THE ENDOPARASITIC MITE *Sternostoma tracheacolum* LAWRENCE (RHINONYSSIDAE) AND THE ENDANGERED GOULDIAN FINCH *Erythrura gouldiae* GOULD (ESTRILDIDAE): A PARASITE-HOST RELATIONSHIP.

by
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DECLARATION

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ABSTRACT

The Gouldian Finch *Erythrura gouldiae* (Gould) is an endemic species to the grassy woodlands of tropical northern Australia. In recent decades it has undergone a substantial decline, both in abundance and distribution. The cause of the decline remains unclear, however, habitat alteration from inappropriate fire regimes and or grazing by cattle, trapping for the avicultural market, disease and parasitism have all been suggested to be involved.

In 1987, the respiratory system inhabiting mite *Sternostoma tracheacolum* Lawrence was discovered in wild populations of the Gouldian Finch. This mite is known to be pathogenic in captive birds, particularly the Gouldian Finch. The prevalence and intensity of infection in wild Gouldian Finches was thought to be high and its presence was found to be associated with respiratory disease (Tidemann *et al.* 1992). Unfortunately, little was known of the biology of *S. tracheacolum* or any of the respiratory system inhabiting mites of vertebrates. Furthermore, little was understood of the parasite-host relationship of these mite groups.

In order to appreciate the potential role of *S. tracheacolum* in the decline of the Gouldian Finch the present study undertook to improve the knowledge of the biology of the parasite and the parasite-host relationship. The investigation involved studies of both naturally infected wild birds and experimentally infected captive reared birds.

The life stages of *S. tracheacolum* from the wild Gouldian Finch are identified and described. The morphology of specimens from the Gouldian Finch is compared with that of specimens described from other wild Australian host species and both captive and wild host species overseas. Significant morphological differences between specimens coming from psittaciform and passeriform hosts are described.

The life history, patterns of infection and the mode of transmission of *S. tracheacolum* are described. The study indicates the following sequence: arrhenotoky, ovoviviparity, egg laying in the lung with subsequent development in the posterior airsacs and a rapid progress from the egg to the adult stage. The stage responsible for transmission is identified as the adult female (non-gravid, non-gorged). Observational data on behaviour and longevity of the infective stage indicates direct transmission via the nares of the host.

S. tracheacolum infrapopulation biology is described in captive reared Gouldian Finches. Following initial infection there was an exponential growth rate and maximum infrapopulation size commonly exceeded 200 mites. In birds that survive these levels of infection there was a

subsequent decline in the size of the infrapopulation until long term infections (i.e. up to two years duration) contain few mites. The mortality rate of mites increases with duration of infection and the transmission rate positively correlates with the size of the infrapopulation. Mite generations are continuous and overlapping with no evidence of synchronisation of reproduction or transmission with host biology.

Gross pathology associated with *S. tracheacolum* infection is described, for individual birds killed at three monthly intervals, over 12 months following initial infection. Occlusion of respiratory passages (trachea, syrinx and primary bronchi) and or secondary pyrogenic infections were a common cause of death in heavily infected birds.

Haematological values (Haemoglobin, Packed Cell Volume, Mean Corpuscular Value, Red Blood Cell count, White Blood Cell count, Thrombocyte count and differential leucocyte counts) of Gouldian Finches infected with *S. tracheacolum* (taken 3, 6, 9 and 12 months following experimental infection) and Canaries (taken 6 months following experimental infection) were not statistically dissimilar to those values obtained from non-infected birds. Cellular haematology is therefore considered to be of limited value in the study of *S. tracheacolum* infection.

The clinical signs of *S. tracheacolum* infection are described over time for Gouldian Finches of known infection size and duration. Infected birds were found to throat clear, sneeze, wheeze (± clicking and gurgling), bill wipe and head shake more often and preen, vocalise, sing, and fly less often than uninfected birds. Infected birds were significantly less able to maintain flight than their uninfected counterparts. The severity of clinical signs was found to be related to the duration and the size of the infection. Some clinical signs are considered to enhance transmission while others have the potential to increase both direct and indirect mortality in wild host populations.

A survey of the intra-nasal mite fauna of wild Gouldian Finches, Masked Finches *Poephila personata*, Pictorella Mannikins *Heteromunia pectoralis*, Long-tailed Finches *P. acuticauda*, Double-barred Finches *Taeniopygia bichenovii*, Zebra Finches *T. guttata* and Budgerigars *Melopsittacus undulatus* from the Northern Territory, Australia revealed twelve new host records for rhinonyssid and kytoditid mites. The prevalence of rhinonyssid infection in these host species ranged from 16.2 to 60.8%, with a corresponding range in the intensity of infection from 1.6 to 26.7 mites per host and a range in the mean parasite burden from 0.26 to 12.7 mites per individual bird. *S. tracheacolum* was found to infect the Gouldian Finch, Pictorella Mannikin, Masked Finch and Budgerigar at a prevalence of 47% (n = 19), 34% (n = 74), 1.4% (n = 85) and 16% (n = 86) and an intensity of 27, 10, 1 and 1.6 mites per host for each species respectively. Both the prevalence and intensity of infection in the Gouldian Finch and the Pictorella Mannikin were significantly higher than that found in the Masked Finch and the Budgerigar. The prevalence and intensity of infection

in the Gouldian Finch and the Pictorella Mannikin were not significantly different. The frequency distribution of mites *S. tracheacolum* in the Gouldian Finch sample was significantly different from the frequency distributions in the Budgerigar and the Masked Finch samples but not significantly different from that in the Pictorella Mannikin sample.

Captive reared Gouldian Finches and Canaries were successfully infected with *S. tracheacolum* obtained from wild Gouldian Finches using an experimental infection technique. Captive reared Budgerigars and wild caught Masked Finches could not be infected by the same technique. The results suggest that Budgerigars are not susceptible (or are resistant) to *S. tracheacolum* mites coming from the wild Gouldian Finch, providing further evidence for sub-specific separation of the two forms. Examination of *S. tracheacolum* mites reared in captive Gouldian Finches and Canaries at 6 months and at 12 months following experimental infection indicated no significant change in external morphology. The data support the proposition that, in the short term, the host does not affect morphological expression in *S. tracheacolum* mites and that observed differences in mites from passerine and psittacid hosts are genetic rather than environmental.

Ivermectin oral dosing is found to be an effective treatment for the control or complete elimination of *S. tracheacolum* infection in captive reared Gouldian Finches. Single dose treatment with ivermectin (i.e. Ivomec®, 0.8 g/l ivermectin) at rates as high as 3.5 µl/g b.w. were administered to both captive reared and wild caught Gouldian Finches without obvious signs of toxicity. The mean percentage of mites killed by the drug increased with increase in the quantity of ivermectin in the oral dose. Complete elimination was achieved at doses above 2.0 µl/g b.w. *S. tracheacolum* eggs can continue development within the carcase of ivermectin killed female mites and stages from larva to adult male have been found within the mother's carcase. The potential for reinfection of the host from mites that have developed in this manner is not known.

The influence of *S. tracheacolum* on mortality and fecundity in the captive reared Gouldian Finch is examined. Groups of experimentally infected birds showed higher mortality rates than uninfected birds and infected birds layed significantly less eggs per number of surviving females over 200 days of infection (for birds initially infected at the beginning of the breeding period) than their uninfected counterparts.

In view of the results of the present study, *S. tracheacolum* is considered to have the potential for significant impact on the population dynamics of the wild Gouldian Finch.

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SUMMARY

Chapter 1: MORPHOLOGY

The life stages of *S. tracheacolum* from the wild Gouldian Finch *Erythrura gouldiae* are identified and described. The external morphology is typical of other endoparasitic mites, having a reduction in sclerotisation in comparison to related external forms. The adult male is much smaller than the adult female and has reduced sclerotisation. The larval stage is a hexapod with poorly developed chelicerae and no idiosomal plates. The nymphal stages are poorly sclerotised and devoid of idiosomal plates. The protonymph has well sclerotised chelicerae with sharp movable digits while those of the deutonymph are poorly developed, end bluntly and are difficult to discern. Deutonymphs are readily sexed on the length of tarsus I, a feature much larger in the female.

S. tracheacolum specimens, of all stages, from the wild Gouldian Finch in Australia differ in dimensions (over a number of external features) in comparison to *S. tracheacolum* adults and immatures described by Guewara-Benitez and Ubeda-Ontiveros (1974) from captive Canaries in Granada, Spain. These differences highlight the morphological variability reported for *S. tracheacolum* by Fain and Hyland (1962), both between host species and between geographic localities (i.e countries and continents).

S. tracheacolum specimens from wild Gouldian Finches captured over 1000 kilometres apart in northern Australia are morphologically similar. Furthermore *S. tracheacolum* specimens from Gouldian Finches are similar to specimens from other known Australian estrildid hosts (i.e. Masked Finch and Pictorella Mannikin). However, specimens from estrildid hosts are significantly different in morphological dimensions (over a number of external features) from specimens from wild Budgerigars collected from the same locations. Consistent variation in the morphology of *S. tracheacolum* specimens coming from passeriform and psittaciform host groups provides a convincing argument for the existence of two subspecies, one infecting passeriforms, the other infecting psittaciforms.

Chapter 2: LIFE HISTORY

S. tracheacolum was found to infect all tissues of the respiratory system, as well as the oesophagus and the body cavity, of Gouldian Finches. Rearing experiments and other evidence suggest that the life cycle, from egg to adult, is completed in less than 6 days. Significant differences were found in the distribution of mites within the host tissues, both between sex and between life stages. These differences are considered to reflect variations in the manner of exploitation of the host by different life cycle stages.

S. tracheacolum is ovoviviparous and lays eggs in the lung of the host. Larvae hatch shortly after oviposition and moult to the protonymph stage without feeding. The protonymph is a blood feeding stage and, following a blood meal in the lung, the female moves to the posterior airsacs to complete development through deutonymph to adult. The males tend to stay within the lung to complete development. Ovigerous female mites tend to occupy the airsacs, the syrinx and trachea of the host while adult non-gravid, non-gorged females tend to be found in the upper respiratory system, particularly the buccal and nasal cavities.

Transmission is accomplished by the adult non-gravid, non-gorged female and this stage is often encountered on the head plumage, bill and nares of infected birds. Observations on behaviour and longevity of survival of the infective stage (i.e. the adult non-gravid, non-gorged female) outside the body of the host indicate a potential for (a) direct transmission between hosts in close proximity and (b) indirect transmission via water, perches or other surfaces. Adult male mites tend to be common in small infrapopulations (i.e. the total number of mites in each host individual) but uncommon, and often absent, in large infrapopulations. These data support an argument for parthenogenesis and an arrhenotokous system of sex determination.

Chapter 3: POPULATION BIOLOGY

S. tracheacolum infrapopulation biology is described in captive reared Gouldian Finches. Following initial infection there was an exponential growth rate and maximum infrapopulation size often exceeded 200 mites. In birds that survive these levels of infection there is a subsequent decline in the size of the infrapopulation until long term infections (i.e. up to two years duration) contain few mites. The mortality rate of mites increases with duration of infection and the transmission rate positively correlates with the size of the infrapopulation. Mite generations are continuous and overlapping with no evidence of synchronisation of reproduction or transmission with host biology.

Chapter 4: PATHOLOGY

Gross pathology associated with *S. tracheacolum* infection is described (for individual birds killed at three monthly intervals) over 12 months following initial infection. Occlusion of respiratory passages (trachea, syrinx and primary bronchi) and or secondary pyrogenic infections were a common cause of death in heavily infected birds.

Chapter 5: HAEMATOLOGY

Haematological values for evaluation of erythrocytes (i.e. PCV, MCV, RBC, MCH and MCHC) haemoglobin, leucocytes (i.e. WBC, % heterophils, % lymphocytes, % monocytes, % eosinophils, % basophils) and thrombocytes are given for captive reared Gouldian Finches. Comparisons between infected Gouldian Finches (taken at 3, 6, 9 and 12 months following experimental

infection) and Canaries (taken at 6 months following experimental infection) and their non-infected counterparts suggest that *S. tracheacolum* parasitism has little or no obvious impact on these haematological values. Consequently, haematology is considered to be of limited value in the study of *S. tracheacolum* infection in wild host populations.

Chapter 6: BEHAVIOUR/ CLINICAL SIGNS

The clinical signs of *S. tracheacolum* infection are described for Gouldian Finches of known infection size (i.e. total number of mites in infrapopulation) and history. Infected birds were found to throat clear, sneeze, wheeze (± clicking and gurgling sounds), bill wipe and head shake more often, and preen, vocalise, sing, and fly less often than their uninfected counterparts. After 3 months of infection, infected and uninfected birds were not significantly dissimilar in their ability to maintain continuous flight. However, after 6 months, infected birds were significantly less able to maintain flight than uninfected birds.

Audible respiratory clinical signs were first detected after approximately 50 days of infection. The mean severity of clinical signs increased to a maximum severity after about 150 days and for surviving birds, the mean intensity of clinical signs remained high for the following 100 to 150 days. In surviving birds there is a subsequent reduction in the severity of clinical signs from between 250 to 300 days following initial infection. For birds surviving beyond 500 days of infection, the clinical signs appear to completely disappear. The increase in the severity of clinical signs is associated with an increase in the size of the mite infrapopulation and the disappearance of clinical signs is associated with a reduction in the size of the mite infrapopulation.

Chapter 7: HOST SPECIFICITY

Twelve new host records for rhinonyssid and kytoditid mites are reported for the Gouldian Finch, Masked Finch *Poephila personata*, Pictorella Mannikin *Heteromunia pectoralis*, Budgerigar *Melopsittacus undulatus*, Long-tailed Finch *P. acuticauda*, Double-barred Finch *Taeniopygia bichenovii*, and the Zebra Finch *T. guttata* from Yinberrie Hills and Newry Station in the Northern Territory, Australia. One nasal mite is a new genus record and a further two are new species records for Australia.

S. tracheacolum was found to infect the Gouldian Finch, Pictorella Mannikin, Masked Finch and Budgerigar at a prevalence of 47% (n = 19), 34% (n = 74), 1.4% (n = 85) and 16% (n = 86) and an intensity of 27, 10, 1 and 1.6 mites per host for each species respectively. Both the prevalence and intensity of infection in the Gouldian Finch were significantly higher than that found in the Masked Finch and the Budgerigar but not the Pictorella Mannikin. The frequency distribution of *S. tracheacolum* in the Gouldian Finch sample population was significantly different from the distribution in the Budgerigar and the Masked Finch but not the Pictorella Mannikin. The

prevalence for rhinonyssid infections in each species examined was 47%, 61%, 32%, 16% 19% 25% and 14%, with an intensity of 26.7, 19, 3.4, 1.6, 4.6, 6.8 and 2 mites per infected host and a mean parasite burden of 12.7, 11.6, 1.1, 0.3, 0.9, 1.7 and 0.3 mites per individual for the Gouldian Finch, Pictorella Mannikin, Masked Finch, Budgerigar, Long-tailed Finch, Zebra Finch and Double-barred Finch respectively. The data indicate that the prevalence and intensity of *S. tracheacolum* infection in the Gouldian Finch are high in comparison to the Budgerigar and the Masked Finch but the values are statistically inseparable from those found in the Pictorella Mannikin.

Chapter 8: HOST SUSCEPTIBILITY

Captive reared Gouldian Finches and Canaries were successfully infected with *S. tracheacolum* obtained from wild Gouldian Finches using an experimental infection technique. Captive reared Budgerigars and wild caught Masked Finches could not be infected by the same technique. The results suggest that Budgerigars are not susceptible (or are resistant) to *S. tracheacolum* mites coming from the wild Gouldian Finch, providing further evidence for sub-specific separation of the two forms.

Examination of *S. tracheacolum* mites reared in captive Gouldian Finches and Canaries at 6 months and at 12 months following experimental infection indicated no significant change in external morphology. The data support the proposition that, in the short term, the host does not affect morphological expression in *S. tracheacolum* mites and that observed differences in mites from passerine and psittacid hosts are genetic rather than environmental.

Chapter 9: DRUG TREATMENT

Ivermectin (i.e. Ivomec®, 0.8 g/L ivermectin) doses as high as 3.5 µl/g b.w. (i.e. 2.52 mg ivermectin/kg b.w.) were administered to aviary bred Gouldian Finches without serious signs of toxicity. No deaths were recorded from 142 captive reared Gouldian Finches (69 adult females, 68 adult males, 3 juvenile males and 2 juvenile females), 20 Budgerigars, 20 Canaries and 28 juvenile and immature wild caught Gouldian Finches following oral doses between 1.2 µl - 3.5 µl ivermectin/g b.w. Abnormal behaviour recorded following oral treatment included excessive bill wiping and head and body shaking. There was no significant change in the body weight (measured to 0.1 g) of treated birds in comparison to non-treated birds within 24-48 hours or within 6-10 days following treatment.

Ivermectin oral dosing was found to be a suitable single treatment for the elimination of *S. tracheacolum* infection in captive reared Gouldian Finches. However, within the range of dose rates tested, repeated treatment regimes must be considered the only confident means of complete

elimination. Small oral doses tested (i.e. < 1.5 µl/g b.w.) showed high variability in *S. tracheacolum* kill rate. The variability was reduced with increase in dose rate.

Ivermectin at appropriate dosages killed all free feeding stages of *S. tracheacolum* (i.e. protonymph and adult). The rapidity of development from larva to protonymph and from protonymph to adult ensured that non feeding stages passed to feeding stages and fed within period of the drug's action. Continued development of mature eggs took place within the carcase of ivermectin killed female mites. Hatching and development from larva to protonymph, to deutonymph and to adult stage was found to occur in this site. This occurrence was common, however, complete development to adult within the carcase of adult females was observed on only two occasions (both were male). The potential for reinfection of treated birds from adult mites surviving within the carcase of dead female mites is considered to be low.

Chapter 10: POPULATION DYNAMICS OF THE HOST

The influence of *S. tracheacolum* on mortality and fecundity in the captive reared Gouldian Finch is examined. Groups of experimentally infected birds showed higher mortality rates than uninfected birds and infected birds layed significantly less eggs per number of surviving females over 200 days of infection (for birds initially infected at the beginning of the breeding period) than their uninfected counterparts.

GENERAL INTRODUCTION

The Gouldian Finch *Erythrura gouldiae* (Gould) is endemic to the grassy woodlands of northern Australia where it is patchily distributed from north-western Queensland, through the Northern Territory, to the Kimberley region of northern Western Australia. Over the past century the species has undergone a substantial decline both in numbers and range (Blakers, Davies & Reilly, 1984). It is currently listed as endangered by the Royal Australian Ornithologists Union (Brouwer & Garnett, 1990) and the International Union for the Conservation of Nature (Garnett, 1992b). Based on available anecdotal and historical evidence, Tidemann, McOrist, Woinarski and Freeland (1992a) suggest that the rate of decline may have increased over the past two decades.

The causes of the species' decline are unclear, as it occupies habitats that have undergone little structural alteration since European settlement. The dominant land use is extensive pastoralism with relatively low cattle densities.

Legal trapping for the avicultural market, habitat alteration through fire or cattle grazing, disease and parasites have all been identified as possible contributing factors to the decline (Garnett, 1992a). However, a causal relationship between any one of these factors and the demise of the Gouldian Finch has not been established.

The present study explores the potential for the decline to be attributable to the endoparasitic mite, *Sternostoma tracheacolum* Lawrence. The reasons for considering this a reasonable line of inquiry are summarised below through a review of what is known of the species' biology.

The short term affects of fire on the Gouldian Finch have been studied by Woinarski (1990). He found that hot fires during the late dry season tended to destroy a large proportion of grass seeds which may disadvantage granivorous birds such as the Gouldian Finch. Tidemann (1990) investigated the effects of cattle grazing on the Gouldian Finch and other co-occurring finches of northern Australia. She found that the abundance of grass finches was inversely related to cattle density and increases in the number of cattle correlated well with the proportion of ground bared of grass and seeds. Although grazing appeared to disadvantage finch species, the Gouldian Finch was not especially affected.

In a study on survivorship and other population parameters of the Gouldian Finch, Woinarski and Tidemann (1992) found that estimates of survivorship in the Gouldian Finch were lower than that in two co-occurring finch species. The disappearance was attributed to either a much higher mortality rate, a much higher emigration rate or a combination of both, in comparison to the other finches

(i.e. the Masked Finch *Poephila personata* (Gould) and the Long-tailed Finch *P. acuticauda* (Gould)).

Gouldian Finches were legally trapped under licence until 1981 in north Western Australia. Trappers returns to the Western Australian Department of Conservation and Land Management and its predecessors, over the period 1972-73 to 1982, clearly indicated a significant reduction in the number of Gouldian Finches captured. However, over the same period there was an increase in the capture of a sympatric finch species (Tidemann *et al.*, 1992a). In following years (i.e. after cessation of trapping) there did not appear to be any significant recovery in numbers (Evans & Bougher, 1987).

Tidemann, Calley and Burgoyne (in press) examined blood smears from northern Australian finches. They failed to find blood parasites (i.e protozoa such as *Plasmodium, Leucocytozoon*, and *Haemoproteus*, microfilariae or trypanosomes) and found that blood cell counts for Gouldian Finches fell within the range encompassed by other finch species.

Tidemann and her associates (1992a) found the endoparasitic mite *S. tracheacolum* in wild Gouldian Finches in 1987, and following a study of the prevalence and histopathology considered that this parasite may have the potential to have caused the Gouldian Finch decline. The circumstantial evidence is strong; however, a conclusive link between the decline of the Gouldian Finch, and the presence of *S. tracheacolum* has not been established.

There are three main reasons why *S. tracheacolum* is thought to be involved in decline of the Gouldian Finch. Firstly, the parameters of infection in comparison to other Australian wild hosts are considered to be aberrant (Tidemann *et al.*, 1992a). Secondly, there is significant histopathological evidence for the association of disease with infection (Tidemann *et al.*, 1992a) and thirdly, *S. tracheacolum* is a common infection in captive birds, particularly the Gouldian Finch (Aeckerlein, 1974).

The discovery of *S. tracheacolum* in the wild Gouldian Finch represents the first record of this parasite in a wild bird in Australia (Tidemann *et al.*, 1992a) though it has been known from captive Gouldian Finches since 1964 (Domrow, 1966) and overseas since 1959 (Cumming, 1959). Previous nasal mite surveys have been undertaken in Australia (e.g. Domrow, 1967; 1969) and a large proportion of Australia's avifauna, including the Gouldian Finch, have been examined (note that the lower respiratory system of birds was not generally examined in previous surveys) yet, no evidence of this parasite has been found. Tidemann *et al.* (1992a) examined some 380 individuals of eight finch and mannikin species from northern Australia as well as a further 240 individuals of 78 genera and 32 families and found *S. tracheacolum* in only three species, the Gouldian Finch, the

Masked Finch and the Pictorella Mannikin *Heteromunia pectoralis* (Gould), all co-occurring species. Tidemann and her associates found that the prevalence and intensity of infection was substantially higher in the Gouldian Finch than in the other host species.

Since *S. tracheacolum* was first discovered, in captive Canaries (Lawrence, 1948), it has often been associated with morbidity and mortality in captive hosts (Keymer, 1982), particularly the Gouldian Finch (Aeckerlein, 1974). Fain and Hyland (1962) considered *S. tracheacolum* to be well tolerated by its wild hosts because lesions had not been found associated with infections. Their observations indicated that only in captive birds did intense parasitism occur, which they attributed to a lowered general health and decreased resistance brought about by captivity. However, Tidemann and her associates (1992a) provided strong histopathological evidence for lesions associated with infection in the wild Gouldian Finch. Based on the apparently high pathogenicity they considered that the parasite-host relationship may be of recent origin.

If *S. tracheacolum* is directly influencing the status of Gouldian Finch populations, future management decisions for conservation of this species may rely heavily on our understanding of both the biology of *S. tracheacolum* and the dynamics of the parasite-host relationship.

There are many possible explanations which could explain the association of disease with *S. tracheacolum* infection in the wild Gouldian Finch. Some probable scenarios include the following:

1. *S. tracheacolum* may be a recently introduced parasite to the Australian native avifauna and is currently having a significant impact on the survival of susceptible host populations, principally the Gouldian Finch. The impact on mortality and fecundity of the Gouldian Finch may be sufficient to have caused the decline of this species in recent decades.

2. *S. tracheacolum* (whether an introduced or a native Australian parasite) may be a vector for a microparasite (i.e. bacterial, viral or fungal infection) that is having a significant impact on the survival of wild Gouldian Finches. This disease may be responsible for the decline of the Gouldian Finch in recent decades.

3. *S. tracheacolum* may be a native Australian parasite and a natural parasite of the wild Gouldian Finch and may be causing disease (due to reduced resistance or tolerance by the host) as a result of some other environmental stress such as an inadequate food resource (e.g. bottle necks in food seed availability at critical times of the year).

4. *S. tracheacolum* may be a natural parasite of wild Gouldian Finches and may have always caused disease and mortality in individual hosts but without adversely affecting the survival of Gouldian Finches at the population level.

There may be serious implications when a parasite is introduced to a new host population. Bird hosts can suffer mortality and or reduced fecundity as a result of parasitic infections and recent theoretical modelling indicates that under certain conditions of mortality and fecundity (caused by the parasite) host populations can fluctuate or even go extinct (Toft, 1991). A good example is the correlation between the accidental introduction of the night mosquito *Culex pipiens fatigans* Say (and certain avian diseases) to Hawaii, and the subsequent lowland exclusion or extinction of several native bird species (Warner, 1968). Since early this century, avian malaria (caused by *Plasmodium*) has been present in Hawaii in epizootic proportions and has had a negative impact on the population dynamics of native forest birds. Currently, avian malaria is a major limiting factor on several host bird populations, restricting both their distribution and abundance (van Riper, van Riper, Goff & Laird, 1986). Toft and Karter (1990) consider that the extinction of bird species in Hawaii was probably a result of a complete lack of resistance to this parasite.

The current prevalence and intensity of infection and the established association of disease with the presence of *S. tracheacolum* could also be explained as a symptom of a declining population under stress from another source or a combination of sources. Inadequate nutrition as a result of recent habitat changes (e.g. timing and intensity of fires influencing the abundance, composition and phenology of grasses) could produce similar levels of infection, in terms of the prevalence and intensity of infection, to those currently being observed. Some parasites are known to interact with the nutritional status of a host through resource competition and thereby potentially reduce the host's ability to mount an effective immunological response (Hudson & Dobson, 1991). For example, Compton (1991) found that mice experimentally infected with *Taenia crassiceps* and fed on identical but varied casein diets have significantly lower dry body weights, after removal of the parasites, than their uninfected partners. As a function of dietary intake, the higher the protein content of the diet the greater the difference between carcass weights of infected and non-infected mice. The weight differences were accounted for by fat which normally accumulates in response to the intake of surplus energy in the form of dietary carbohydrate and protein. There is also evidence that in some parasites the nutritional status of the host may influence the course of the infection via both the population dynamics and reproductive output of the parasite (Compton, 1991).

Finally, *S. tracheacolum* may have always caused significant respiratory disease in wild Gouldian Finches, but without causing a change in the parasite-host relationship that could account for the observed decline in host populations.

Parasites do not necessarily evolve towards a lowered level of pathogenicity. Some ancient parasites are known to have remained pathogenic to their hosts of long association (Toft & Karter, 1990). Parasites are considered to have the potential for as much impact on their hosts as predators. In so doing they must also have the potential to regulate their host populations (Toft, 1991). Toft and Karter (1990) consider that there are many potential outcomes for the evolution of virulence in parasites and that a lowered virulence is only one of these outcomes. Therefore, the apparently high level of virulence exhibited by *S. tracheacolum*, in its association with the Gouldian Finch, may not necessarily indicate a parasite-host association of recent origin.

If *S. tracheacolum* is the primary cause of the decline of the Gouldian Finch then management for the conservation of this species may require artificially improving resistance in host individuals, elimination of infection in wild populations or at least control of infection in wild birds. Any one of these strategies may ultimately become essential to prevent the extinction of existing wild populations. Given our current knowledge of the biology of the host and the parasite, antiparasitic drug treatment of individual birds may be the only feasible short term technique available for this task. Furthermore, an ability to control or eliminate *S. tracheacolum* infection in host individuals may be a useful tool for the experimental study of the parasite-host relationship in the wild. Woinarski and Tidemann (1992) suggest that the mortality rate due to *S. tracheacolum* in wild birds could be assessed by direct comparison between the two known remaining breeding populations, from one of which *S. tracheacolum* is eliminated.

A number of authors (e.g. Cumming, 1959; Murray, 1966; Guewara-Benitez & Ubeda-Ontiveros, 1974; Jolivet, 1975; Kummerfeld & Schäfer-Nolte 1987; Szeleszczuk & Kruszewicz, 1987) have reported on the efficacy of systemic drugs and inhalations in the control of *S. tracheacolum* in captive bird species, particularly the Gouldian Finch. A number of recent reports have indicated that the drug ivermectin is effective in the control of *S. tracheacolum* infection (e.g. Kummerfeld & Hinz, 1982; Kummerfeld & Schäfer-Nolte 1987). Favourable results have also been reported with the use of ivermectin on a range of pathogenic mite species such as Airsac mite, *Kytodites nudus* (e.g. Grimm & Centurier, 1985), Scaly mite, *Knemidokoptes pilae* (e.g. Madill, 1987) and Chicken mite, *Dermanyssus gallinae* (e.g. Zeman, 1987).

No studies have yet investigated the proportion of mites *S. tracheacolum* killed by specific doses of ivermectin or the effect of the drug on each of the life stages. If recommended doses do not eliminate *S. tracheacolum* infection in the host, it would be necessary to quantify the impact of the drug on the demography and size of individual mite infrapopulations in order to predict the outcome for the infection, as well as the ongoing infectivity of treated birds to susceptible non-treated birds.

The Parasite

S. tracheacolum is a gamasid mite belonging to the family Rhinonyssidae. This group of mites are respiratory tract parasites of birds. Most species inhabit the nasal cavities, but aside from some incidental occurrences, only *S. tracheacolum* is known to inhabit the lower respiratory system.

Of all the rhinonyssids known *S. tracheacolum* is the least host specific. It is also probably the most variable in form between and within host species, and between geographic localities (Fain & Hyland, 1962).

Radovsky (1969) in a study on the adaptive radiation in the parasitic Gamasida considered that the unusual habit of *S. tracheacolum* to occupy the lower respiratory system of its hosts and the lack of apparent host specificity 'may indicate that a rapid radiation into different host associations is taking place in conjunction with the invasion of a new parasitope'.

Beyond taxonomic studies, a little information exists on the general biology of the Rhinonyssidae. This is due in part to the difficulty in obtaining information and data without sacrifice of the host. Sampling techniques have been used on live hosts, e.g. flushing of nasal cavities with water (Yunker, 1961), and tracheal swabs have be used to diagnose *S. tracheacolum* infection (e.g. Greve, 1978), but no suitable technique currently exists for the collection of mites from the lower respiratory system of live birds. Descriptive studies have been made on the life stages of several rhinonyssids, though very few are complete (Mitchell, 1963) and little is known of the life history and the biology of transmission for most species (Krantz, 1978). Most studies indicate that the life history is completed within the respiratory system of the host and that transmission is direct between host individuals (Hyland & TerBush, 1963).

The Host

Until recent studies (e.g. Tidemann, 1987; Woinarski & Tidemann, 1992; Price, 1992; Tidemann, Boyden, Elvish, Elvish & O'Gorman, 1993; Lawson, 1993; Tidemann & Woinarski, 1994) little was known of the life history and ecology of the Gouldian Finch. However, a wealth of information exists on the biology of captive populations (e.g. Cayley, 1932; Immelmann, 1965).

The Gouldian Finch is a brightly coloured but small grass finch of the family Estrildidae. It feeds on native grass seeds, particularly seeds of *Sorghum* spp. (Tidemann, 1987) and is the only Australian finch known to nest almost exclusively in tree hollows (Tidemann *et al.*, 1992).

Breeding begins at the end of the northern Australia's 'wet' season (in late February to early March) and continues through the 'dry' season, till as late as August or September. Snappy Gums, *Eucalyptus brevifolia,* and Salmon Gums, *E. tintinans,* with hollows created by termite activity, are

favoured for nest sites but both the size of hollows and their height above ground can influence nest site choice (Tidemann *et al.*, 1993).

Although the precise drinking requirements of the Gouldian Finch are not known (Evans, Neems & Pagendam, 1989) they appear to drink at least once per day and nesting sites are probably restricted to within a few kilometres of a water source (Tidemann, 1992a).

Eggs are incubated by both parents and hatch after two weeks. Nestlings are fed for about three weeks prior to fledging. Major nest losses occur as a result of predation but some nests are also abandoned (Tidemann, 1992). Lawson (1993) found that the breeding biology (studied at two localities in the Northern Territory) was not dissimilar to that of other ecologically similar species. The spatial pattern of nest sites is clumped and the reproductive output correlates with the amount of wet season rainfall and the distribution of rainfall within the wet season though the precise relationship is not well understood (Lawson, 1993).

In the late dry/early wet season Gouldian Finches disperse from breeding sites. During this period birds are thought to move in response to patchiness of food availability in the landscape. This is likely to be influenced by interacting factors such as fires, rainstorms, water availability and variations in vegetation phenology (Woinarski, 1990). Based on anecdotal sighting records and comparisons of relative wing size, Woinarski and Tidemann (1992) suggest that the area of dispersal of Gouldian Finches may be larger than that for other co-occurring finch species.

The Study

Historical information on the abundance of wild Gouldian Finches is largely anecdotal prior to the last decade (e.g. Heumann, 1926) so the rate at which wild populations have declined can only be guessed. The current rarity of Gouldian Finches, combined with our paucity of knowledge of their patterns of dispersal make estimates of population parameters by conventional techniques inaccurate. There is scant evidence to show current population trends at any known breeding sites. Field based experiments, designed to understand the role of *S. tracheacolum* in the decline, such as the assessment of survival rates of birds following parasitic manipulation in host individuals, are largely impractical. However, Gouldian Finches are popular aviary birds and large numbers are kept, both in Australia and overseas. The availability of captive bred birds make aviary based experimentation at least feasible, if not necessarily the best reflection of the natural situation. Therefore, the laboratory enclosure may provide the only convenient tool for a study of the biology of *S. tracheacolum* and the parasite-host relationship.

With respect to the foregoing, the present study seeks to satisfy the following objectives.

1. Improve knowledge of the biology of *S. tracheacolum* with particular attention to the life history, the recognition of the life stages and the biology of transmission.

2. Improve understanding of the parasite-host relationship between *S. tracheacolum* and the Gouldian Finch with a particular emphasis on the population biology of the parasite and its effect on the host.

3. Determine whether *S. tracheacolum* is a recently introduced parasite (i.e. following European settlement) or a native parasite of the Australian avifauna.

4. Assess the potential for the control of *S. tracheacolum* in individuals and populations of the wild Gouldian Finch using the acaricide, ivermectin.

5. Develop a model of the *S. tracheacolum*-Gouldian Finch relationship. Provide parameter estimates for use in the development of stochastic models. Such models may aid in the assessment of the potential for *S. tracheacolum* to cause population decline in the Gouldian Finch, and determine theoretical outcomes for host and parasite populations under specific management regimes.

These objectives have been achieved through a combination of independent studies, both descriptive and experimental. The overall structure of the thesis separates the research into three parts.

Part I presents foundation studies on the biology of the parasite (i.e. **Chapter 1: Morphology**; **Chapter 2: Life History** and **Chapter 3: Infrapopulation Biology**).

Part II provides the host perspective on parasitism, measured in terms of **Pathology (Chapter 4) Haematology (Chapter 5)** and **Behaviour/ clinical signs (Chapter 6)**. Chapters 3 to 6 and chapter 9 rely on data collected from experimentally infected captive Gouldian Finches that were subsequently monitored over periods of up to one year. The methodology is set out in the **Experimental Design**. **PARTs I** and **II** are essential elements in the development of an understanding of the parasite-host relationship.

PART III, Chapter 7: Host Specificity examines parameters of rhinonyssid infection in wild Gouldian Finches, co-occurring host species and host species overseas. **Chapter 8: Host**

Susceptibility examines the susceptibility of captive and wild bird species to infection. **Chapter 9: Drug treatment** investigates the efficacy of ivermectin in the control and elimination of *S. tracheacolum* in the captive Gouldian Finch and assesses the potential for the use of this drug in wild host populations. **Chapter 9: Population Dynamics of the Host** uses data and observations gathered from all other aspects of the study in an attempt to estimate population parameters necessary for the development of a model for the parasite-host interaction.

In conclusion, three major questions are addressed pertaining to the parasite-host relationship.

1. Is *S. tracheacolum* responsible for the decline of the wild Gouldian Finch?

2. Is the association of *S. tracheacolum* and the Gouldian Finch of recent origin?

3. If *S. tracheacolum* is responsible for the decline, what management strategies can be implemented to secure a future for the wild Gouldian Finch.

For the most part each chapter is self-contained with a structure that includes introduction, methodology, results and discussion. To ensure continuity between chapters and to reduce duplication some cross referencing is also made.

PART I THE PARASITE

Chapter 1. MORPHOLOGY

1.1 INTRODUCTION

S. tracheacolum was originally described by Lawrence (1948) from female specimens infecting captive Canaries in South Africa. It was redescribed by Furman (1957), Fain (1957), and Fain and Hyland (1962) to account for additional characters omitted from the original description and to encompass observed levels of morphological variation.

Fain and Hyland (1962) found considerable variation between female specimens from different host species and different geographic localities. Important variations were also found among specimens from captive Canaries, but from widely separated localities. They considered that geographical or biological isolation of the host probably plays a larger role in the production of variation than host species or host individuals.

Fain and Hyland (1962) used morphological evidence to suggest that wild birds are the natural hosts for *S. tracheacolum* and that the Canary may be secondarily infested in different geographic localities. The House Sparrow, *Passer domesticus* was thought to act as a host for the transfer of mites between wild and captive groups.

Guevara-Benitez and Ubeda-Ontiveros (1974) studied female specimens from captive Canaries in Spain and made comparisons with morphological variation reported by Fain and Hyland (1962) for specimens from captive Canaries in South Africa, Italy, Brazil and Belgium. Based on morphological similarity, they considered infections in Granadan Canaries may have originated from the importation of infected Canaries from Belgium.

Descriptive studies of rhinonyssid mites are usually taxonomically orientated and consequently few deal with the morphology of immature stages. The most detailed and comprehensive study to date is that of Mitchell (1963) for *Rhinonyssus rhinolethrum* (Trouessart). Mitchell described all life stages, i.e. larva, protonymph, deutonymph and adult male and female, and sexed deutonymphs based on morphological characters.

For the genus *Sternostoma*, comprising more than 60 described species, there are few published descriptions of the immature stages. No study has described all stages and most have not made distinctions between successive nymphal stages or the sex of deutonymphs. Castro (1948) described the nymph of *S. angrensis* (Castro); Strandtmann (1951) briefly described the larva and nymph of *S. boydi* Strandtmann; Furman (1957) described the larva and nymph of *S. strandtmanni* Furman; Hyland (1962) briefly described a nymph of *S. porteri* Hyland; Feider and Mironescu (1968) made

a detailed description of the larva of *S. borceanum* Feider & Mironescu; Pence (1972) described the larva and protonymph of *S. spatulatum* Furman; Guevara-Benitez and Ubeda-Ontiveros (1974) described the larva and nymph of *S. tracheacolum*; Guevara-Benitez and Ubeda-Ontiveros (1975) described the larva of *S. fulicae* Fain & Bafort and Domrow (1979) described the protonymph leg setation of *S. cuculorum* Fain. Guevara-Benitez and Ubeda-Ontiveros' description of the life stages of *S. tracheacolum* was insufficient to determine whether one or two nymphal stages were present and the limited number of specimens available did not allow nymphs to be sexed.

Rhinonyssid males are uncommon in infections and most species descriptions include an account of the adult female only. Within *Sternostoma,* only a few males have been described: *S. kelloggi* Hyland & Clark (Hyland & Clark, 1959), *S. spatulatum* (Pence, 1972), *S. sternahirundo* Butenko (Butenko, 1974), *S. tracheacolum* (Medda, 1957; Guevara-Benitez & Ubeda-Ontiveros, 1974) and *S. isabelae* (Ubeda-Ontiveros & Guevara-Benitez, 1980). Medda (1957) made only a very brief description of *S. tracheacolum* males from the captive Canary in Italy while Guevara-Benitez and Ubeda-Ontiveros (1974) presented a detailed description of a single male specimen from the captive Canary in Spain.

The present study identifies and describes all life stages of *S. tracheacolum* from the respiratory system of the wild Gouldian Finch. The descriptive detail presented is sufficient for rapid recognition of each life stage, a necessary foundation for subsequent studies of the life history, demography and population dynamics of this species. Each life stage is compared with that described for *S. tracheacolum* from the captive Canary in Spain by Guevara-Benitez and Ubeda-Ontiveros (1974). Morphological variability is described between female specimens from known Australian native and overseas hosts. Variability of mites from wild Australian hosts is used as evidence to explore questions relating to the source and age of the association between *S. tracheacolum* and the wild Gouldian Finch.

1.2 METHODS

Mites were obtained from wild birds caught by mist netting or by shooting with a .22 calibre cartridge containing light shot. Other mites came from captive bred Gouldian Finches and Canaries that were experimentally infected, subsequently maintained in an aviary environment, then killed by lethal anaesthetic injection.

Dissections were conducted under a dissecting stereoscope. *S. tracheacolum* were removed from host tissues and stored in 70% alcohol for a minimum period of six weeks prior to clearing and mounting. Clearing involved the immersion of mites in Nesbitt's fluid at 45^{o} C for periods ranging between 30 minutes and 3 hours. Mites were then mounted in a small drop of Hoyer's medium under cover slip pressure. Translucent, non fed larvae and protonymphs were mounted directly in

Hoyer's medium without initial clearing. Morphological observations were made with a binocular microscope to a magnification of 400X. Measurements were taken with the aid of an eyepiece grid calibrated for each objective magnification and unless otherwise stated are presented in micrometers. Drawings were prepared with the aid of a drawing tube.

Morphological measurements, following Fain and Hyland (1962), were taken from adult female mites from wild caught Gouldian Finches captured at Newry Station, NT (16° 08' S 120° 05' E), Yinberrie Hills, NT (14° 08' S 132° 05' E) and Littleton Station, Qld (18° 30'S, 142° 30' E). These data were compared to similar measurements taken of mites from wild-caught Budgerigars *Melopsittacus undulatus,* Pictorella Mannikins *Heteromunia pectoralis* and Masked Finches *Poephila personata* captured at Newry Station. The Statistical Analysis System (SAS Institute INC., 1988) was used for statistical analysis. Comparisons were made between the groups using ANOVA (PROC GLM). Significant differences at the 0.05 probability level were identified using Tukey's studentized range test (TUKEY).

Mean measurements of female *S. tracheacolum* from wild and captive psittaciform and passeriform hosts reported by Fain and Hyland (1962), mean measurements of mites reported by Guevara-Benitez & Ubeda-Ontiveros (1974) from the captive Canary from Granada, Spain and mean measurements of mites reported by Blasco-Sabio & Portús-Vinyeta (1974) from the captive Canary from Barcelona, Spain were combined with mean measurements reported here for mites from Australian wild and captive birds. Idiosomal measurements were omitted due to large dimensional variation. Host species with missing measurements were also omitted leaving a matrix of 24 host groups and 17 measurement variables. The resulting data set was ordinated using PCA (principal components analysis) (PROC FACTOR).

1.3 LIFE STAGES

There are five stages in the life cycle of *S. tracheacolum*: egg, larva, protonymph, deutonymph and adult. The adults are easily distinguished from immature stages by the presence of idiosomal plates on both the dorsal and ventral surfaces. The male is best recognised by its small size relative to the female and the presence of a genital pore opening at the level of the anterior sternal plate. The larva is a hexapod. The first nymphal stage, or protonymph, is most easily recognised by the presence of sclerotised chelicerae with sharp movable digits, similar in form to those of the adult female but smaller in size. The chelicerae of the second nymphal stage, or deutonymph, are poorly sclerotised, end bluntly and are difficult to discern.

Table 1.1 ***S. tracheacolum.*** **Dimensions of 10 adult non-gorged and 10 gorged adult females from the wild Gouldian Finch** ***E. gouldiae*** **(measurements are in microns).**

	Non-gorged		Gorged	
	Mean	Range	Mean	Range
Length of idiosoma	443	(396-467)	633	(558-720)
Width of idiosoma	237	(213-274)	355	(305-406)
Length of podosomal plate	249	(243-253)	249	(240-253)
Width of podosomal plate	195	(188-203)	195	(185-208)
Length of opisthosomal plate	128	(123-140)	128	(123-135)
Width of opisthosomal plate	62	(58-68)	63	(60-68)
Length of gnathosoma	109	(100-118)	110	(98-118)
Width of gnathosoma	82	(75-95)	78	(75-83)
Length of palps	39	(38-40)	38	38
Total length of chelicera including fixed digit	131	(125-135)	133	(125-138)
Length of movable digit of chelicera	13	(13-15)	13	(13-15)
Length of leg I	283	(274-305)	278	(264-294)
Length of leg IV	265	(253-284)	263	(243-284)
Width of leg I	55	(50-58)	55	(53-58)
Width of leg IV	45	(43-50)	45	(43-48)
Length of sternal plate	114	(110-125)	113	(105-125)
Width of sternal plate	97	(88-105)	90	(83-100)
Length of genital plate	112	(103-117)	113	(100-122)
Width of genital plate	81	(75-85)	81	(75-88)
Length of pretarsal claw of leg II	24	(20-25)	-	
Length of pretarsus of leg I	51	(48-53)	-	

Table 1.2 ***S. tracheacolum.*** **Dimensions of 10 adult males from the wild Gouldian Finch** ***E. gouldiae*** **(measurements are in microns).**

	Mean	Range
Length of idiosoma	310	253-345
Width of idiosoma	185	150-233
Length of podosomal plate	182	165-202
Width of podosomal plate	137	125-150
Length of opisthosomal plate	90 (n=3)	95-110
Width of opisthosomal plate	67 (n=3)	65-70
Length of gnathosoma	60	50-70
Width of gnathosoma	51	48-55
Length of palps	28	25-30
Total length of chelicera including fixed digit	54	33-68
Length of movable digit of chelicera	23 (n=1)	
Length of leg I	174	155-183
Length of leg IV	148	130-163
Width of leg I	38	38-40
Width of leg IV	32	30-38
Length of sternal plate	73 (n=1)	
Width of sternal plate	57 (n=2)	50-63
Length of genital plate	73 (n=1)	
Width of genital plate	40	32-55
Length of pretarsal claw of leg II	12	10-13
Length of pretarsus of leg I	12	8-15

Figure 1.1 Adult stages *Sternostoma tracheacolum*

Female A, dorsal view; B, ventral view

Male C, dorsal view; D, ventral view

Egg E, ventral view of gravid female; F, egg following oviposition

CD = Cheliceral digit

CH = Chelicera

G = Gnathosoma

GP = Genital plate

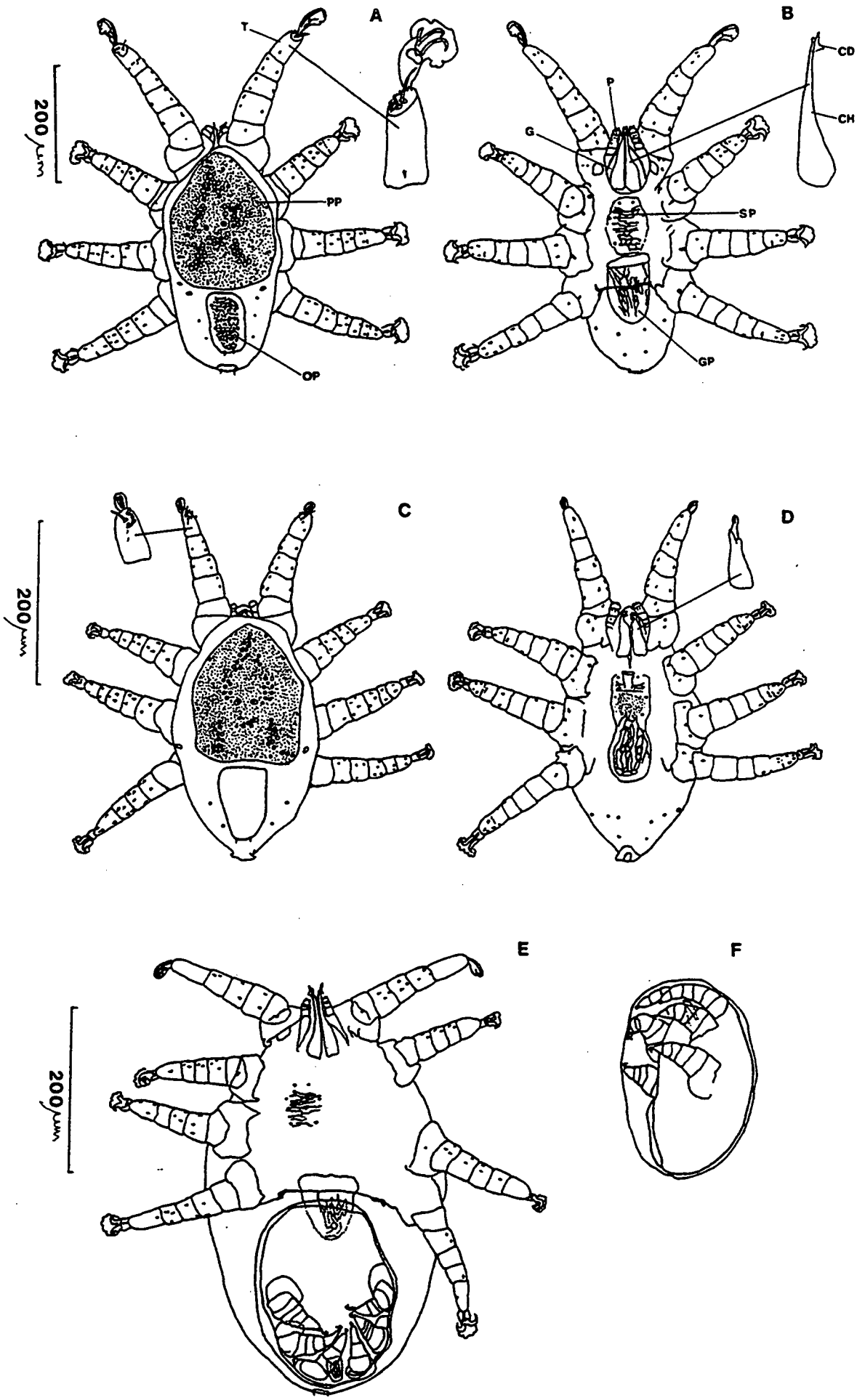
OP = Opisthosomal plate

P = Palp

PP = Podosomal plate

SP = Sternal Plate

T = Tarsus


A
T
PP
OP
200 µm
B
CD
CH
P
G
SP
GP
C
200 µm
D
E
200 µm
F

1.3.1 Female (Table 1.1; Figure 1.1A, B, E)

The adult female is the largest stage. Sclerotisation is weak and the boundaries of plates are often difficult to discern. The following account is a brief description of the adult female and follows that of Fain and Hyland (1962). The podosomal plate is pentagonal to triangular in shape, pointing anteriorly, rounded at the edges and patterned. The opisthosomal plate is elongate and patterned. The sternal plate is rectangular with sclerotisation that becomes less distinct towards the borders. A network of lines cover about two thirds of the plate. The genital plate is rounded in outline and is covered with a well defined network of lines with a longitudinal orientation. The anus is terminal with a small plate. The gnathosoma is almost completely ventral. Palps protrude beyond the level of the dorsal idiosoma and curve inward. The chelicerae are swollen at the base and, viewed dorsally, curve inwards towards the middle of their length then laterally towards the movable digit. The claw of tarsus I is greatly elongated and poorly developed. The claws of tarsus II-IV are large and well developed.

Idiosomal dimensions of the gravid female, 631 (527-749) by 349 (316-409), and the gravid female, with egg containing a developed larva, 631 (608-655) by 393 (363-437), are similar to those of the non-gravid blood gorged female but much larger than the non-gorged female 423 (396-446) by 208 (185-229). The egg, observed through the female idiosoma, measures 316 (201-374) by 238 (174-282) to 262 (241-282) by 210 (195-226) when the egg contains a clearly well developed but unhatched larva.

1.3.2 Male (Table 1.2; Figure 1.1C, D)

The adult male is considerably smaller than the adult female and little variation is detectable in idiosomal dimensions between newly moulted and blood fed specimens. The podosomal and opisthosomal plates are similar in shape to those of the adult female. The opisthosomal plate is poorly sclerotised, often with indistinct or undetectable boundaries. The genital plate is rounded and covered with a network of lines. The sternal plate is similar to that of the adult female and has indistinct boundaries. The genital pore opens at the level of the anterior margin of the sternal plate. The anal plate is terminal. The gnathosoma is ventral and only the palps protrude beyond the level of the anterior margin of the idiosoma. The chelicerae are small, bulbous at the base and well sclerotised. The movable digit is modified, probably for sperm transfer. All legs are short relative to the female. The claw of tarsus I is greatly reduced. The claws of tarsus II-IV are reduced but normal in shape.

1.3.3 Larva (Table 1.3; Figure 1.2A, B)

The larva has six legs and is similar in size to the non-fed protonymph. No plates can be discerned on either the dorsal or ventral idiosoma. The anus is terminal with no plate. The chelicerae are

Table 1.3 ***S. tracheacolum.*** **Dimensions of 10 larvae from the wild Gouldian Finch** ***E. gouldiae*** **(measurements are in microns).**

	Mean	Range
Length of idiosoma	327	264-365
Width of idiosoma	225	183-238
Length of gnathosoma	55	50-60
Width of gnathosoma	50	45-53
Length of palps	26	25-28
Total length of chelicera including fixed digit	48	40-53
Length of leg I	149	123-160
Length of leg III	130	123-140
Width of leg I	45	38-55
Width of leg III	43	35-48
Length of pretarsal claw of leg II	8	8
Length of pretarsus of leg I	8	5-10

Table 1.4 ***S. tracheacolum.*** **Dimensions of 10 protonymphs from the wild Gouldian Finch** ***E. gouldiae*** **(measurements are in microns).**

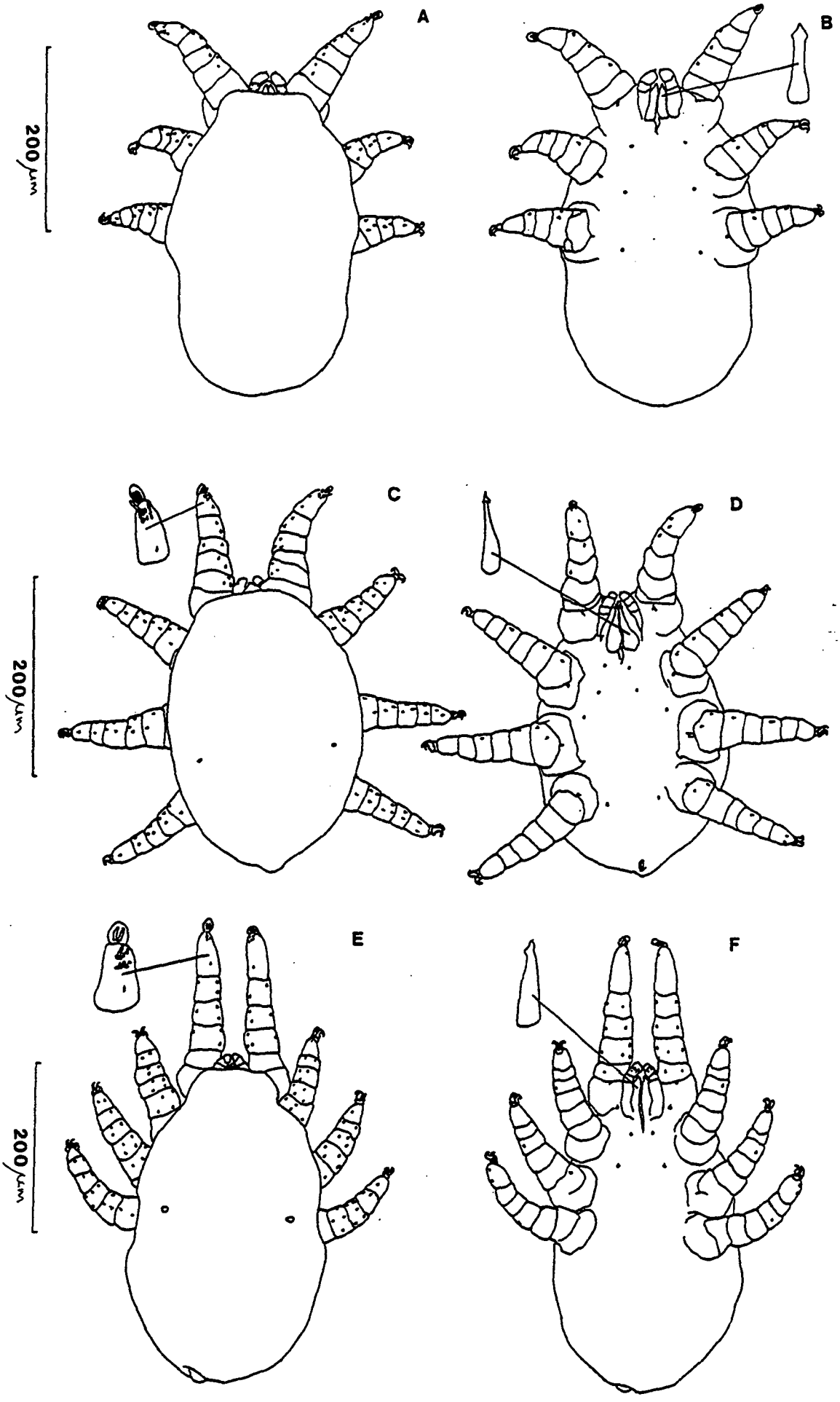
	Mean	Range
Length of idiosoma	315	274-355
Width of idiosoma	210	183-253
Length of gnathosoma	63	58-68
Width of gnathosoma	52	48-53
Length of palps	27	25-28
Total length of chelicera including fixed digit	65	63-70
Length of movable digit of chelicera	approx. 5	
Length of leg I	156	138-175
Length of leg IV	139	113-165
Width of leg I	44	40-48
Width of leg IV	39	35-45
Length of pretarsal claw of leg II	15	13-18
Length of pretarsus of leg I	11	8-15

Figure 1.2 Non-adult stages of *Sternostoma tracheacolum*

Larva A, dorsal view; B, ventral view

Protonymph C, dorsal view; D, ventral view

Deutonymph E, female dorsal view; F, female ventral view


A
B
C
D
E
F
200 µm
200 µm
200 µm

simple and poorly sclerotised. If present, the digit is greatly reduced and weakly sclerotised. Tarsus I bears a reduced claw. Tarsi II-III bear strong but small claws.

1.3.4 Protonymph (Table 1.4; Figure 1.2C, D)

No plates can be discerned on the dorsal or ventral idiosoma. The gnathosoma is similar to the female. Chelicerae are well sclerotised and smaller but similar in shape to those of the adult female. The digits are sharp-pointed and similar in shape to the adult female. The anus is terminal without an obvious plate. The claw of tarsus I is considerably reduced. The claws of tarsi II-IV are small but well developed.

1.3.5 Deutonymph (Tables 1.5 - 1.7; Figure 1.2E, F)

Plates can not be discerned on the dorsal or ventral idiosoma. The chelicerae are weakly sclerotised and difficult to discern. The palps protrude well beyond the level of the idiosoma. The first pair of legs tend to be held forward in the live specimens; in the live protonymph they often tend to be splayed laterally. The anus is terminal with a small plate. Deutonymphs can be sexed on the size of tarsus I and the ambulacral apparatus of tarsus I. Both these characters are significantly larger in the female deutonymph. All measured characters of the female deutonymph tend to be larger than those of the male deutonymph. Tarsus I of the female deutonymph is larger and more robust that tarsus II-IV (Table 1.7).

1.4 COMPARATIVE MORPHOLOGY

1.4.1 Comparative morphology of the life stages of *S. tracheacolum* from the wild Gouldian Finch and the captive Canary from Spain.

Adult female mites from the Canary from Spain have larger idiosomal dimensions, e.g. length 694 (362-999); a longer opisthosomal plate, 152 (135-164); a narrower genital plate, 49 (42-58); shorter chelicerae, 100 (93-119) and shorter movable digits 6.4 (5.8-7.5) than mites from the Gouldian Finch. Most notable is the difference in length of the cheliceral digit, almost half the size of those from the Gouldian Finch.

Adult male mites from the Gouldian Finch conform to the description presented by Guevara-Benitez and Ubeda-Ontiveros (1974) for a single specimen from the Canary from Spain though there are dimensional differences. Idiosomal dimensions of the specimen from the Canary fall within the range observed for specimens from the Gouldian Finch. However, the podosomal plate, opisthosomal plate and gnathosoma are much larger and the palps, chelicerae and legs are much longer. Guevara-Benitez and Ubeda-Ontiveros noted that tarsus I was larger and thicker than tarsus IV in the mite from the Canary. Tarsus I and IV are similar in size in specimens from the Gouldian Finch. Furthermore, the ambulacral apparatus in mites from the Gouldian Finch is much smaller than in mites from the Canary. Guevara-Benitez and Ubeda-Ontiveros record 22 for the ambulacral

Table 1.5 ***S. tracheacolum.*** **Dimensions of 10 female deutonymphs from the wild Gouldian Finch** ***E. gouldiae*** **(measurements are in microns).**

	Mean	Range
Length of idiosoma	406	406-446
Width of idiosoma	259	233-294
Length of gnathosoma	92	87-100
Width of gnathosoma	68	65-70
Length of palps	29	25-40
Total length of chelicera including fixed digit	51	40-55
Length of leg I	240	228-250
Length of leg IV	199	187-217
Width of leg I	54	50-55
Width of leg IV	44	43-45
Length of pretarsal claw of leg II	21	18-25
Length of pretarsus of leg I	17	13-20

Table 1.6 ***S. tracheacolum.*** **Dimensions of 10 male deutonymphs from the wild Gouldian Finch** ***E. gouldiae*** **(measurements are in microns).**

	Mean	Range
Length of idiosoma	344	305-370
Width of idiosoma	210	183-225
Length of gnathosoma	70	63-75
Width of gnathosoma	54	53-60
Total length of chelicera including fixed digit	not measured	
Length of leg I	174	165-180
Length of leg IV	150	140-160
Width of leg I	40	38-43
Width of leg IV	33	28-33
Length of pretarsal claw of leg II	14	13-15
Length of pretarsus of leg I	9	7-10

Table 1.7 ***S. tracheacolum.*** **Length of tarsi I-IV of 10 male and 10 female deutonymphs from the wild Gouldian Finch** ***E. gouldiae*** **(measurements are in microns).**

	Tarsus I	Tarsus II	Tarsus III	Tarsus IV
Female deutonymph	68 (63-78)	50 (43-60)	49 (38-55)	48 (38-60)
Deutonymph-adult female moult	76 (68-82)	52 (48-57)	53 (50-55)	55 (50-63)
Male deutonymph	40 (35-43)	38 (33-43)	38 (35-40)	40 (38-43)
Deutonymph-adult male moult	40 (35-43)	38 (35-40)	39 (33-45)	37 (38-45)

length of tarsus I and 30, 30 and 32 for tarsi II-IV respectively. Specimens from the Gouldian Finch have an ambulacral length of 12 (8-15) for tarsus I and 20 (17-25) for tarsus IV.

The larva described by Guevara-Benitez and Ubeda-Ontiveros (1974) is larger than the larva described from the Gouldian Finch. The idiosoma is larger, 450 (351-454) by 318 (270-366); the gnathosoma is larger, 71 (69-73) by 61 (58-64); the palps are longer, 39 (39-40), and the legs are longer, wider and carry larger ambulacra. Only the chelicerae are similar in size between larvae specimens from the two host species.

Description of the nymph by Guevara-Benitez and Ubeda-Ontiveros (1974) resulted from the examination of 9 nymph specimens. The chelicerae of their description are similar to that of the protonymph from the Gouldian Finch. However, the dimensions of the idiosoma, legs and gnathosoma are similar to those of the female deutonymph from the Gouldian Finch. Guevara-Benitez and Ubeda-Ontiveros observed a podosomal plate, but were unable to determine its size and shape precisely; an opisthosomal plate, with a sclerotised zone similar to the female; a sternal plate, poorly sclerotised with borders that are difficult to appreciate and the initiation of a genital plate in the nymph specimens. They also observed that the ambulacra of tarsus I was not reduced but similar to those of tarsus II, III and IV. In contrast, the tarsus I ambulacral apparatus of the female deutonymph from the Gouldian Finch is moderately reduced in comparison to that of tarsi II-IV. The ambulacral apparatus on tarsus I of the protonymph and male deutonymph however is greatly reduced compared to the ambulacra of legs II-IV and no idiosomal plates were observed on either the protonymph or deutonymph specimens.

1.4.2 Comparative morphology of female *S. tracheacolum* from native Australian hosts.

S. tracheacolum has been recorded from four species of wild native Australian birds: the Gouldian Finch, Pictorella Mannikin, Masked Finch (Tidemann *et al.*, 1992a) and the Budgerigar (Chapter 7: Section 7.3, Australian wild hosts). Morphological measurements of adult female mites from these host species are presented in Tables 1.8 to 1.11. Mean measurements and range for adult female mites from wild Gouldian Finches collected at three widely separated localities in northern Australia are presented in Table 1.11.

No differences, significant at the 0.05 probability level, were found between mites from the estrildid hosts (i.e. Pictorella Mannikin, Masked Finch and Gouldian Finch from all localities) for measurements of the following features: podosomal plate, opisthosomal plate, genital plate, palps, chelicerae, cheliceral digit, legs I and IV and gnathosoma. Measurements on the sternal plate were omitted from analysis due to the small number of measurements obtained. Visual comparison of measurements obtained for the sternal plate did not indicate apparent differences in the dimensions between mites from any of the estrildid hosts.

Table 1.8 Dimensions of adult female *S. tracheacolum* from the wild Pictorella Mannikin *H. pectoralis* (n = 4) from the Northern Territory, Australia (measurements are in microns).

	No. mites	Mean	Range	SD
Length of idiosoma	9	538	477-629	47.9
Width of idiosoma	9	289	223-346	42.8
Length of podosomal plate	16	254	228-264	10.6
Width of podosomal plate	14	196	175-215	9.8
Length of opisthosomal plate	13	133	128-141	4.4
Width of opisthosomal plate	12	65	60-70	3.5
Length of gnathosoma	11	106	100-118	6.0
Width of gnathosoma	15	77	70-93	6.5
Length of palps	14	38	35-40	1.4
Total length of chelicera including fixed digit	8	132	125-135	3.7
Length of movable digit of chelicera	7	13	10-15	1.5
Length of leg I	3	287	284-294	5.8
Length of leg IV	10	250	220-274	16.1
Width of leg I	14	54	50-60	2.25
Width of leg IV	15	45	40-48	2.4
Length of sternal plate	5	115	113-117	1.7
Width of sternal plate	2	98	95-100	3.5
Length of genital plate	15	111	105-116	3.6
Width of genital plate	13	81	73-93	5.0

Table 1.9 Dimensions of adult female *S. tracheacolum* from the wild Masked Finch *P. personata* (n = 1) from the Northern Territory, Australia (measurements are in microns).

	No. mites	Mean	Range	SD
Length of idiosoma	9	538	391-690	100.2
Width of idiosoma	7	284	228-355	53.9
Length of podosomal plate	9	248	238-264	8.0
Width of podosomal plate	8	194	168-208	12.6
Length of opisthosomal plate	5	129	116-138	8.9
Width of opisthosomal plate	5	67	60-78	6.9
Length of gnathosoma	6	104	98-113	6.0
Width of gnathosoma	7	83	75-98	8.5
Length of palps	6	39	38-41	1.2
Total length of chelicera including fixed digit	6	132	120-138	6.4
Length of movable digit of chelicera	6	13	13-15	0.8
Length of leg I	7	291	274-315	14.9
Length of leg IV	6	266	248-294	17.2
Width of leg I	9	54	49-60	3.5
Width of leg IV	9	46	38-53	4.6
Length of sternal plate	3	108	102-117	7.6
Width of sternal plate	1	87	87	-
Length of genital plate	10	114	107-122	4.8
Width of genital plate	7	82	77-83	2.3

Table 1.10 Dimensions of adult female *S. tracheacolum* from the wild Budgerigar *M. undulatus* (n = 5) from the Northern Territory, Australia (measurements are in microns).

	No. mites	Mean	Range	SD
Length of idiosoma	6	604	558-660	42.2
Width of idiosoma	6	260	233-315	32.8
Length of podosomal plate	8	270	253-284	11.8
Width of podosomal plate	7	192	170-203	14.4
Length of opisthosomal plate	9	157	143-163	6.7
Width of opisthosomal plate	9	65	58-75	6.2
Length of gnathosoma	6	98	90-107	6.6
Width of gnathosoma	6	69	53-90	13.9
Length of palps	6	39	38-43	2.0
Total length of chelicera including fixed digit	5	112	90-120	12.4
Length of movable digit of chelicera	5	13.2	12-15	1.1
Length of leg I	3	305	294-315	21.4
Length of leg IV	6	296	284-305	30.4
Width of leg I	5	61	58-65	3.6
Width of leg IV	6	49	45-53	2.7
Length of sternal plate	6	137	113-155	15.8
Width of sternal plate	4	80	65-90	11.7
Length of genital plate	9	129	123-135	4.4
Width of genital plate	9	62	58-70	4.3

Table 1.11 Dimensions of adult female *S. tracheacolum* from the wild Gouldian Finch *E. gouldiae* from Yinberrie Hills and Newry Station, Northern Territory and Littleton Station, Queensland, Australia (measurements are in microns).

	Newry Station Mites = 6 Hosts = 6	Yinberrie Hills Mites = 6 Hosts = 2	Littleton Station Mites = 5 Hosts = 2
	Mean (Range)	Mean (Range)	Mean (Range)
Length of idiosoma	514 (416-639)	499 (426-568)	609 (568-660)
Width of idiosoma	308 (243-396)	274 (223-325)	289 (233-365)
Length of podosomal plate	240 (223-264)	249 (235-264)	258 (250-274)
Width of podosomal plate	195 (180-210)	197 (185-213)	195 (178-203)
Length of opisthosomal plate	124 (113-133)	130 (115-137)	136 (135-138)
Width of opisthosomal plate	63 (53-70)	63 (58-65)	58 (58)
Length of gnathosoma	109 (100-113)	104 (93-113)	103 (100-105)
Width of gnathosoma	80 (73-88)	75 (73-78)	78 (75-80)
Length of palps	38 (33-40)	37 (35-40)	39 (38-40)
Total length of chelicera including fixed digit	131 (125-138)	133 (125-138)	137 (135-138)
Length of movable digit of chelicera	13 (13)	13 (13)	13.5 (13-15)
Length of leg I	274 (253-294)	297 (294-305)	284 (284)
Length of leg IV	259 (240-274)	268 (253-284)	246 (240-253)
Width of leg I	52 (50-53)	55 (53-55)	54 (50-55)
Width of leg IV	43 (40-45)	44 (43-45)	46 (43-50)
Length of sternal plate	110 (100-118)	112 (105-115)	112 (107-113)
Width of sternal plate	104 (100-108)	102 (95-108)	-
Length of genital plate	114 (100-125)	110 (98-115)	113 (105-120)
Width of genital plate	78 (70-85)	80 (75-85)	85 (80-90)

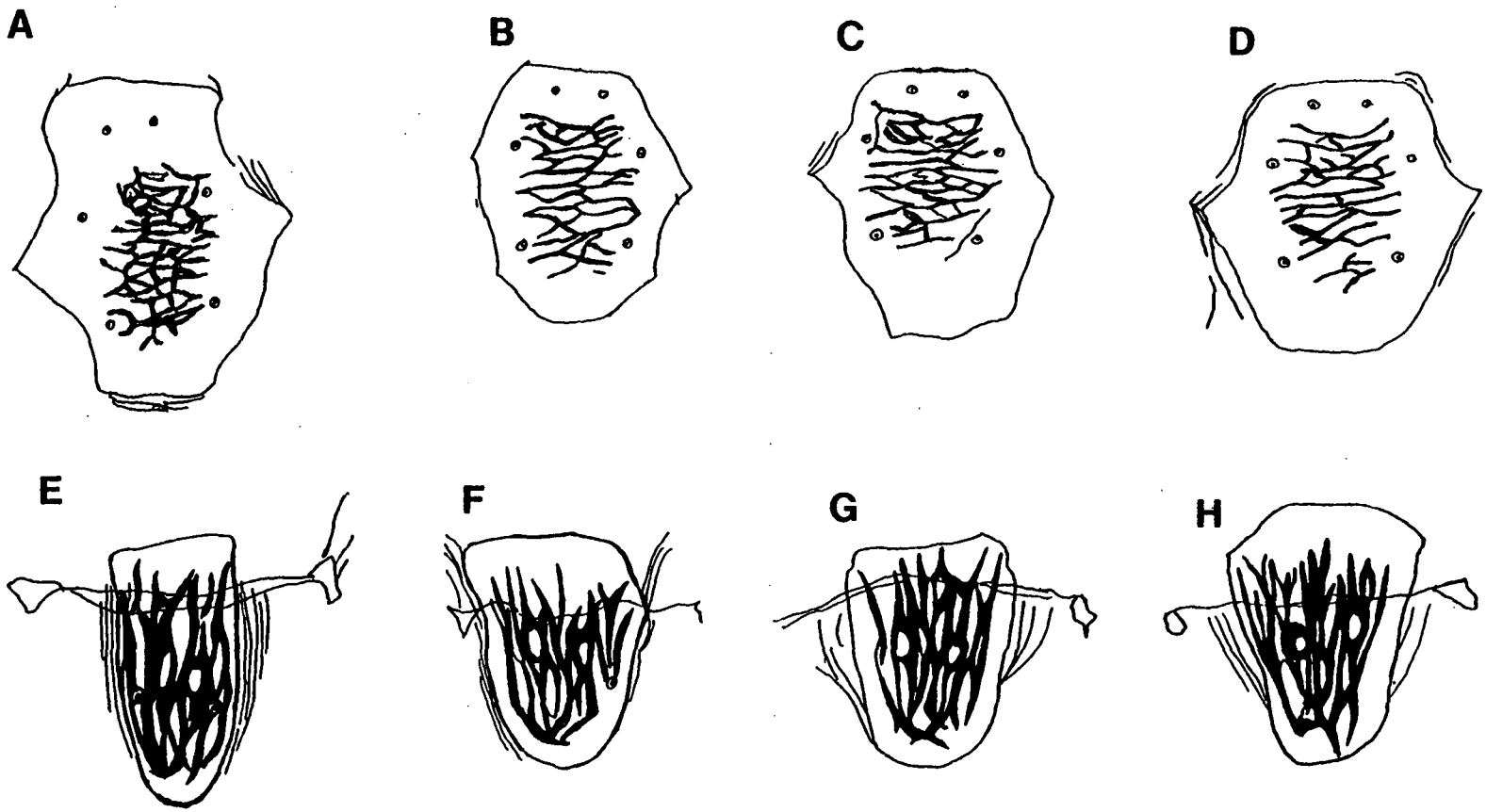


Figure 1.3 ***Sternostoma tracheacolum*** **Sternal and genital plates:** specimens from wild birds; Budgerigar (A and E); Gouldian Finch (B and F); Pictorella Mannikin (C and G); Masked Finch (D and H).

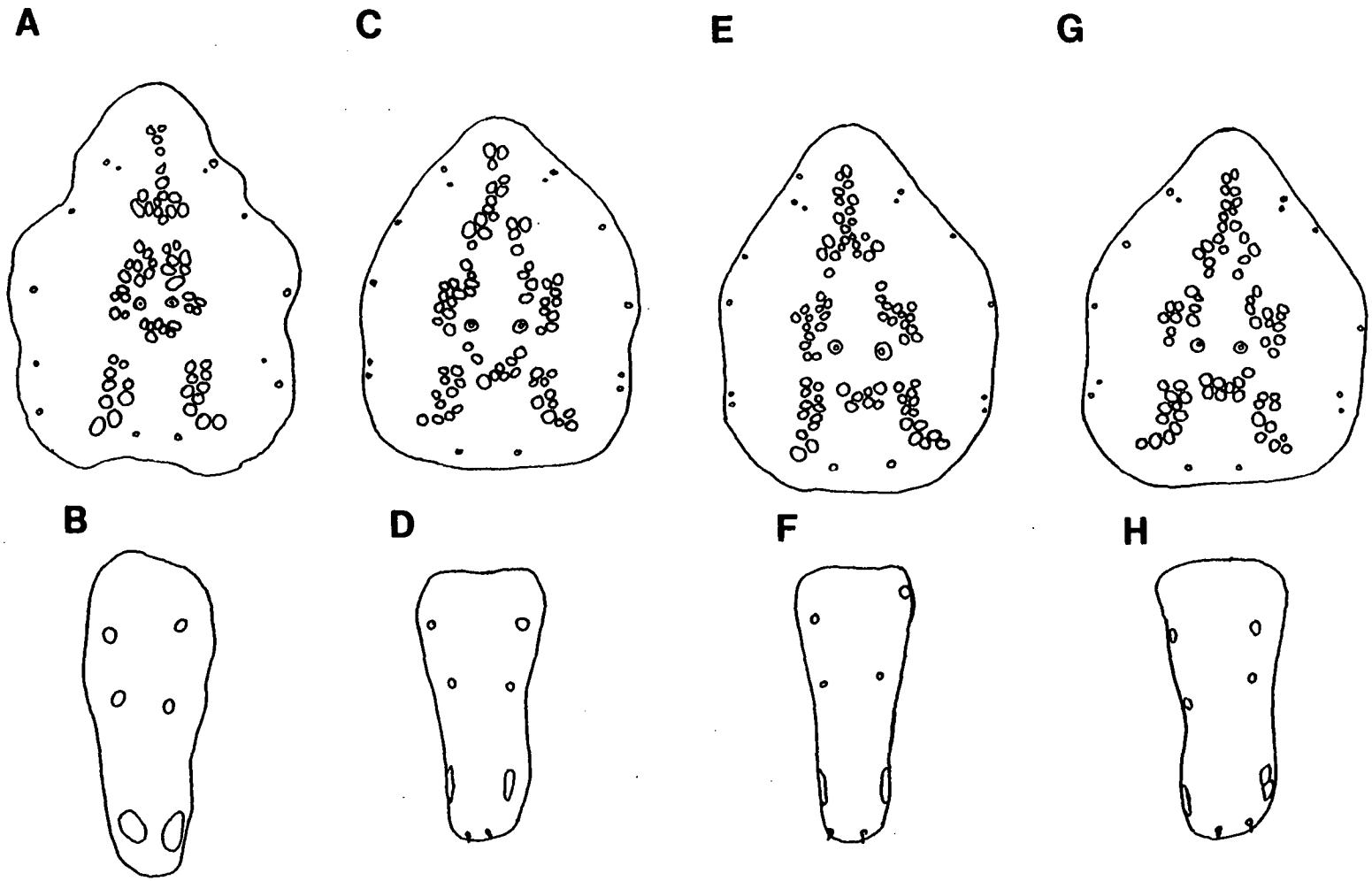


Figure 1.4 *Sternostoma tracheacolum* Podosomal and opisthosomal plates: specimens from wild birds; Budgerigar (A and B); Gouldian Finch (C and D); Pictorella Mannikin (E and F); Masked Finch (G and H).

Significant differences were found between mites from Budgerigars and estrildid hosts for the following measurements: length of podosomal plate, length of opisthosomal plate, length and width of gnathosoma, length of chelicerae, width of leg I, length of leg IV and the length and width of the genital plate (Table 1.12). Mites from all estrildids differed significantly from Budgerigar mites in the length of the opisthosomal plate, length of the chelicerae, width of leg I and the length and width of the genital plate. Visual examination of measurements obtained for the sternal plate indicate a large apparent difference between mites from the Budgerigar and all the estrildid hosts. By comparison with the estrildids, mites from the Budgerigar appear to have a longer and narrower sternal plate (Fig. 1.3). Patterns on the genital plate (Fig. 1.3), podosomal plate and the opisthosomal plate (Fig. 1.4) vary between the Budgerigar and the estrildids, these features being similar within the estrildids. Mites from the Budgerigar lack a pair of short setae at the posterior margin of the opisthosomal plate, a feature present in mites from all estrildid hosts.

Table 1.12 Significant differences (ANOVA) in dimensions between adult female *S. tracheacolum* from Budgerigar (final column) and other known Australian wild hosts. Measurements with the same symbol are not significantly different. Mean measurements are presented for each character. See Tables 8 - 11 for mite and bird samples sizes.

	Gouldian Finch (Yinberrie)	Gouldian Finch (Newry)	Gouldian Finch (Littleton)	Masked Finch (Newry)	Pictorella Mannikin (Newry)	Budgerigar (Newry)
Length of podosomal plate	*249	*240	‡258	*248	*254	‡270
Length of opisthosomal plate	*130	*124	*136	*129	*133	‡157
Length of gnathosoma	‡104	*109	‡103	‡104	‡106	‡98
Width of gnathosoma	‡75	‡80	‡78	*83	‡77	‡69
Total length of chelicera including fixed digit	*133	*131	*137	*132	*132	‡112
Width of leg I	*55	*52	*54	*54	*54	‡61
Length of leg IV	‡269	*259	*246	*266	*250	‡296
Length of genital plate	*110	*114	*113	*114	*111	‡129
Width of genital plate	*80	*78	*85	*82	*81	‡62

1.4.3 Comparative morphology of adult female *S. tracheacolum* from Australian and overseas hosts.

An ordination of mean morphological measurements for mites from Australian and overseas hosts is shown in Figure 1.5. The first axis (Factor 1) was mainly related to the chelicera and cheliceral digit length, gnathosoma length and genital plate width and accounted for 35.9% of the variation. The two subsequent axes accounted for a further 27.5% and 10.5% of the variation respectively. They were related to leg I width and length and gnathosoma width (Factor 2) and genital plate length (Factor 3).

Figure 1.5 Ordination of *Sternostoma tracheacolum* measurements.

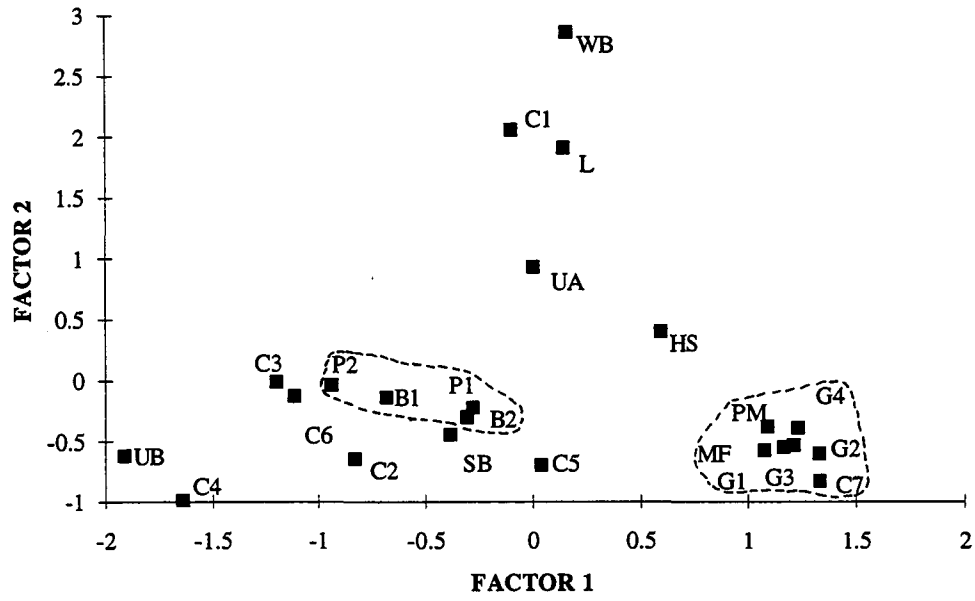
Wild hosts: L = Lark *Macronyx croceus* Vieillot **Emberizidae**, from central Africa; WB = *Icterus bullocki* (Swainson) **Emberizidae** and Tricolored Blackbird *Agelaius tricolor* (Audubon) **Emberizidae** from California, U.S.A.; UA = Bank Swallow *Riparia riparia* (L.) **Hirundinidae**; Eastern Meadow lark *Sturnella magna* (L.) **Emberizidae**, Song Sparrow *Melospiza melodia* (Wilson) **Emberizidae,** Field Sparrow *Spizella pusilla* (Wilson) **Emberizidae,** Indigo Bunting *Passerina cyanea* (L.) **Emberizidae** and House Sparrow *Passer domesticus* L. **Passeridae** from Michigan, U.S.A.; UB = Vesper Sparrow *Pooecetes gramineus* (Gmelin) **Emberizidae**, *M. melodia* and *P. cyanea* from Michigan, U.S.A.; HS = *P. domesticus* from Michigan, U.S.A.; P1 = Madagascar Lovebird *Agapornis cana* (Gmelin) **Psittacidae** and P2 = *Agapornis* sp. **Psittacidae** from Madagascar (Fain & Hyland, 1962). G1 = Gouldian Finch *E. gouldiae* **Estrildidae** from Yinberrie Hills, NT; G2 = *E. gouldiae* from Newry Station, NT; G3 = *E. gouldiae* from Littleton Station, Qld; B1 = Budgerigar *Melopsittacus undulatus* (Shaw) **Psittacidae** from Newry Station, NT; PM = Pictorella Mannikin *Heteromunia pectoralis* **Estrildidae** from Newry Station, NT and Masked Finch *Peophila personata* **Estrildidae** from Newry Station, NT, Australia (This study).

Captive hosts: B2 = Budgerigar from the Antwerp Zoo, Belgium; SB = Yellow-winged Sugarbird *Cyanerpes cyaneus* (L.) **Emberizidae**, from the Antwerp Zoo, Belgium (originally from Brazil); C1 = Canary *Serinus canarius* (L.) **Fringillidae** from South Africa; C2 = Canary from Brazil; C3 = Canary from Belgium; C4 = Canary from New Jersey, U.S.A. (Fain & Hyland, 1962). C5 = Canary from Barcelona, Spain (Blasco-Sabio & Portús-Vinyeta, 1974). C6 = Canary from Granada, Spain (Guevara-Benitez & Ubeda-Ontiveros, 1974). C7 = Canary from Australia (experimentally infected with *S. tracheacolum* from the wild Gouldian Finch from Newry Station); G4 = Gouldian Finch from Australia (experimentally infected with *S. tracheacolum* from the wild Gouldian Finch from Newry Station, NT (This study).

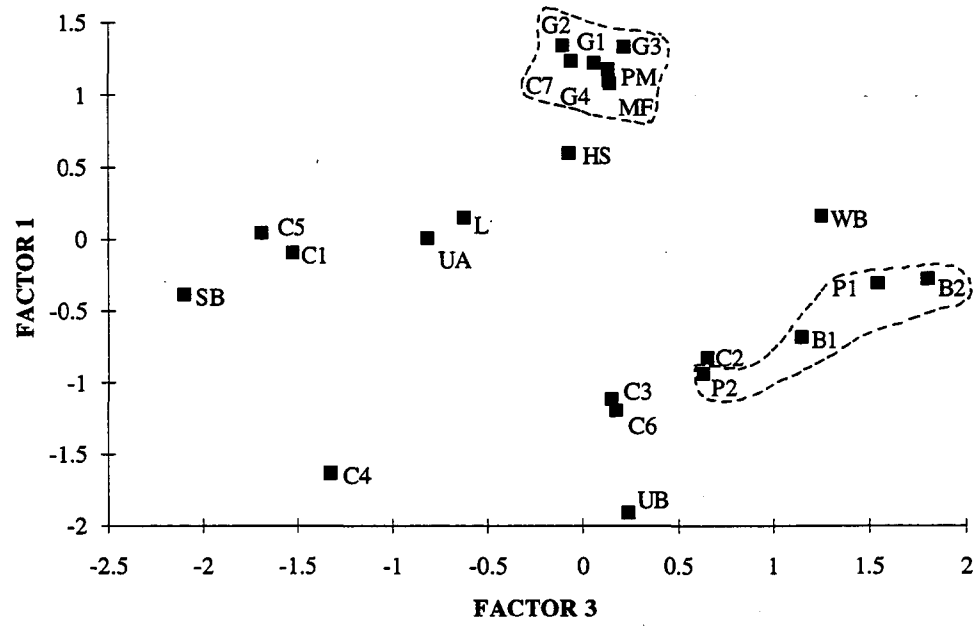
Dashed lines enclose values for mites from Australian wild and captive estrildid and fringillid hosts from this study (i.e. G1, G2, G3, G4, PM, MF and C7) and from psittacid hosts (i.e. P1, P2, B1 and B2) from this study and from Fain and Hyland (1962).

Figure 1.5 Ordination of *Sternostoma tracheacolum* measurements

Factor 2 vs Factor 1



Factor 1 vs Factor 3



S. tracheacolum from estrildids are clustered at high values of Factor 1. Their values are higher than values for mites from all other hosts and host species but lie closest to mites from the House Sparrow. Budgerigar mites lie at middle values of Factor 1, some distance from the estrildids. Of particular note is the closeness of Budgerigar mites (B1) to mites from other recorded psittacid hosts: Budgerigar from Belgium (B2); Love Bird *Agapornis cana* Gmelin (P1) and *Agapornis* sp. (P2) from Madagascar. With regard to Factor 3, mites from estrildids are again closely grouped. Psittacids lie in a loosely associated group at higher values of Factor 3. Mites from the House Sparrow and or the Canary lie between estrildid and psittacid groups with regard to values of all Factors.

With regard to all Factors, mites from estrildid finches and both captive Canaries and Gouldian Finches (experimentally infected with mites from the wild Gouldian Finch) show tight clustering within the ordination of mean morphological measurements. With regard to Factor I the estrildid mite group lies outside the range of values scored for mites from other host species. The mites from this group tend to have a wider genital plate, longer chelicerae and longer cheliceral digits. With specific regard to these features, mites from the House Sparrow appear to be most similar to the estrildid group.

1.5 DISCUSSION

1.5.1 Life stages of *S. tracheacolum* from the wild Gouldian Finch

Sexual dimorphism in adults is pronounced. The male is small and the opisthosomal plate is poorly sclerotised in comparison to the female. However, the best feature to use for rapid separation from other life stages is the presence of the male genital pore. Blood gorged and or gravid females are readily recognised with the naked eye by their large size. The developing egg can be often seen through the translucent idiosoma though examination at the microscopic level is generally necessary for confident separation of gravid and non-gravid specimens. The non-gravid, non-gorged female, the adult male and the immatures necessarily require at least partial clearing and subsequent examination under the light microscope for reliable recognition. The larval stage is readily recognised as a hexapod but at low magnification is easily confused with the newly moulted protonymph. The nymphs are recognised by the lack of discernible idiosomal plates. The protonymph and deutonymph can be distinguished on the form of the chelicerae and cheliceral digits; strong chelicerae in the feeding protonymph and weak vestigial chelicerae in the non-feeding deutonymph. Deutonymphs are readily sexed on the length of tarsus I, a feature much longer in the deutonymph female. For the purposes of demographic and population studies on *S. tracheacolum* no rapid technique for recognising stage and sex exists. Reliable identification requires the protracted procedure of clearing, mounting and subsequent examination under the compound light microscope.

1.5.2 Comparative morphology of life stages of *S. tracheacolum* and other *Sternostoma* spp

The morphologies of life stages of *S. tracheacolum* from the Gouldian Finch are typical of those described for other *Sternostoma* spp. The larval stage shows little or no development of the idiosomal armature, has a reduced setation and is weakly sclerotised. The larval stage of *S. strandtmanni* (see Furman, 1957), *S. boydi* (see Strandtmann, 1951), *S. spatulatum* (see Pence, 1972), and *S. fulicae* (see Guevara-Benitez & Ubeda-Ontiveros, 1975) are also poorly developed and devoid of plates. In contrast, the larva of *S. borceanum* is a robust mite with strong claws and idiosomal plates similar to the adult female.

S. tracheacolum nymphs are similarly delicate and typical in comparison to other *Sternostoma* nymphs. Furman (1957) noted for the nymph of *S. strandtmanni* that no idiosomal plates were visible either by standard or phase microscopy and that the claws of tarsus I were greatly reduced in comparison to tarsus II-IV. The protonymph of *S. spatulatum* (Pence, 1972) and the nymph of *S. boydi* (Strandtmann, 1951) also lack plates.

1.5.3 Comparative morphology of female *S. tracheacolum* from the wild Gouldian Finch and overseas hosts

Distinct morphological differences between immature mites from the Gouldian Finch and the Canary from Spain are difficult to interpret, particularly with respect to the presence of idiosomal plates in specimens from the Canary. However, these differences are also reflected by important differences in the morphology of adult mites from the two host species.

Adult female mites from the Canary from Spain show similarity with a group of mites recognised by Fain and Hyland (1962) from Canaries from Belgium. The major distinguishing feature is the cheliceral digit length which is only half that of mites from Canaries from South Africa. By contrast, mites from the Gouldian Finch have affinities with mites with extremely large cheliceral digit length. These mites are similar to those from Canaries from South Africa. Fain and Hyland considered that, given the relative stability of the cheliceral digit length in specimens from the same locality, mites from Canaries from Belgium may have constituted a new species. However, after finding specimens from other host species with cheliceral digit lengths lying between the two extremes they concluded that the differences could be accounted for by within-species variation. It is clearly evident, from the comparison of mite life stages from the wild Gouldian Finch from Australia and the Canary from Spain, that important differences occur not only in the adult female but in all life stages and over several characters. Both the male and the immatures from the Gouldian Finch appear to be less robust than those from the Canary from Spain. Combined with the knowledge that adult female mites from the two host species represent extremes in the length of the cheliceral digit considered (by Fain and Hyland) to be a very stable character, it is tempting to suggest that they belong to separate subspecies. But until more information is available on the

males and immatures from other host species, and all specimens can be examined by the same author, it would be unwise to propose such a division at this stage.

1.5.4 Comparative morphology of female *S. tracheacolum* from native Australian hosts

Interpretation of the variation in the morphology of *S. tracheacolum* from wild Australian birds appears to be a little more straight forward. No differences are detectable between mites from the three recorded estrildid hosts or between mites from estrildid specimens from localities separated by up to 1000 km. Nor are there any significant differences between these mites and mites from wild caught Gouldian Finches that have been reared in captive bred Canaries for over 6 months (Chapter 8: Host Susceptibility), or captive bred Gouldian Finches for over two years.

On the other hand, mites coming from Budgerigars captured in the same locality as the wild estrildid hosts, are significantly different (over a number of measurements) from mites of estrildid hosts. Measured independently, the differences are not large, though viewed as a whole, a Budgerigar mite is distinctly different from an estrildid mite. Budgerigar mites from Newry Station, NT are more similar to mites found in two captive reared Budgerigars found dead at the Antwerp Zoo, Belgium in 1958 (1 mite) and 1961 (4 mites) and mites from *Agapornis* sp. (3 mites) and *A. cana* (2 mites) from Madagascar (Fain & Hyland, 1962) than to mites from Australian estrildid finches. Fain and Hyland note that mites from the captive Budgerigar are inseparable from mites from the Lovebirds of Madagascar and that all mites from psittaciforms can be differentiated from the passeriforms (both wild and captive reared) by the subequal lengths of legs I and IV. Based on the consistency of this character and the different nature of the hosts they consider that mites from the psittaciform hosts may constitute a distinct subspecies.

Morphological evidence of mites from psittacid and estrildid host species in Australia supports the proposition for separation of *S. tracheacolum* into psittaciform host and passeriform host species. Additional supporting evidence for the separation comes from the experimental study of host susceptibility. Captive reared Budgerigars do not appear to be susceptible to experimental infection by *S. tracheacolum* originating from the wild Gouldian Finch, yet captive bred Gouldian Finches and Canaries are readily susceptibility to infection (Chapter 8: Host Susceptibility). The Budgerigar, Masked Finch, Pictorella Mannikin and the Gouldian Finch overlap in their distributions, occupy similar habitat, and observations from the present study indicate reasonable opportunity for interspecific transmission (Chapter 2: Section 2.7, Transmission) yet the morphological evidence suggests that the two groups of mites are genetically isolated populations. By contrast, morphological similarity of mites from the estrildid host species (Gouldian Finch, Masked Finch and Pictorella Mannikin) suggests that they are not genetically isolated by host species or geographic location.

In the present study, only specimens from the Budgerigar were found to be devoid of a pair of small setae at the level of the posterior margin of the opisthosomal plate. From the account of *S. tracheacolum* by Fain and Hyland (1962) the same appears to be the case for all mites recorded from psittaciform hosts when compared to all mites from passeriform hosts.

For the purposes of this study and to reduce confusion in the following chapters, the morphological form of *S. tracheacolum* infecting wild Gouldian Finches, Masked Finches and Pictorella Mannikins in Australia will be referred to as the 'Passerine form' and the morphological form of *S. tracheacolum* infecting wild Budgerigars will be referred to as the 'Psittacine form'.

1.5.5 Implications of the study of *S. tracheacolum* morphology for an 'introduction hypothesis'

In an attempt to interpret the cause of heavy infection by *S. tracheacolum* in wild Gouldian Finches and the presence of associated respiratory disease, Tidemann *et al.* (1992a) suggested that *S. tracheacolum* may be a recent introduction to Australia, arriving either naturally by migratory birds or accidentally by the importation of aviary birds prior to mandatory quarantine procedures. Access to wild birds by the latter would have occurred through accidental or deliberate release of infected birds into the wild. The morphological study of *S. tracheacolum* from wild Australian birds yields results that are inconsistent with this suggestion. For the suggestion to retain validity a recent introduction of two distinct morphological types would have been necessary, one form now present in the psittaciforms, (represented by the Budgerigar) and one form present in the passeriforms (represented by the Gouldian Finch, Pictorella Mannikin and the Masked Finch).

There is no reason to suspect that *S. tracheacolum* has not been present in wild Budgerigar for a considerable period of time. There is no obvious gross pathology associated with infection, measures of intensity and prevalence do not appear to be aberrant in comparison to other known hosts (Chapter 7: Section 7.3.2, Prevalence of infection) and the morphological type present is typical of *S. tracheacolum* from other psittaciform hosts, as well as captive Budgerigars since 1958.

On the other hand the morphological consistency observed in specimens from several estrildid host species and collected over widely separated localities in northern Australia is consistent with the suggestion of a recent introduction and a rapid spread of the mite in recent decades. If the suggestion by Tidemann and her associates (1992a) that *S. tracheacolum* is recently introduced to Australia is not to be rejected out of hand, it would be necessary to modify the proposed scenario.

The 'Passerine form' of *S. tracheacolum* may have evolved in passeriform hosts overseas and has only recently (since European settlement) been introduced to Australia. The 'Passerine form' is potentially pathogenic in some species of estrildid finches (especially the Gouldian Finch). Based

on morphological similarity of mite specimens, the introduction could have been effected by the Canary *S. canarius* or the House Sparrow *P. domesticus*.

Chapter 2. LIFE HISTORY

2.1 INTRODUCTION

Little is known of the life history or biology of transmission of acari that parasitise the respiratory system of vertebrates. Some progress has been made with the halarachnids e.g. *Pneumonyssus* (Hull, 1956; 1970; Furman *et al.*, 1974) and *Orthohalarachne* (Furman & Smith, 1973), but few studies have yet focused on the Rhinonyssidae.

Porter and Strandtmann (1952) in a study on the rhinonyssids *Ptilonyssus nudus* and *Neonyssus hirsti*, and the speleognathid *Speleognathus sturni* in nestling House Sparrows, *Passer domesticus*, suggested that transmission was direct from infected hosts by 'billing' or while parent birds were feeding their young. They considered that direct transfer was probably obligatory for the Rhinonyssidae due to the extreme sluggishness and susceptibility to desiccation in observed species. However, for the Speleognathidae which are very agile and more resistant to desiccation, they 'could conceivably leave one host and make their way unassisted to another'.

Murray (1966) found *S. tracheacolum* in nestling Gouldian Finches which provided further support for transmission at the nest site. In contrast, TerBush (1963) found a prevalence of 2% for *Larinyssus orbicularis* infecting very young Herring Gulls, *Larus argentatus*, compared to a 50% prevalence in second year birds and a 63% prevalence in birds aged over three years. TerBush considered that, at least in the Herring Gull, transmission does not commonly take place in the nest but elsewhere and at a different time in life. Similar differences were observed by Amerson (1967) in the prevalence of *Larinyssus* and *Sternostoma* between immature and adult Sooty Terns, *Sterna fuscata.* Amerson observed nasal mites around the choana of several adult birds and on the glottis of the trachea in three cases from a collection of 257 birds. He suggested that mites moving to this locality from the nasal cavity would be easily transmitted when regurgitated food is fed to nestlings. On the available evidence, transmission in the Rhinonyssidae appears to be direct. However, the mode of transfer, and whether mites play an active or passive role in their transferral is less understood and remains open to speculation.

Gamasid parasites have evolved towards a simplification of the typical acarine life cycle that has involved a reduction in both the number of separate stages and the number of active stages. Egg, larva, protonymph, deutonymph and adults occur in all known species although the egg or both the egg and larva stage may be completed before birth (Radovsky, 1969).

There is also a tendency among the endoparasitic gamasids for specialisation of the immature stages for transmission. The reproductive adults are generally specialised for internal parasitism

where immature, and especially non feeding stages, may be free to evolve attributes specifically adapted for transmission (Radovsky, 1969). Immatures of the Entonyssidae are more common in the trachea than in the lungs where the adults occur (Fain, 1961) and similar distributions have been found in some species of the Halarachnidae (Radovsky, 1969). Larvae of the halarachnids such as *Pneumonyssus simicola* (see Hull, 1970) and some rhinonyssids such as *R. rhinolethrum* (Mitchell, 1963) have large well developed claws that are in some cases larger than those of the adult female. These features are potentially useful in moving between hosts (Radovsky, 1969). Observed *Sternostoma* larvae show no features that could be described as particularly useful in transmission. They are weakly developed with reduced claws and, given the suggestion that mites may be transferred from parent bird to offspring via food regurgitation, the larva cannot necessarily be disqualified as a potential candidate for transmission. The larva of *S. borceanum* is an exception with long legs and sclerotised plates that are similar in appearance to the adult female. Indeed, variations in the morphology of immature rhinonyssids suggest that the stage and/or the mode of transmission may even vary between species.

Our limited knowledge of the longevity of the life cycle from egg to adult in endoparasitic mites of vertebrates comes mainly from *in vitro* rearing experiments. There has been some success in the rearing of halarachnids but attempts to culture rhinonyssids have failed. Porter and Strandtmann (1952) were able to keep adults of *Neonyssus hirsti* alive for up to two weeks in physiological saline at room temperature, but without reproduction. They observed that mites desiccate and die within a few minutes when placed on a dry surface exposed to free air. *S. tracheacolum* has also been noted to desiccate rapidly outside the body of the host (Kummerfeld & Hinz, 1982). Hull (1956) reared larvae of the monkey lung mite *P. simicola* to nymphal stage in normal saline at room temperature and Furman, Bonasch, Springsteen, Stiller and Rahlmann (1974) were able to rear larvae in 0.85% saline which developed to adult stage after 5 days. Furman and Smith (1973) cultured a larva of *Orthohalarachne diminuata* (Doetschman), taken from the nares of the California sea lion, to the adult stage in physiological saline within 11-12 days.

The previous studies of endoparasitic gamasids indicate a tendency for rapid development from the larva to adult stage. The need for high humidity appears to be important although simple saline solutions or moist environments may not be sufficient to stimulate oogenesis and egg laying. Adults of *Sternostoma* are delicate, sluggish and have never been observed outside the body of a living bird (Amerson, 1967; Porter & Strandtmann, 1952); removed from the host they are extremely short lived. For this reason the live chorio-allantoic membrane (CAM) of the domestic chick has some appeal as a possible culturing vessel. Not only does the CAM provide a constant humidity and a suitable temperature for rhinonyssid mites but also a well vascularised membrane which may be suitable for mite feeding. The CAM has been widely used in the culturing of bacteria and viruses

(Ganote *et al.*, 1964) and more recently for the culture of certain trematodes species (Fried, 1962; Leno & Holloway, 1986).

Parthenogenesis is known to occur in most suborders of the Acarina and arrhenotoky is a frequent mode of reproduction in specific families. Arrhenotoky involves the development of haploid males from unfertilised eggs and diploid females from eggs receiving spermatozoa. In thelytoky, mainly females are produced and males are either absent, rarely found or if present usually do not mate (Oliver, 1971). Arrhenotoky appears to be the predominant form of reproduction within the Gamasida (Oliver, 1971) though thelytoky is also known to be common in certain taxa (Krantz, 1978). Mode of reproduction is usually demonstrated cytologically (e.g. Hansell, Mollison & Putman, 1964; Helle & Bolland, 1967) though most information regarding sex determination comes from experiments with laboratory cultures (e.g. Filipponi, 1964; Regev, 1974). The type or types of reproduction employed by the Rhinonyssidae have not been determined, though several authors have noted the rarity of males, particularly *S. tracheacolum*, in observed infections (e.g. Lawrence, 1948; Stephen, Kaschula & Canham, 1950). For many species, males are not yet known.

The present study investigates the life cycle of *S. tracheacolum* with particular emphasis on the biology of transmission, the duration of the life cycle and the spatial distribution of mite infrapopulations (i.e. the total number of mites in individual hosts) within the host. The analysis of the spatial patterns of infection is based on a data set containing information on stage and site details for mites from 84 *S. tracheacolum* infections. The duration of individual life stages and the life cycle from egg to adult is investigated through a combination of CAM rearing experiments and examination of chemically killed gravid mites retained within the respiratory system of live hosts.

2.2 METHODS

2.2.1 *In vitro* culturing

Fertile eggs were collected from a local hatchery and incubated at a temperature of 37-38^{o} C and a relative humidity of 60-68%. After 7 days, eggs were candled to determine fertility. A window, 1 cm^2, was drilled in the blunt end of the egg and a slit was cut in the shell membrane and moistened with a sterile physiological saline solution. While separating the slit with sterile forceps, a gravid mite taken from the respiratory system of a freshly killed bird was carefully placed on the CAM with a micro spatula. The eggshell was replaced and sealed with hot liquefied paraffin and the egg returned to the incubator. At various intervals eggs were examined and live mites were recovered. Following examination under the dissecting stereoscope mites were placed on freshly prepared egg CAMs.

2.2.2 Chemically killed female mites

When ivermectin (Ivomec®) is administered orally to captive Gouldian Finches infected with *S. tracheacolum* large proportions of mite infrapopulations are killed, but the egg of killed female mites does not die but continues to develop (Chapter 9: Section 9.3.2, An abnormal development site for *S. tracheacolum* following ivermectin treatment of the host). All stages from hatched larva to adult male may thus be found within the carcass of the mother. Given a knowledge of the time elapsed between drug administration and subsequent killing of the host to assess the efficacy of the acaricide action, minimum times for egg to latter stage development can be determined.

2.2.3 Life history

A dataset was compiled from information on 6143 mites from 84 *S. tracheacolum* infrapopulations from both wild and captive bred Gouldian Finches. The mean intensity of infection was 73 mites per host (Range = 1-359 mites). The sex, age, head colour and experimental history for each infected bird, along with the total number of mites and the number of mites found dead in each infection, are listed in Appendix III.

A record was made of the site (i.e. nasal cavity, buccal cavity, upper trachea, lower trachea, syrinx, bronchus, lung, posterior airsac, thoracic airsac, anterior airsac or body cavity), stage (i.e. egg, larva, protonymph, deutonymph, adult male or adult female), type (i.e. egg, larva, larva-protonymph moult, protonymph, protonymph-deutonymph moult, deutonymph, deutonymph-male moult, deutonymph female moult, adult male or adult female, non-gravid or gravid and gorged or non-gorged) and whether the mite was live or dead at the time of host death.

For comparative purposes some of the host sites were lumped. The oesophagus and the buccal cavity were grouped as 'buccal cavity'. The cervical and interclavicular airsacs, including humerus airsac extensions, were grouped as 'anterior airsacs' and the anterior and posterior thoracic airsacs were grouped as 'thoracic airsacs'. The 'type' larva-protonymph was classified as protonymph, protonymph-deutonymph as deutonymph, deutonymph-male as adult male and deutonymph female as adult female to conform to 'stage' categories. An adult female mite was recorded as gravid when an egg membrane could be detected through the idiosomal exoskeleton. An obviously bloated female mite was recorded as gorged and a non-bloated female mite, even if old blood could be seen within the caeca, was classified as non-gorged. Missing values were recorded in the 'type' category for 200 of 4810 females and were ignored in subsequent calculations. These were dead mites that had disintegrated to the point where no determination could be made on either the state of engorgement or the reproductive condition prior to death.

A small percentage (<1%) of mites were lost or completely destroyed during dissection, storage, clearing or slide mounting. If the stage and sex of the mite was not known it was allocated to the

category containing the highest frequency for that specific site. If more than one mite from the same site was lost or destroyed they were allocated to 'stage' and 'type' categories at the same ratio recorded for other mites from the same site.

A lung and 50% of the nasal cavity tissue were not examined for 10 Gouldian Finches (used in a study of histopathology). As the distribution of mites was not significantly different between the right and the left side of the respiratory system ($\chi^2 = 2.05$, df = 1, $P = 0.15$, Hosts = 16, Mites = 739), the frequency and the allocation of mites to 'stage' and 'type' categories for the unexamined lung and nasal cavity were assumed to be the same as those recorded for the examined side. The lung and the side of the nasal cavity examined was determined by the toss of a coin.

Summed raw frequencies for all 84 infections were used to examine stage, sex, site and mortality data. The analysis assumes the localisation of mites and the proportions of dead mites to be independent of the size of the infrapopulation or host parameters such as sex or breeding condition.

Feeding status categorised as either translucent non fed, containing fresh red blood or containing old black blood was recorded for 1567 mites and used to assess the feeding requirements of each mite stage.

2.2.4 Transmission

During the period January 1992 to October 1993, examinations were made of the drinking water from various enclosures of infected Gouldian Finches. The water was usually collected daily and filtered through a 100 micron mesh. Trapped items were examined under the dissecting microscope and mites found (live or dead) were cleared, mounted and examined microscopically.

The head plumage, external nares and mandibles of infected Gouldian Finches were regularly examined using either a 10X magnification hand lens or by holding the bird under a dissecting microscope. A record was made of both the position of the mite on the host and the time of the observation.

Mites coming from either freshly dissected Gouldian Finches and Canaries, removed from the plumage, anterior nares or mandibles of Gouldian Finches or found on the surface of drinking water from enclosures containing infected Gouldian Finches were subjected to various regimes of temperature and humidity to determine the longevity of survival outside the host.

2.2.5 Analysis

Programs in the Statistical Analysis System (SAS Institute INC., 1988) were employed for data manipulations and statistics. Descriptive statistics, means and standard deviations, were calculated using PROC MEANS. Frequencies and proportions were calculated using PROC TABULATE. Chi-square (χ^2) tests were performed on frequency tables using PROC FREQ with the CHISQ option.

2.3 SITE

2.3.1 All mites

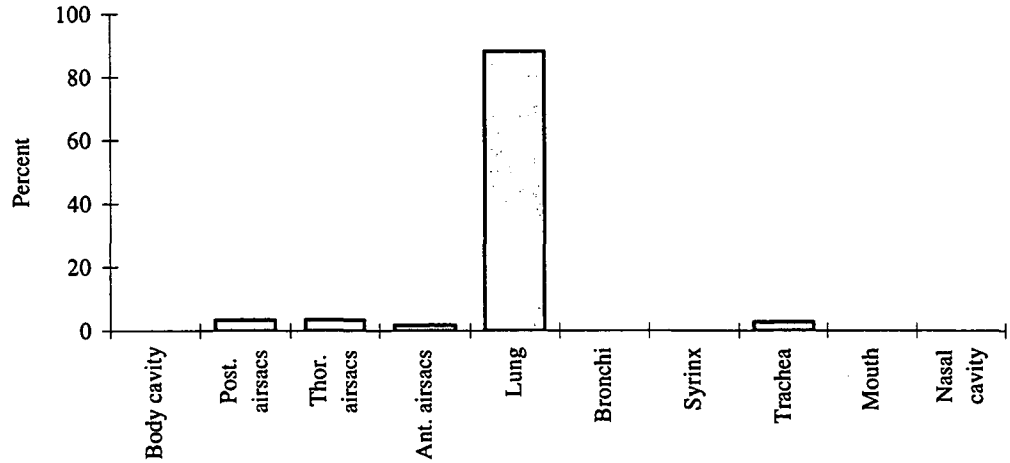
Live *S. tracheacolum* were found within the respiratory system, digestive system and the general body cavity of the host. Mites were never found embedded in tissues. Outside the body of the host mites were found on both the bill and the head plumage (Section 2.7, Transmission). Within the respiratory system mites were found in the nasal cavity, buccal cavity (primarily in the region between the larynx and the palatal folds at the opening of the nasal passage), trachea, syrinx, primary bronchi, air passages of the lungs and all major airsacs including the cervical, interclavicular, anterior and posterior thoracic, and abdominal airsacs. Very occasionally mites were found in the proximal region of the pneumatisized humerus and within the oesophagus. Within the general body cavity mites were found on mesentery adjacent to or directly on the liver, kidneys, intestine and the ovary or testes.

2.3.2 Females

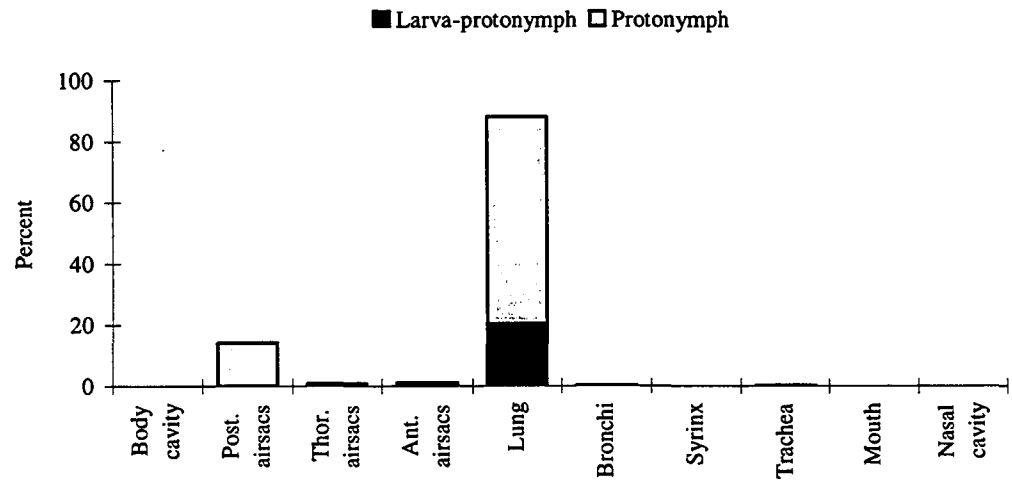
Adult females were found throughout the respiratory system. They were found in the nasal cavity, buccal cavity and the oesophagus of the host and were the only stage to be found in these sites. The most common sites were the trachea and the airsacs (Figure 2.2B). The deutonymph-female moults were found in the posterior airsacs and the lungs. They were more common in the posterior airsacs but not significantly ($\chi^2 = 3.1$, df = 1, $P = 0.08$). Two localities, the trachea and the anterior airsacs, accounted for 63.6% of gravid females. Otherwise, gravid females occurred in all other sites except the buccal and nasal cavities. The distribution of gravid and non-gravid females within the trachea (upper 50% versus lower 50%) was significantly different ($\chi^2 = 22.3$, df = 1, $P < 0.00001$). Gravid females were significantly more common in the lower trachea than the upper trachea. There was a significant association between site and reproductive condition of the females ($\chi^2 = 745$, df = 9, $P < 0.0001$), with significantly fewer gravid mites in the posterior airsacs ($P < 0.0001$), lungs ($P = 0.001$), mouth ($P = 0.0003$) and the nasal cavity ($P < 0.0001$) and significantly more gravid mites in the anterior airsacs ($P < 0.0001$), syrinx ($P < 0.0001$) and trachea ($P = 0.0008$). Conversely, the frequency of non-gravid mites was significantly higher in the posterior airsacs, lungs, mouth and nasal cavity and significantly lower in the anterior airsacs, syrinx and trachea. Of 376 females found in the mouth and nasal cavity none were gravid and of 457 females found in the posterior airsacs only 11 were gravid.

Figure 2.1 ***S. tracheacolum.*** **Localisation of immature stages in the respiratory and other tissues of Gouldian Finches** ***E. gouldiae.*** A, larva; B, protonymph; C, deutonymph.

A. Larva (n = 111)



B. Protonymph (n = 704)



C. Deutonymph (n = 200)

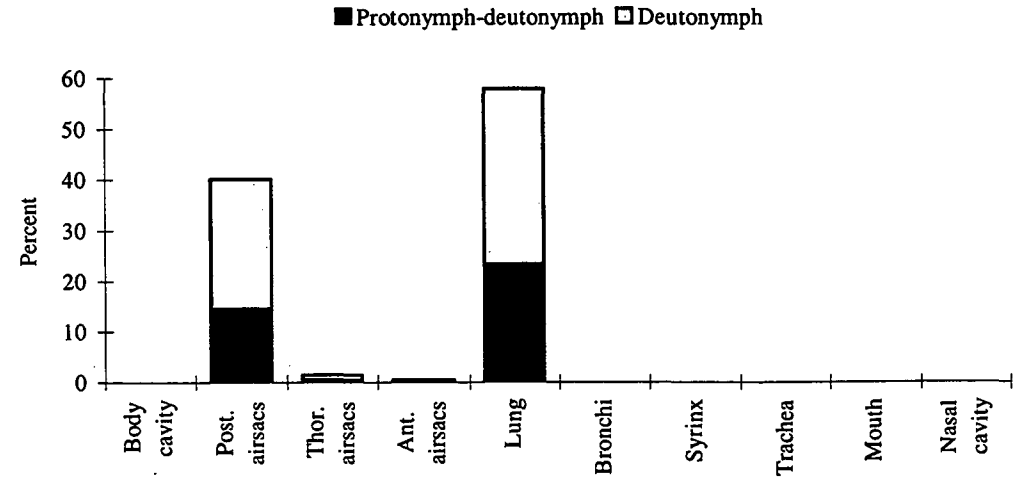
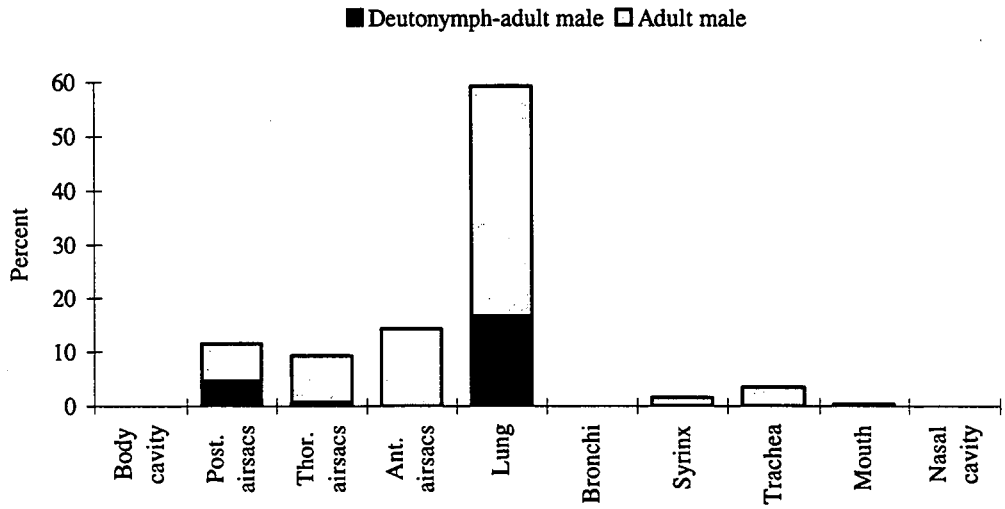
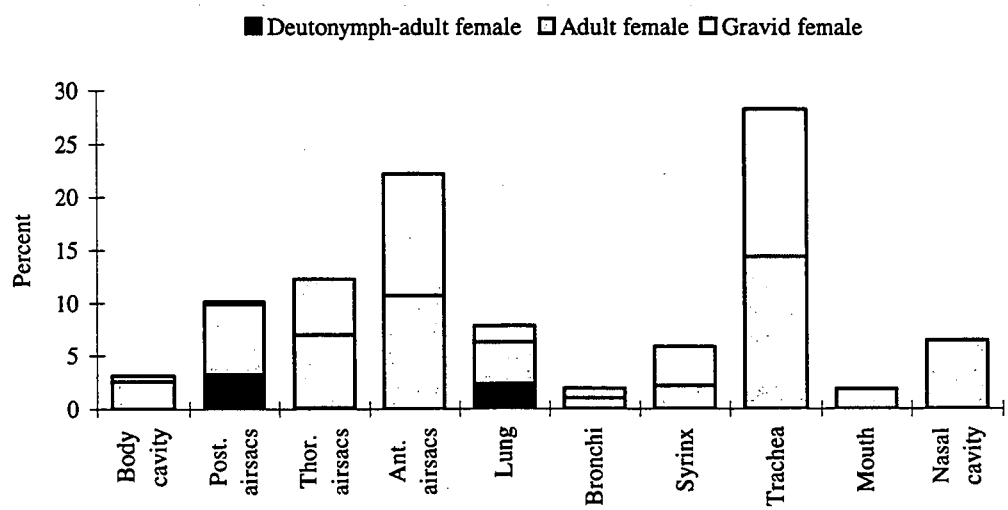


Figure 2.2 ***S. tracheacolum*****. Localisation of adult mites in the respiratory and other tissues of Gouldian Finches** ***E. gouldiae***. A, Male; B, Female.

A. Male (n = 258)



B. Female (n = 4508)



2.3.3 Males

Adult males were found throughout the respiratory system but not within the nasal or buccal cavity (Figure 2.2A). The majority (58%), were found in the lungs but they were also found in the anterior and posterior airsacs. Deutonymph-male moults were found mainly in the lungs (73%), but were also in the posterior airsacs. They were significantly more common in the lungs ($\chi^2 = 5.1$, df = 1, $P = 0.02$) than in the posterior airsacs.

2.3.4 Immatures

Mite eggs were found on only seven occasions: in the lung (n = 5), posterior airsac (n = 1) and thoracic airsac (n = 1). Larvae were found in the lungs (87%), and rarely in the posterior and anterior airsacs (Figure 2.1A). Protonymphs were found primarily in the lungs (63%), though also less commonly in the thoracic and posterior airsacs (Figure 2.1B). The larva-protonymph moults were found exclusively in the lungs.

Deutonymphs were found in the lungs and the posterior airsacs (Figure 2.1C). Protonymph-deutonymph moults were evenly spread between these sites. However, male deutonymphs were significantly more common in the lungs (90%) than elsewhere in the respiratory system ($\chi^2 = 6.6$, df = 1, $P = 0.01$) and female deutonymphs were significantly more common elsewhere (78%), than in the lungs ($\chi^2 = 4.3$, df = 1, $P = 0.04$).

2.3.5 Site and life history

Site data indicate both stage and sex specific selection for sites within the respiratory system. Adult females appear to be least selective, though based on their reproductive condition, significant site selection is evident. Aside from teneral adults, non-gravid females occur more frequently in the upper respiratory system. Within the buccal and nasal cavities females are exclusively non-gravid. Adult males select the lungs over other tissues of the respiratory system, particularly the upper respiratory system. Development of the immature stages takes place in the lungs and the posterior airsacs. Larvae develop exclusively within the lungs and probably hatch in this locality. Within the deutonymph stage there is evidence of sexual selection for development sites; females favouring the posterior airsacs and males favouring the lungs.

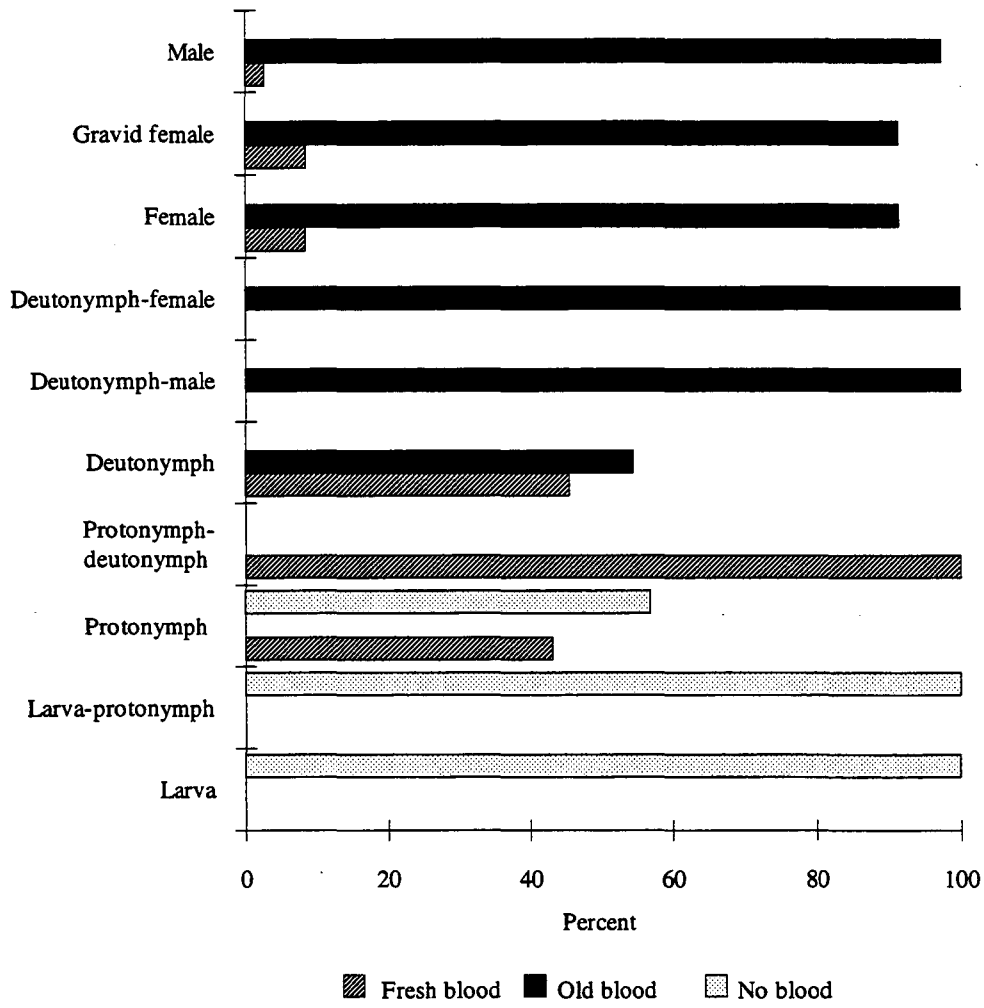
2.4 FEEDING

Percentage data for the feeding status of mites within stages are shown in Figure 2.3.

2.4.1 Larvae

All larvae and larva-protonymphs were translucent in appearance indicating that larvae do not feed on host blood prior to moulting.

Figure 2.3 ***S. tracheacolum.*** **Feeding status of live mites at time of host dissection:** male (n = 37); gravid female (n = 500); non-gravid female (n = 664); deutonymph-female (n = 63); deutonymph-male (n = 14); deutonymph (n = 11); protonymph-deutonymph (n = 23); protonymph (n =195); larva-protonymph (n = 43) and larva (n = 11).



2.4.2 Protonymphs

The protonymph does feed on host blood and was found either translucent and similar in size to the larva, or gorged and bright red in colour. The absence of protonymphs containing old blood (mites black in appearance) suggests that moulting takes place rapidly following a blood meal.

Blood fed protonymphs were significantly more common in the lungs than the posterior airsacs ($\chi^2 = 22.6$, df = 3, $P = 0.00005$) and non-fed specimens were not found outside the lungs. No other notable differences were detectable for within stage feeding status between localities.

2.4.3 Deutonymphs

Deutonymphs were found containing either fresh blood or old blood and, given the rudimentary nature of the feeding apparatus (Chapter 1: Section 1.3.5, Deutonymph), it is probable that specimens containing fresh blood represent an undigested carry-over from the protonymph blood meal.

2.4.4 Adults

There was no evidence of blood feeding in either the male or female deutonymph-adult moult. The majority of adult mites contained old blood and only a small percentage (male = 2.7%, n = 37; female = 8.6%, n =1164) contained fresh blood. There was no significant difference in the feeding status between male and female mites. However, adult females often contained small amounts of fresh blood, in addition to old blood, which suggests they may be feeding often on small amounts of blood, rather than taking large blood meals followed by long non-feeding periods. The feeding status of gravid and non-gravid mites was identical.

2.5 MORTALITY

Mite infrapopulations often contained dead mites that were not voided from the respiratory system by mechanical means such as mucous production and coughing. These comprised everything from recently dead but intact mites to disintegrated mite fragments of indiscernible stage and sex. Most dead mites were found free though others were bound in a tenacious mucous (particularly those in the upper respiratory system) or surrounded by host histolytic tissue (particularly those in the lung and posterior airsacs).

2.5.1 Distribution of dead mites within the host's respiratory system

Dead mites were found in all sites, but in comparison with the distribution of live mites, significantly lower than expected frequencies were found in the anterior air sacs ($\chi^2 = 38.7$, df = 11, $P = 0.00006$), nasal cavity ($\chi^2 = 27.5$, df = 11, $P = 0.004$) and both the upper ($\chi^2 = 22.6$, df = 3, $P = 0.0005$) and lower trachea ($\chi^2 = 56.4$, df = 11, $P < 0.00001$). Higher than expected

frequencies of dead mites were found in the lung (χ^2 = 128.7, df = 11, $P < 0.00001$) and posterior airsacs (χ^2 = 105.7, df = 11, $P < 0.0001$).

2.5.2 Stage specific mortality

Mortality was obvious in all stages. Most notable was the high percentage of male mites found dead (29.5%, n =261), over twice the percentage observed for other life stages and significantly higher than that observed for females (8.69%, n = 4810; χ^2 = 104.19, df = 1, $P < 0.0001$). The percentage of immatures found dead was 8.8%, 12.3% and 11.9% for the stages larva (n = 114), protonymph (n = 741) and deutonymph (n = 210) respectively. Figure 2.4 shows the 'type' component of mites found dead. A high percentage of mites died during moult. The proportion of deutonymph-adult female moults found dead was significantly higher than the proportion of adult females found dead (χ^2 = 142.0, df = 4, $P < 0.0001$) and a significantly smaller proportion of gravid female mites were found dead than non-gravid females (χ^2 = 65.0, df = 3, $P < 0.0001$).

2.6 DURATION OF THE LIFE CYCLE

2.6.1 *In vitro* rearing

Table 2.1 shows observation records for successful maintenance of adult female mites and the partial rearing of immature mites on the chorioallantoic membrane (CAM) of the domestic chick embryo. Many attempts failed due to death of the chick embryo following the mite introduction procedure. However, a sufficient number of egg series did survive to gauge the suitability of the CAM for further investigation as a vessel for maintaining and rearing rhinonyssid mites.

Egg laying on the CAM of the chick embryo indicates that at least *in vitro*, *S. tracheacolum* is ovoviviparous. The maximum period for maintenance of the adult female was 9 days 21 hours. Adult females tended to survive on the CAM while the chick embryo remained alive, consequently dead mites were recovered from dead chick embryos. There was evidence of adult mite faeces on the CAM, and the presence of blood like material seen through the translucent idiosoma suggests that mites were able to feed on the vascular membrane. A small patch of free blood was observed on the second CAM used for maintaining adult female F15 (see Table 2.1).

The minimum time recorded between egg laying and subsequent hatching of a larva was 39 hours 30 minutes (F18). This represents the period of time between the last observation of an ovigerous female and the first observation of a free larval stage associated with the same adult female mite. The minimum time observed for development from unhatched egg to protonymph was 4 days 21 hours for the egg from female F16. Of two larvae that moulted to protonymph both failed to feed on the CAM and one was dead at the time of examination.

Figure 2.4 ***S. tracheacolum*****. Percentage of mites found dead of each life cycle stage within the respiratory and other tissues of the Gouldian Finch** ***E. gouldiae*****:** larva (n = 163); larva-protonymph (n = 144); protonymph (n = 590); protonymph-deutonymph (n = 82); deutonymph (n = 132); deutonymph-male (n = 54); deutonymph-female (n = 260); non-gravid female (n = 2657); gravid female (n = 1693) and male (n = 204).

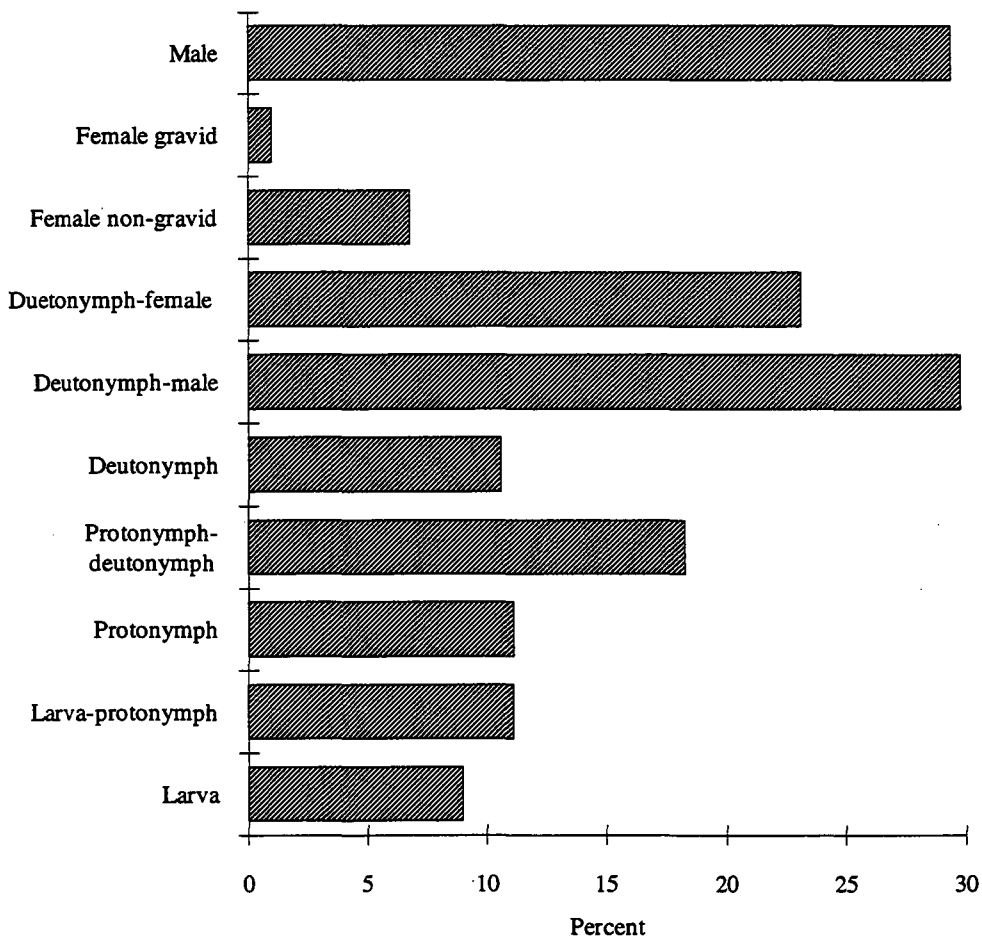


Table 2.1 Observation records for successful maintenance of adult female mites and the partial rearing of immature mites on the chorioallantoic membrane (CAM) of the domestic chick embryo.

DAY 1	DAY 3	DAY 5	DAY 8	DAY 10
1700 hrs 1 gravid female F1 (from trachea of a Canary)	1725 hrs 1 female (live) 1 larva (live)			
1800 hrs 1 gravid female F2 (from trachea of a Canary)	1800 hrs 1 female (live) 1 egg (movement of enclosed larva)			
1700 hrs 1 gravid female F15 (from trachea of a Canary)	1100 hrs 1 gravid female	1400 hrs 1 female 1 egg (movement of enclosed larva)		1400 hrs 1 female (live) 1 protonymph (live)
1700 hrs 1 gravid female F16 (from trachea of a Canary)	1500 hrs 1 gravid female	1600 hrs 1 female 1 egg (containing developed larva)		1400 hrs 1 female (live) 1 protonymph (dead)
1700 hrs 1 gravid female F14 (from syrinx of a Canary)	1300 hrs 1 gravid female	1400 hrs 1 female 1 larva (dead)		1100 hrs 1 female (live)
800 hrs 1 gravid female (from anterior airsac of a Canary)	1000 hrs 1 female 1 egg		1000 hrs 1 female (live) 1 larva (dead)	
1800 hrs 1 gravid female F18 (from anterior airsac of a Canary)	0930 hrs 1 female 1 larva		1500 hrs 1 female Immature not recovered	

2.6.2 Other indicators of the duration of the life cycle duration

Eggs of 159 ivermectin killed gravid female mites were observed to have continued development within the mother's carcass (Chapter 9: section 9.3.2, An abnormal development site for *S. tracheacolum* following ivermectin treatment of the host). One hundred and fifty hatched mites had reached protonymph stage, 6 had reached deutonymph and 3 had reached adult male stage. Table 2.2 shows the stage reached by each developing mite and the maximum time period elapsed for development to have taken place. An adult male was observed in the carcass of its dead mother 6 days following ivermectin treatment of the host. However, no hosts were examined earlier than this date after treatment. Figure 2.5 shows typical orientation of adult and immature mites within the carcass of dead female mites.

Table 2.2 The occurrence of immature and adult male *S. tracheacolum* within the carcass of ivermectin killed gravid female *S. tracheacolum* following oral treatment of host Gouldian Finches with ivermectin.

Host sex, maturity/ ivermectin dosage	Stage of mite/ Number found in host within adult females				Time elapsed between drug administration and dissection of the host (days)
	L	P	D	M	
Female, adult / 2.46 µl/g bw	9	32	3	1	6
Female, juvenile / 3.15 µl/g bw	3	12	0	0	10
Male, juvenile / 2.17 µl/g bw	0	2	0	0	7
Male, juvenile / 2.71 µl/g bw	3	4	0	0	11
Male, adult / 2.85 µl/g bw	1	12	0	1	14
Female, adult / 2.8 µl/g bw	0	4	0	0	8
Male, adult / 2.0 µl/g bw	0	8	0	0	8
Male, adult / 2.0 µl/g bw	3	36	1	1	9
Male, adult / 2.0 µl/g bw	1	5	1	0	10
Male, adult / 2.0 µl/g bw	1	2	0	0	10
Female, adult / 3.5 µl/g bw	1	28	1	0	14
Female, adult / 3.5 µl/g bw	0	3	0	0	12
Male, adult / 1.12 µl/g bw	0	2	0	0	7

(L = larva; P = protonymph; D = deutonymph; M = adult male; The frequency of larval stages are those following hatching)

2.7 TRANSMISSION

2.7.1 Stage responsible for transmission

All data and observations indicate that the life stage responsible for transmission is the adult non-gorged, non-gravid female. All mites found within the nasal and buccal cavities were adult non-gorged, non-gravid females. This stage was significantly more common in the upper respiratory system than elsewhere within the body of the host and all mites found on the external surface of the host and subsequently examined (n = 26) were adult non-gorged, non-gravid females.

2.7.2 The infective stage on the external surface of the host

Adult non-gorged, non-gravid females (infective stage) were regularly observed on the external nares, the mandibles and the head plumage of infected birds. All mites were observed to carry the first pair of legs in the air and wave them vigorously. Of 46 mites observed on the external surface of hosts, 21 were on the lip of the host's external naris, 10 on plumage between the eye and the naris, 9 on the upper mandible and 6 within the external naris on soft tissue. The following accounts represent specific observations.

- A mite removed from the outer naris region of an infected female Gouldian Finch was placed on the mid upper mandible region of another infected female Gouldian Finch. The mite moved actively on the bill and entered the right naris 8 minutes later. It did not exit the naris during continuous observations over the following 5 minutes before the bird was returned to the aviary.

- A mite was observed moving back and forth between the plumage of the forehead and the upper mandible of a male Gouldian Finch. Throughout the observation the first pair of legs was waved vigorously in the air as in questing behaviour (See Plate 2.1C). Fifteen minutes later the mite re-entered the naris and came out again one minute later. The mite took up a position on the lip of the naris with the first pair of legs pointing outwards. Questing behaviour continued for a further 21 minutes before the bird was returned to the aviary.

- A mite was observed on the anterior lip of the right naris of an adult female bird (See Plate 2.1A). Twenty minutes later the mite was observed on the upper mandible moving anteriorly. The bird was re-examined every half hour for a further 3 ½ hours but no mites were observed.

- Two mites were observed on the anterior lip of the right naris of an adult male Gouldian Finch. The bird was removed from the aviary in order to photograph the mites. Aside from a short foray onto the head plumage immediately behind the naris (see Plate 2.1B) both mites maintained a position on the lip of the naris during a half hour observation period.

Mites were observed on the external surface of Gouldian Finches in all months of the year and between 0800 and 1800 hours when observations were made. They were observed on both male and female birds in both breeding and non breeding condition. However, the presence of mites on the external surface of the host was related to the size and duration of the infection (Chapter 3: Section 3.3.3, Transmission of *S. tracheacolum*) and can confirm diagnosis of *S. tracheacolum* infection in Gouldian Finches without the necessity for sacrifice and autopsy of the host (Chapter 6: Behaviour/ Clinical Signs).

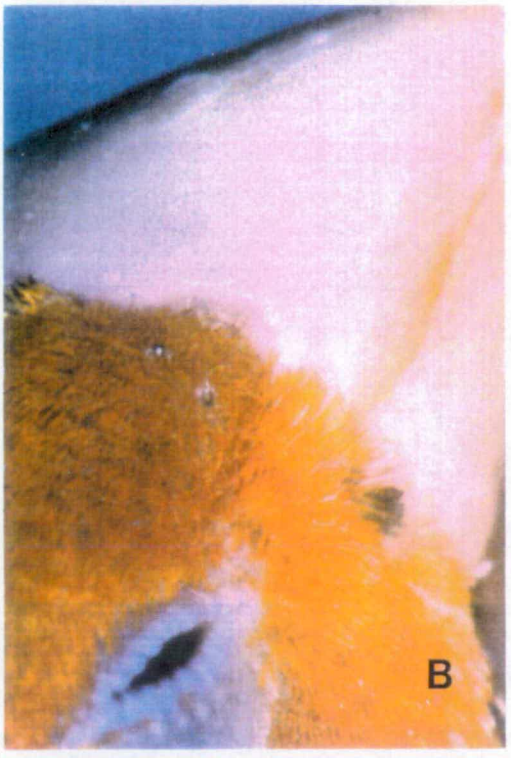
Plate 2.1 *S. tracheacolum.* On the external body of the Gouldian Finch *Erythrura gouldiae.*

A. A female mite *S. tracheacolum* in the naris of an orange headed female Gouldian Finch.

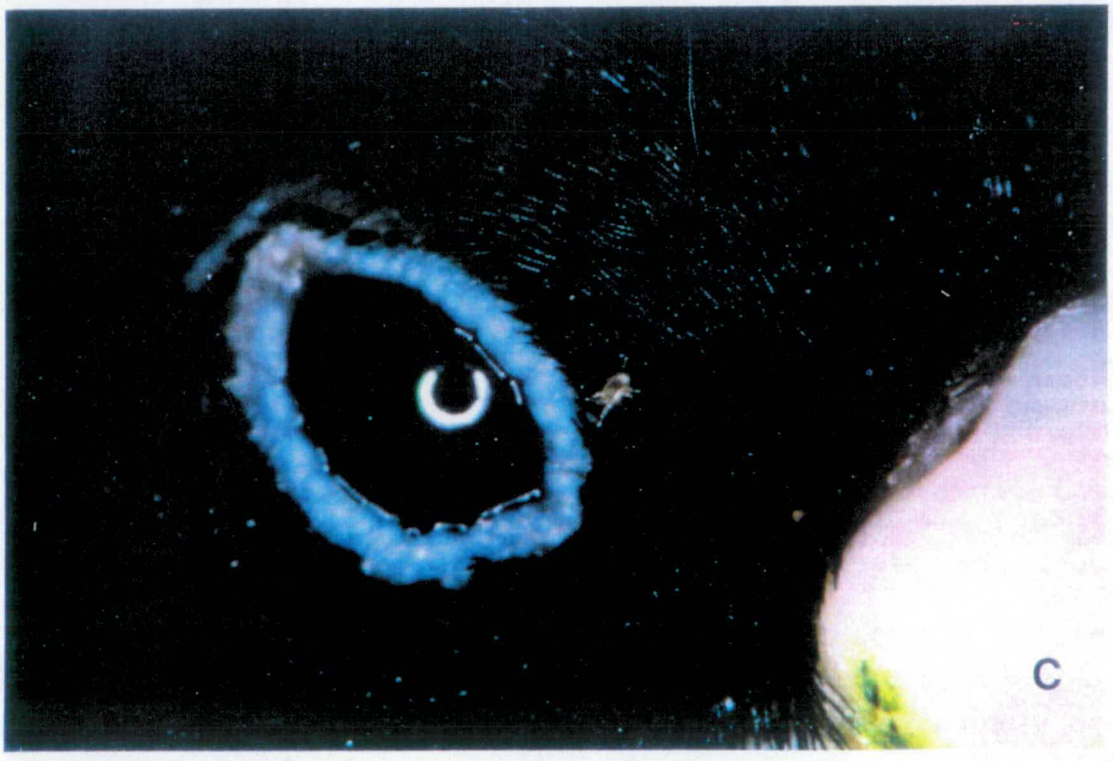
B. Female mites *S. tracheacolum* on the forehead plumage of an orange headed male Gouldian Finch.

C. A female mite *S. tracheacolum* on the head plumage of a black headed male Gouldian Finch.

A



B



C

2.7.3 The infective stage on the surface of aviary drinking water

Non-gorged, non-gravid mites were found in the drinking water provided for infected captive Gouldian Finches. They were usually found floating on the surface on the water. The majority were alive and active at the time of examination though some were found dead. Dead mites were intact and not discoloured so were assumed to have died at a time after leaving the host. Quantitative data on mites in drinking water is dealt with in Chapter 3 Section 3.3.3.1, Transmission of *S. tracheacolum* and the duration of infection.

2.7.4 Longevity of survival of the infective stage outside the host

Opportunities to observe mites outside hosts were available on many occasions. However, planned experiments were not practicable because collection was based on chance and the number of available mites could not be predicted. The following are specific accounts of observations made on mites removed from the body of the host.

- Five non-gorged, non-gravid female mites from the syrinx and trachea of a freshly dissected Gouldian Finch were placed in a tissue culture dish with moist cotton wool and held in an incubator at 37° C and a humidity of 60%. Seventeen and a half hours later they were re-examined and all found to be dead. Two mites had walked up the side of the dish and towards the centre of the underside of the lid where they remained adhered.

- Five non-gorged, non-gravid female mites from the syrinx and trachea of a freshly dissected Gouldian Finch were floated on tap water in a tissue culture dish and held in an incubator at 37° C and 60% humidity. When re-examined 20 hours and 45 minutes later they were all dead.

- Five non-gorged, non-gravid female mites from the nasal cavity of a freshly dissected Gouldian Finch were placed on damp filter paper in a tissue culture dish and held in an incubator at 37° C and 60% humidity. They were all dead when re-examined 20 hours and 45 minutes later.

- Five non-gorged, non-gravid female mites from the nares of a female Gouldian Finch were floated on the surface of tap water in a tissue culture dish and held at room temperature. They were still alive when re-examined 8 hours later.

Table 2.3 Observations on the duration of survival of female non-gorged, non-gravid mites *S. tracheacolum* removed from the external nares, plumage and mandibles of Gouldian Finches and held in a dry tissue culture dish at 25 C.

Time of mite collection from host	Total period mite known to be alive (Hours/ Minutes)
0922	6/28
0923	6/27
0940	5/35
0940	5/35
0945	8/45
0958	9/32
1118	8/47
1120	24/40

Table 2.4 Observations on the activity and duration of survival of an adult non-gorged, non-gravid female mite *S. tracheacolum* removed from the external nares of a Gouldian Finch *E. gouldiae* and maintained in a dry tissue culture dish at a temperature of 25 C.

Time (Hours/Minutes)	Observation
0	removed from the external naris of a Gouldian Finch
0/5	active, on base of dish
0/15	active, on wall of dish
0/20	active, climbing vertical wall dish
0/35	active, on wall of dish
0/50	active, on wall of dish
1/20	active, on underside of dish lid
1/40	active, on underside of dish lid (replaced on base of dish)
1/55	active, on underside of dish lid
2/25	active, on underside of dish lid
3/0	active, attempting to move under lid to outer wall of dish
3/15	active, on underside of dish lid
3/30	active, on underside of dish lid (replaced on base of dish)
4/0	stationary/ moving front legs/ active after dish was jolted
4/15	stationary/ moving front legs/ moving after dish was jolted
4/35	moving slowly
5/05	stationary/ slowly moving all legs
5/20	moving/ rear legs slowly
5/45	stationary/ slight movement in all legs
5/55	stationary/ slight movement of some legs
6/20	stationary/ slight leg movement
6/35	no movement/ no response to jolting/ presumed dead

- Five non-gorged, non-gravid female mites collected over a 10 minute period from the head plumage and mandibles of infected Gouldian Finches were floated on the surface of tap water in a tissue culture dish at 25° C. Two died after 5 hours. The third died after 8 hours, the fourth after 23 hours and the last mite died after 25 hours.

- Over a period of 4 days several non-gorged, non-gravid female mites were collected from the external surface of infected Gouldian Finches and held individually in dry tissue culture dishes at 25° C. The total period for which each of these mites was known to be alive is shown in Table 2.3. The observations recorded for a specific mite are presented in Table 2.4.

- A live non-gorged, non-gravid mite collected from a water bowl provided for an enclosure of infected Gouldian Finches survived for 4 ½ hours floating on the surface of tap water at room temperature.

- Two non-gorged, non-gravid mites from the nasal cavity of a female Gouldian Finch were placed on a piece of filter paper one hour after the death of the host. If turned on their backs they would immediately right themselves. The mites always walked towards a light source (or towards the heat of the light source) aimed horizontally across the filter paper. If presented with a piece of cotton the mites would grasp it.

- Ten non-gorged, non-gravid mites removed from the nasal cavity of a dissected Gouldian Finch were divided into two equal groups. One group was placed on the surface of tap water and the other group was placed on dry filter paper. Both were held in tissue culture dishes at 20° C. Mites on filter paper were all dead within 3 ½ hours. Of the mites on the water surface, 2 died within 22 hours, 1 within 23 hours and the last 2 died some time between 50 and 69 hours following removal from the host's nasal cavity.

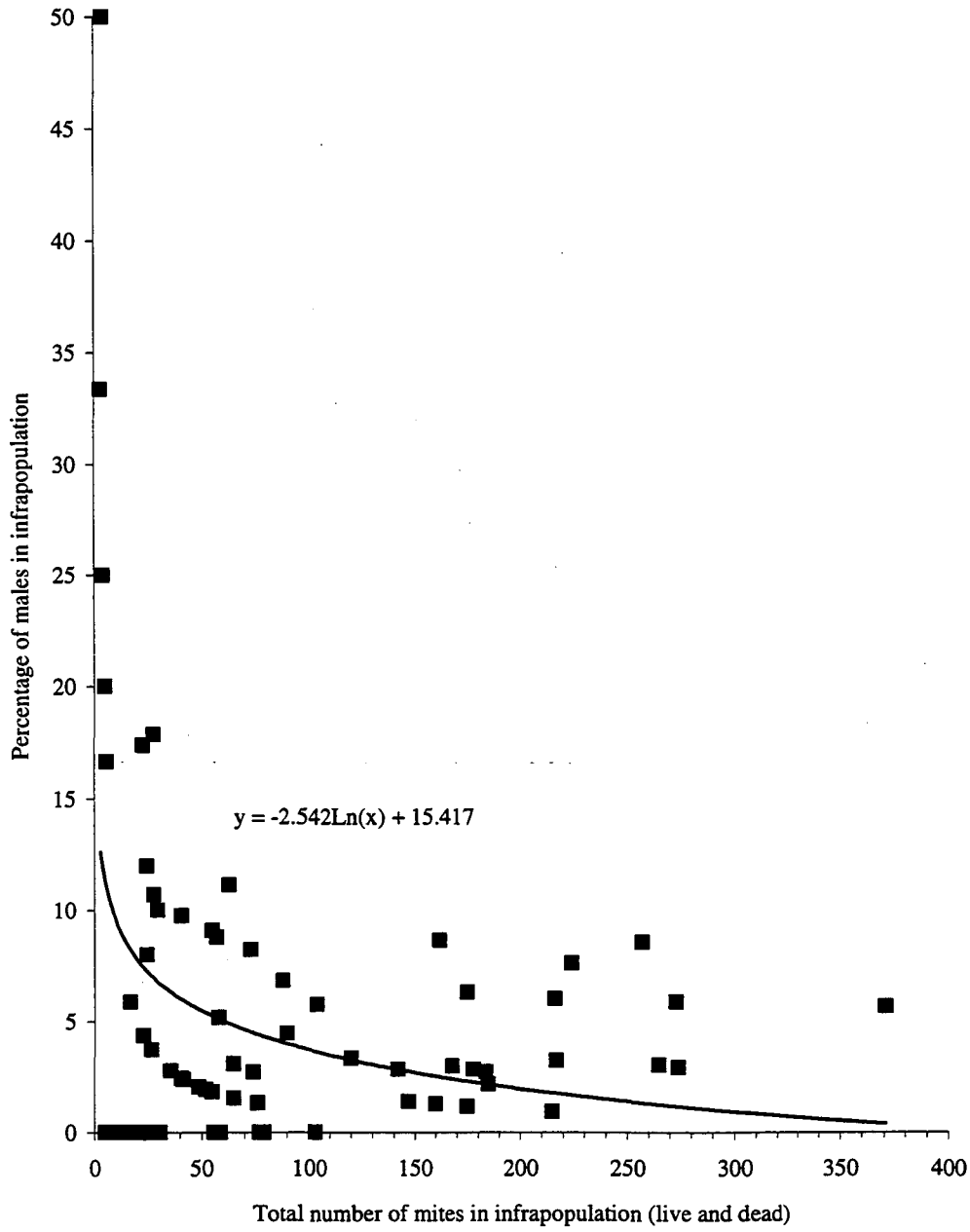
2.7.5 Transmission in the nest

Gouldian Finch nestlings from infected parents, examined prior to fledging, were often found to be infected with mites. On all occasions (n = 20) the mites were adult females. However, examination of the external bodies of nestlings did not reveal mites. The occurrence of mites in nestling birds is further dealt with in Chapter 3: Section 3.3.2, Infrapopulation growth of *S. tracheacolum* and Section 3.3.3 Transmission of *S. tracheacolum.*

2.8 PARTHENOGENESIS

The number of male mites found in infections was always small and males were completely absent from 24 infrapopulations comprising more than 2 mites (Hosts = 75; Infrapopulation Range = 3-103 mites). The mean ratio of adult male to adult female mites was 1:18 with a range from 0:85 for

Figure 2.6 The presence of male mites in *S.tracheacolum* infections of the Gouldian Finch *E. gouldiae*: Percentage of male mites in the total infrapopulation (Infrapopulations of total size less than 3 mites are excluded).



an infrapopulation of 103 mites to 1:1 for an infrapopulation of 3 mites. The mean percentage of male mites (live and dead) from entire infrapopulations was 5.27% (R = 0-50) for 75 infections with a mean size of 81.73 mites (Infrapopulation Range = 1-371). With increase in the size of the infection there appears to be a corresponding decrease in the percentage of males present in the infrapopulation (Figure 2.6). Very small infrapopulations may contain a large proportion of adult male to adult female mites.

Following ivermectin treatment of *S. tracheacolum* infected Gouldian Finches there is a change in the proportion of males in the infrapopulation (Chapter 9: Section 9.3.3, Impact of ivermectin on infrapopulation structure and location). Adult male mites were significantly more common in pooled stage frequency data for 24 infections examined following oral ivermectin treatment of the hosts (n = 1237, males = 107) than males from similarly pooled data from 84 normal infections (n = 6143, males = 261; $\chi^2 = 33.29$, df = 5, $P < 0.0001$). Of 3 ivermectin killed female mites, where development of eggs continued to adult stage within the mother's carcase, all enclosed adults were males. Following the kill of 93.3% of an infrapopulation of 263 mites, 56 male mites were found representing an adult male to adult female ratio of 1:3.

2.9 DISCUSSION

2.9.1 Transmission of *S. tracheacolum*

From the results of this study it is evident that the adult non-gravid, non-gorged female is the mite life stage responsible for transmission. Increased proportions of non-gorged, non-gravid females in the upper respiratory system, combined with the absolute monopoly of this stage in the nasal and buccal cavity, most likely reflect a movement of the infective stage to the exterior surfaces of the host. Certainly, no other life stage was found outside the host and artificial infection experiments indicate that non-gravid, non-gorged females from the nares of the host are capable of surviving and founding a new infection in a naive host (The Experimental Design: 6. Experimental infection procedure, P. 66).

Observations on the longevity of non-gravid, non-gorged females (from the nares and the external surfaces of the host) indicate their suitability for prolonged exposure to ambient conditions; an attribute not particularly obvious in other life stages. The larva, protonymph, deutonymph, adult male and the gorged (gravid or non-gravid) female can survive for a few hours in water (indication from general observations during many dissections) but rapidly desiccate in the absence of moisture. In contrast, adult non-gravid, non-gorged females show an ability to survive for periods in excess of 2 days in moist conditions and for over 24 hours in dry conditions following their removal from the host. Non-gravid, non-gorged females from the nares undertake forays onto the bill and head plumage of the host and are able to return to the nares. Observations indicate their potential to

remain on the bill and the plumage for many hours before retreating to the humid safety of the nasal cavity.

The behaviour of the non-gravid, non-gorged female also lends support to the hypothesis that it is the stage responsible for transmission. It is both the most agile and the most active of all mite stages. On the external surface of the host it demonstrates questing behaviour. Adult gorged females are active in the moist conditions of the host respiratory system though are sluggish on dry substrates. Relative to the non-gorged female, their bodies are huge and rotund, probably causing a serious hindrance to mobility on dry substrates.

The freeing of the infective stage of *S. tracheacolum* from dependence on a high humidity level and/ or moist surfaces, combined with an aptitude for exploratory behaviour and an ability to survive for extended periods outside the host allows further modes of transmission to be considered. It appears that *S. tracheacolum* is not a passive participant in the process of transmission but has the potential to actively seek a new host. It seems unlikely that regurgitated food is a common vehicle for transmission between parent birds and feeding offspring. The mechanical action of this activity alone may be sufficient to destroy a delicate mite such *S. tracheacolum*. A mite surviving transferral to the crop of a nestling bird must then survive further mechanical and biochemical dangers during migration to the trachea. The most probable modes of transfer are (i) direct transfer from the nasal cavity of an infected bird to the nasal cavity of a recipient bird via the external naris of each bird, and (ii) indirect transfer from the nasal cavity of an infected bird to the nasal cavity of a recipient bird via the external naris, but including a period on water, perches or nest material. Direct transmission would be effected by direct contact between birds in close proximity, such as paired birds and parent birds and nestlings. Indirect transmission provides a pathway between unrelated birds within a species and also between species.

The probability of transmission in the nest, between paired birds, and between parent birds and their nestling offspring is obviously high. This is well illustrated by the high prevalence of infection in newly fledged Gouldian Finches (Chapter 3: Section 3.3.3, Transmission of *S. tracheacolum*; Murray, 1966). Direct transmission at other times and in different localities would depend on the behaviour of the host species being considered (e.g. level of gregariousness).

In contrast, the probability of indirect transmission via a common drinking site must be considered very low, though nonetheless, provides an obvious link between susceptible species. A combination of the prevailing environmental conditions and the drinking behaviour of susceptible host species will determine the potential and probability for indirect transmission. At Gouldian Finch breeding sites in northern Australia drinking sites are usually limited during the late dry season (April to October) (Woinarski & Tidemann, 1992). Often they are shallow with a small surface area (e.g.

natural springs, water holes and pastoral bore sites). Gouldian Finches, and other finches including Pictorella Mannikins and Masked Finches visit these sites in large numbers in the early mornings during the dry season (Evans, Neems and Pagendam, 1989). The limitation on water sites combined with the strong flocking behaviour of these host species at drinking sites is likely to enhance indirect *S. tracheacolum* transmission.

In captive environments, increased host densities increase the potential for transmission outside the nest site. Observational data suggest that Gouldian Finches often roost in small groups and often in direct contact with each other. The availability of perches and roosting sites and the surface area of drinking sites are considerably reduced in comparison to natural situations. For captive populations, the probability for indirect transmission between unrelated birds and between susceptible species would be enhanced. Most accounts of *S. tracheacolum* infections in aviary and other captive situations suggest a rapid spread.

Although the adult female is responsible for transmission in *S. tracheacolum* it may not necessarily be the transmissible stage in other species of the Rhinonyssidae or even other species of *Sternostoma*. *S. tracheacolum* inhabits the lower respiratory system and is bound to the lungs for reproduction and feeding. All other rhinonyssids occur in the nasal cavities of their hosts. The only other species of *Sternostoma* that has been examined by the author is *Sternostoma paddae* Fain 1956 (Chapter 7: Section 7.3, Australian wild hosts) which infects wild Gouldian Finches, Long-tailed Finches and Masked Finches. Two of 3 infections (1 Long-tailed Finch, 1 Masked Finch and 1 Gouldian Finch) comprised single deutonymphs. So, although the mode of transmission in *S. paddae* may be similar to that of *S. tracheacolum*, the deutonymph stage or an earlier stage is the most likely candidate for transmission. Unfortunately, the extremely low prevalence and intensity of *S. paddae* infection in wild Australian hosts would make a serious investigation of life history and transmission difficult.

2.9.2 Male *S. tracheacolum* and parthenogenesis

The small percentage of male *S. tracheacolum* in very large infections and the high proportion of males to females found in small infections provides a strong argument for both parthenogenesis and a haploid-diploid arrangement for sex determination. If we assume that the infective stage (i.e. non-gravid, non-gorged female mites found in the upper respiratory system) are virgins, then an arrhenotokous system would dictate the sex of first progeny (from a successfully transferred mite to an infection-free host) to be male. The sex of subsequent progeny from the mating of diploid females and haploid males would be female. Arrhenotoky could account for the higher proportion of males found in very small infections and the rapid decrease in the proportion of males with increase in the size of infection.

The data are not conclusive because small infections are often completely devoid of male mites. However, more than one infective stage may be responsible for the founding of a new infection. This is especially pertinent to birds infected in the nest and or birds that nest or roost colonially; those infected at drinking sites are more likely to be founded by a single female mite. If several mites are responsible for founding an infection we may find that examination of the host prior to mite reproduction would yield an all-female infrapopulation whereas examination following reproduction would yield an infrapopulation containing a large proportion of male mites. In subsequent generations the proportion of males would fall dramatically. Unmated females within the respiratory system may be responsible for the continued production of males with the small but highly variable sex ratio being influenced by chance fluctuation in numbers of unmated females that do not leave the host.

Increased production of male mites from eggs of ivermectin-killed hosts also provides circumstantial evidence for arrhenotoky. The high proportion of male mites found dead in the respiratory system of treated hosts may indicate that adult males may be short lived in comparison to females and have a high turnover rate. If males are killed rapidly following ivermectin treatment of the host then surviving unmated females may produce eggs that develop to male mites and similarly, ivermectin-killed, unmated ovigerous females may also produce male mites within their carcases. The evidence is inconclusive and further study would be necessary to confirm an arrhenotokous system.

2.9.3 The chorio-allantoic membrane of the domestic chick as a site for the rearing of endoparasitic mites

The chorio-allantoic membrane of the domestic chick may have application for further studies of the life cycle, reproductive rate and the mechanism for sex determination of *S. tracheacolum*. Potentially, the technique may also be useful in the study of other avian endoparasitic mites. Experimental evidence suggests that *S. tracheacolum* protonymphs may not be capable of feeding on the CAM. However, there is no reason to suggest that they would not survive and develop on the CAM following a blood meal. Blood gorged specimens obtained fresh from the posterior airsacs of a host could be placed on a prepared CAM and examined daily to determine the duration of development from the protonymph to the adult male or female. The adult female appears capable of feeding on the CAM and could conceivably be maintained indefinitely in this situation. Examination at weekly intervals, when mites were removed to a new CAM, would provide an opportunity to assess the reproductive rate of virgin females and the sex of their progeny. Comparisons could be made on the sex of eggs from virgin females raised from the protonymph stage on the CAM, those from non-gorged, non-gravid females from the nares (i.e. infective stage) and those from females from the lower respiratory system that may or may not have mated. The rarity of males in most infections limits their potential to opportunistic use in rearing experiments.

Another technique that may prove to be a useful tool in the study of life cycle duration is ivermectin drug treatment of the host (i.e. continued development of the egg within the carcase of ivermectin killed females). There is considerable scope for varying the quantity of drug administered and proportion of mites killed. Furthermore, alternatives to oral administration (e.g. intramuscular injection) may increase the speed at which the drug is absorbed into the blood stream and hence improve the accuracy of determining time to stage duration.

2.9.4 Larvipary or ovovivipary in *S. tracheacolum*?

Parasitic mites are usually larviparous (Krantz, 1978) and for the most part *S. tracheacolum* has been assumed to be larviparous. Observations on developed larva within the egg of gravid females, combined with a high frequency of larvae found free, and the lack of eggs reported in host tissues (e.g. Stephan *et al.*, 1950; Medda, 1958; Vaccari & Ballarini, 1963) suggests larviparity.

Some authors (e.g. Guevara-Benitez & Ubeda-Ontiveros, 1974; Szeleszczuk & Kruszewicz, 1987) have found eggs free in host tissues. Guewara-Benitez and Ubeda-Ontiveros (1974) found several free larvae in infected Canaries but found only one larva enclosed in a free egg. Because the host was a drug treated bird they considered the case anomalous. Szeleszczuk and Kruszewicz (1987) also observed eggs in the respiratory system of infected Gouldian Finches and Canaries in Poland.

Observational data from CAM rearing experiments in the present study suggest that in all cases *S. tracheacolum* lays eggs, that the eggs contain well developed larvae and they hatch rapidly following oviposition. All data indicate *S. tracheacolum* to be ovoviviparous and not larviparous. The rapidity of hatching following oviposition explains the rarity of eggs found in dissected hosts such as 7 from 84 infected Gouldian Finches in the present study, 1 from 14 infected Canaries in Spain (Guewara-Benitez & Ubeda-Ontiveros, 1974) and none from 78 infected Canaries, 1 European Siskin *Carduelis spinus* (L.) and 1 Gouldian Finch in Italy (Vaccari & Ballarini, 1963).

2.9.5 Site specific development of *S. tracheacolum* life stages in the respiratory system of the host

The importance of the lung as a site for oviposition and early development of immatures may be paramount. Parasitic mites that lay eggs usually select a specific host tissue for oviposition (Krantz, 1978). Although little information is available on oviposition and development of endoparasitic mites, at least for *S. tracheacolum*, site selection for egg laying is apparent. *S. tracheacolum* eggs were found primarily in the lung (though on two occasions eggs were found in airsacs). Observational data suggest that eggs are laid in the lung exclusively and it is unlikely that eggs laid elsewhere in the respiratory system would survive beyond the protonymph stage. Protonymphs have small feeding apparatus and show little mobility. The surface tissues of the trachea, syrinx, primary

bronchus and the airsacs may not provide a membrane with sufficient superficial vascularisation for blood feeding by the protonymph. The occurrence of eggs in the airsacs is therefore considered to be aberrant, and probably due either to the rupture of a gravid female idiosoma during host dissection (leaving the egg to be found free) or an anomalous oviposition during changes in the environmental conditions following host death.

High proportions of non-gravid, non-gorged females in the posterior airsacs probably reflect the completion of development in this site. Whether these 'teneral adults' become gravid and remain within the lower respiratory system of the host or move to the upper respiratory system and become infective is not known, though density-dependent factors are most likely involved. Non-gravid, non-gorged females are found in the nares of juvenile, immature and adult Gouldian Finches and at all times of the year though they are not generally found in the nares of hosts carrying small infrapopulations.

Both gravid and non-gravid females tend not to be found in the lungs but are prevalent in the airsacs and the trachea. The tendency for female mites to be found in the airsacs rather than the lungs may be a function of the inability of the host to produce an effective immune response in this site. The airsacs are essentially large membranous bags that are poorly vascularised and lack a mucosal lining. Conversely, the lungs are highly vascularised, highly reticulated organs that contain small lumina where mucosa can operate effectively to remove foreign material. Large gravid females probably only visit the lungs to oviposit or take a blood meal.

By laying the egg in the lung *S. tracheacolum* mites ensure that the protonymph has ready access to a food source. The claws of the larval stage can be used to maintain position within the confined spaces of the air passages. Following blood engorgement female protonymphs then move into the posterior airsacs to complete development in what could be described as an immunologically privileged site.

The smaller male protonymphs tend to remain within the lung to complete development and probably only range beyond the lungs in search of females. Life in the lungs may be substantially less perilous for adult males, which are very small and have a reduced external armature. Similar comments could apply to the larva and the unfed protonymph.

2.9.6 The rate of development from egg to adult in *S. tracheacolum*

The data from CAM rearing and ivermectin dosing experiments indicate that the life cycle of *S. tracheacolum* is completed rapidly. Development from egg to adult probably occurs in less than 6 days. Rapid hatching of the larva ensures only a limited amount of time is available for the host to void the egg from the respiratory system. The presence of fresh blood in the caeca of deutonymphs

also suggests a rapid moult period following the protonymph blood meal. Rapid development from egg to adult is also a feature of other endoparasitic mites. For example the development of *P. simicola* (from the lungs of the rhesus monkey) from larva to adult can take place within 5 days (Furman *et al.*, 1974) and *O. diminuata* (from the nares of the Californian sea lion) can develop from larva to adult within 11-12 days (Furman & Smith, 1973).

2.9.7 Stage and sex specific mortality rates in *S. tracheacolum*

Results from the examination of mites found dead in the host's respiratory system indicate that the death rate of mites, either natural or host-induced, is probably highest during moulting, particularly during the protonymph-deutonymph and the deutonymph-adult moult periods. It is not understood why such a high proportion of male mites were found dead in infections, however, it may reflect a high turnover with a sex differential in susceptibility to the host immune responses.

2.9.8 Blood feeding by *S. tracheacolum*

S. tracheacolum is clearly a typical gamasid in terms of blood feeding. The protonymph and the adult are both feeding stages and have chelicerae equipped for that task. The larva and the deutonymph have rudimentary feeding apparatus and both are short lived and non-feeding. The feeding pattern of the adult female is more difficult to interpret. Given that they often contained old black blood with small amounts of fresh blood in the anterior caeca it is probable they take many small blood meals throughout their lives in preference to a reduced number of large blood meals. The former behaviour would have an advantage in the avoidance host immune responses, whether internally activated following a blood meal or through the production of tenacious mucous on the feeding substrate.

2.9.9 Conclusion

A study of the population biology of *S. tracheacolum* first requires an ability to identify the parasite and its component life stages (Chapter 1: Morphology) with a subsequent understanding of at least the fundamental elements of its life history and mode of transmission (this chapter). Following these prerequisites the infrapopulation and demographic data from parasite infections can be interpreted. Chapter 3 interprets these data from infections of known duration in order to plot the course of a 'typical infection' and determine the outcome for the parasitic infrapopulation.

EXPERIMENTAL DESIGN

Chapter 3: **Population Biology**, Chapter 4: **Pathology**, Chapter 5: **Haematology**, Chapter 6: **Behaviour/Clinical Signs** and Chapter 9: **Population Dynamics** rely on data and observations collected from an aviary based experiment undertaken in 1992 and repeated in 1993. The design and methodology of this experiment is set out below.

1. Aim of the experiment

(a) To investigate infrapopulation biology of *S. tracheacolum* in Gouldian Finch hosts.

(b) To determine the influence of infection by *S. tracheacolum* on the fecundity and mortality of Gouldian Finches.

(c) To describe the pathogenesis in Gouldian Finches attributable to infection by *S. tracheacolum.*

(d) To describe the influence of *S. tracheacolum* infection on the behaviour of Gouldian Finches and determine the period to onset of respiratory distress/ impairment and other clinical signs associated with infection.

2. Experimental enclosures

An aviary was specially constructed for the purposes of the study. The floor area measured 14 x 4m and supported 6 separate enclosures. One half of the roof area was covered by corrugated iron sheeting. The rear and the sides were enclosed by cement sheeting. The remainder (1/2 of the roof area and the front of the aviary) was covered by a fine wire mesh and a double layer of translucent plastic. The facility was orientated to the north to obtain maximum sunshine hours for enclosures and to take advantage of solar heating. Maximum internal temperatures were partially regulated by a electric fan and ducting system that circulated cooler external air. Minimum internal temperatures were partially regulated by a series of electric fan heaters. The daily internal temperatures were recorded with a max-min thermometer (recorded temperatures are summarised in Table 1).

All enclosures were similar in size (approximately 2m wide, 3m deep and 2.4m high) and orientation. Enclosures housing control birds were separated from those containing experimentally infected birds by a thin but complete wall of cement sheeting. The wall prevented direct contact between control and experimentally infected birds, thereby reducing the potential for transmission of *S. tracheacolum* between these groups. All enclosures experienced similar conditions of light (controlled by natural factors) and temperature (partially controlled by electric heating and cooling equipment). Each enclosure was provided with ample quantities of clean dry grass for nesting material and 6 nest boxes (of identical size and design), placed high on the side and rear walls.

With regard to the size and location of perches, feeding bowls and other aviary furniture, all enclosures were similar.

Table 1. Aviary temperature range during the course of the 1992 and 1993 aviary experiments.

Month	Minimum Temperature Mean (Range)	Maximum Temperature Mean (Range)
1992		
February	16.8 (11-20)	31.5 (24-35)
March	18.3 (12-21)	34.5 (24-45)
April	18.0 (15-20)	33.2 (29-38)
May	15.5 (14-19)	29.9 (25-33)
June	13.3 (11-16)	28.5 (26-31)
July	14.3 (12-17)	28.3 (24-33)
August	12.8 (12-15)	27.0 (23-30)
September	14.2 (10-16)	28.6 (24-35)
October	16.5 (12-19)	33.1 (23-42)
November	16.6 (12-20)	32.7 (24-40)
December	17.5 (16-19)	32.0 (25-35)
1993		
February	16.2 (14-20)	33.8 (22-40)
March	15.6 (14-18)	32.2 (25-38)
April	15.2 (13-18)	31.0 (24-36)
May	15.8 (13-18)	30.1 (22-34)
June	16.4 (13-19)	28.2 (23-33)
July	17.4 (13-20)	27.9 (23-30)
August	17.6 (14-20)	30.5 (24-34)
September	18.1 (16-21)	33.3 (26-40)
October	17.9 (17-20)	32.9 (28-36)
November	18.3 (16-23)	32.0 (25-40)
December	17.6 (14-20)	32.5 (24-42)

3. Experimental procedure

(a) 1992

On 20 December 1991, 100 sexually mature (captive reared) first year Gouldian Finches were purchased from a commercial aviculturist in south eastern Queensland. The supplier confirmed that *S. tracheacolum* had not been detected in the breeding stock during more than 20 years of operation. Following transport to Hobart the birds were initially housed in small cages at the Zoology Department, University of Tasmania and maintained at 24^{o}C on a 12 hour light/dark cycle.

A random sample of 10 birds (5M; 5F) was killed by lethal anaesthetic injection and examined for *S. tracheacolum* infection. No mites were found. From the remaining collection of birds, 72 birds (36M; 36F) were randomly selected and divided into 6 groups, each comprising 6 males and 6 females. Each group of 12 birds was then allocated to either a control enclosure (enclosures 1, 2 and 3) or an experimental enclosure (enclosures 4, 5 and 6) in the specially constructed aviary.

Birds were introduced to the aviary between 14 and 17 January 1992. All received a 25 µl oral dose of ivermectin (dosage range, 1.36-1.88 µl/g b.w. Ivomec®) on 10 January, prior to transfer to the aviary, and again on 20 January, while in the aviary. Birds from enclosures 4, 5 and 6 were each experimentally infected with a single adult female mite on 6 February. This infection procedure was repeated on 12 February. At fortnightly intervals until 20 July, both control and experimentally infected birds were caught, weighed and examined. From 6 February (subsequently referred to as day 1 of infection, 1992) observations were made on host fecundity, mortality, behaviour and clinical signs of disease.

Between 15 and 26 May 1992, 5 control birds (4 M; 1F) from enclosure 3, and 5 experimentally infected birds (4M; 1F) from enclosure 4 were killed and dissected (subsequently referred to as the '3 months sample'). Between 28 and 31 July, 6 control birds (3M; 3F) from enclosures 1 and 2, and 6 experimentally infected birds (3M; 3F) from enclosures 5 and 6 were killed and dissected (subsequently referred to as the '6 months sample').

On December 10, 1992 all remaining birds (both control and experimentally infected) were transferred to a temperature and light controlled room (24°C; 12h light/12h dark) and housed in small cages (4 birds per cage). This move was necessary to enable other birds to be installed in the aviary for continuing experiments. Control and experimentally infected birds were housed in separate cages. One experimentally infected female bird was killed and examined on 14 April 1993, one male bird on 16 April 1993, one male bird on 1 September 1993 and one male on 21 February 1994.

(b) 1993

On 12 February 1993, 50 adult captive reared Gouldian Finches, 20 captive reared Budgerigars and 20 captive reared Canaries were purchased from the same aviculturist in south east Queensland. Thirty six of the Gouldian Finches (18M; 18F), were first year adults and 12 (6M; 6F) were second year birds that had bred during the previous season. Birds were initially housed in small cages at the Zoology Department, University of Tasmania, under the same conditions as the 1992 birds.

A sample of 5 birds was killed and examined for *S. tracheacolum*. No evidence of infection was found. Following a procedure of random allocation, 40 birds were divided into 4 groups, each comprising 4 male and 4 female first year birds and 1 male and 1 female second year bird. Two groups were placed in control enclosures (enclosures 1 and 2) and two groups were placed in experimental enclosures (enclosures 4 and 5).

Between 16 and 17 February 1993, all control and experimental birds received a 2.0 µl/g b.w. oral dose of ivermectin (overall dosage range, 28-40 µl Ivomec®) and were transferred to the aviary on

18 February. Experimental infection of birds from enclosure 4 and 5 was carried out on 2 and 3 March (3 March is subsequently referred to as day 1 of infection, 1993).

Between 6 and 7 December 1993, 4 control birds (2M; 2F) from enclosure 2, and 3 experimentally infected birds (2M; 1F) from enclosure 4 were killed and dissected (subsequently referred to as the '9 months sample'). Between 17 and 24 February 1994, 5 control birds (3M; 2F) from enclosure 1, and 4 experimentally infected birds (2M; 2F) from enclosure 4 were killed and dissected (subsequently referred to as the '12 months sample').

Budgerigars and Canaries were randomly allocated to either control (6 birds per species) or experimental groups (14 birds per species). All birds were given a 2.0 µl/g b.w. dose of ivermectin (total dosage range: Budgerigars, 72-120 µl; Canaries, 34-44 µl Ivomec®) between 9 and 10 March 1993. Budgerigars from experimental groups were each infected with 2 adult female mites (1 gravid; 1 non-gravid) on 19 February 1993. Experimental Canaries were similarly infected on 17 March. The experimental groups were housed in the aviary from 19 March to 27 September 1993 and subsequently housed in a temperature and light controlled room at 24°C and a 12 hour light/dark cycle. Control groups were housed in small cages (3 birds per cage) throughout the period 19 March 1993 to 16 September 1993. Between 16 and 17 September 1993, 5 experimentally infected Canaries (2F; 3M) and 3 control Canaries (3F) were killed and dissected. Fourteen experimentally infected Budgerigars (11M; 3F) and 5 control Budgerigars (2M; 3F) were killed and dissected between 17 and 20 September 1993.

Prior to transfer of birds to the aviary, all individuals of each host species received a unique combination of coloured leg bands for subsequent identification. At the same time an examination was made to record 'initial conditions' of each bird (plumage colour, bill colour, moult characteristics, wing length, tail length, weight and presence of ectoparasites etc).

All birds (control and experimentally infected) received an identical diet comprising a dry seed mixture of approximately 40% Pannicum, 25% Japanese Millet, 30% Canary seed and 5% Niger, Rape and Linseed). Each enclosure was supplied with fine shell grit, bush charcoal and cuttlefish pens. Clean water and fresh green vegetables were provided daily.

4. Preliminary assessment of the experimental infection procedure

Preliminary studies were undertaken to assess the potential for experimental infection of Gouldian Finches and other known host species. Initial trials focused on Canaries. Live mites were obtained from the upper respiratory system of freshly killed wild Gouldian Finches (see Table 3) and directly transferred to the mouth of individual Canaries. After various intervals of time, birds were killed and dissected (Table 2-A). *S. tracheacolum* mites were recovered from all birds that were

experimentally infected. No mites were recovered from two birds purchased from the same avicultural breeder but not experimentally infected with *S. tracheacolum.* Although the previous infection history of experimentally infected birds was not known, the results of the experiment supported the notion that a simple transfer of mites, directly from an infected bird to an uninfected bird, would be an effective means of experimentally establishing an infection in a new host. Similar experiments were then conducted on captive reared Gouldian Finches with equally favourable results (Table 2-B).

Table 2. Results of initial trials on the efficacy of experimental infection techniques: A, Canaries; B, Gouldian Finches.

Recipient	Date of experimental infection	Technique of experimental infection	Date of euthanasia of recipient	Number and stage of mites recovered
A. Canaries				
Adult female	15 March 1990	4F in mouth	22 March 1990	5F
Adult female	"	"	20 April 1990	23F+I
Adult female	"	"	15 May 1990	32F+I
Adult male	20 April 1990	2F in mouth	11 July 1990	45F+I
Adult female	"	3F in mouth	23 July 1990	7F
"	"	2F in mouth	31 July 1990	14F+I
"	15 May 1990	4F in mouth	20 August 1990	5F
B. Gouldian Finches				
Juvenile female W	3 October 1990	6F in mouth	12 October 1990	4F live
"	"	"	"	"
Juvenile male W	"	"	15 October 1990	77*
Adult male (B) C	31 January 1992	3F in nares	1 February 1992	3F dead
Adult female (O) C	"	5F in nares	"	5F
Adult male (O) C	1 February 1992	1F in naris	3 February 1992	1F live
Adult male (B) C	6 March 1992	10F in mouth	12 March 1992	1F,1P live

C, captive reared; W, wild caught; (B), black head plumage; (O), orange head plumage; F, adult female; P, protonymph; I, immature stages; *, number of mites live and stages present was not determined (bird obviously supported a pre-existing infection).

Given the scope of the project and the limitations imposed by the availability of birds for experimental purposes, time constraints and ethical considerations, the success of specific techniques could not be appropriately evaluated. At the time of designing the aviary based experiment little was known of the biology of *S. tracheacolum* and the stage responsible for transmission, nor differences in the level of host resistance (between individuals birds and between species) and the survival rate of individual mites following contact with a new host. Furthermore, any experimental interpretation of these factors would be influenced by the period of time between experimental infection and the point at which the host was killed for examination.

In the absence of known survivorship and reproductive potential of mites, direct transfer of mites between birds appeared to be quite suitable for the establishment and maintenance of an infected captive host population. However, to achieve the aims of the aviary experiment it was necessary to be confident of the success of the technique in all individual birds. Such rigour was unfortunately not possible.

As a best-bet approach in the face of some uncertainty, birds used in the aviary experiment were each experimentally infected with 2 adult female mites (1 non-gravid female, 1 gravid). The possible outcome in the new host was the survival and reproduction of both mites, only a single mite or no mites. In the event of the death of both mites, prior to reproduction and successful establishment of an infection in a host, that host would either remain uninfected throughout the experiment or would become infected through natural transmission from one or more of the successfully infected hosts sharing the same enclosure.

5. Source of *S. tracheacolum* mites used in experiments

S. tracheacolum mites used in experimental work were originally collected from wild Gouldian Finches caught at Yinberrie Hills, Northern Territory (Table 3). These hosts were killed and dissected and all live female mites were used to experimentally infect captive reared Gouldian Finches and Canaries. The captive reared birds were subsequently used as a source of mites for ongoing experiments. As birds were killed to provide mites for specific experiments, further birds were experimentally infected to maintain an ongoing source of mites.

Table 3. Original source hosts, Gouldian Finches *E. gouldiae*, for mites *S. tracheacolum* used in the establishment of experimental infections. All birds were collected by mist nesting at Yinberrie Hills, NT on 5 September 1990.

Host Sex	Host Age	Date Host euthanased	Number of adult *S. tracheacolum* collected
Male	Immature	3 October 1990	22
Female	"	4 October 1990	37
Male	"	13 November 1990	33
Female	"	20 December 1990	35
"	Adult	1 May 1991	39
"	"	3 May 1991	27

6. Experimental infection procedure

A heavily infected Gouldian Finch can yield sufficient mites for the experimental infection of up to 30 other birds. Prior to experimental infection, a bird from the stock of infected birds (showing respiratory clinical signs characteristic of heavy infection) was killed and dissected. Live adult mites were removed from the nares, trachea and the anterior airsacs. They were placed in sterile

tissue culture dishes containing a physiological saline and kept at 37^{o} C. Mites were then examined and cleaned of mucus and other debris using fine probes and micro spatulas. The mites were held in physiological saline for up to an hour prior to their transfer to recipient birds. Only active mites were chosen for transfer.

Two stereo dissecting microscopes were required for the procedure. One was used to examine and collect mites. Recipient birds, restrained by hand, were examined under the other. While the bill of a recipient bird was propped open (with a paperclip) a mite (held on the end of a micro spatula) was placed in its mouth. Mites were placed under the tongue or on the side of the mouth posterior to the bill. The procedure was repeated (within one minute) for the transfer of a second mite. Following the procedure, recipient birds were returned to the aviary.

7. Ivermectin pre treatment procedure

Informative observations in the aviary experiment relied on the absence of pre-existing *S. tracheacolum* infections in both control and experimentally infected birds. If control birds were to yield *S. tracheacolum* infection then data from the experiment would be rendered, for the most part, useless. Although birds used in the major aviary experiment came from a breeding stock where *S. tracheacolum* had not been detected for a considerable period of time it was deemed prudent to pre-treat them with an effective acaricide. Ivermectin, (Ivomec®), was chosen for this purpose (See Chapter 9: Drug Treatment). Doses administered were those that were known to be non-toxic to hosts but effective in killing mites. All birds were administered pure oral doses with the aid of a microlitre syringe.

8. Limitations of the experiment

One limitation of the experiment was the potential for varying effectiveness of the experimental infection technique. Housing birds in groups was a fundamental requirement for the study of the impact of *S. tracheacolum* on host fecundity. However, birds that were not successfully infected by the experimental technique were likely to become infected naturally from birds that were successfully infected by the same technique. Complete failure of the technique in individual birds and, perhaps even the failure of only one of the two mites to establish and reproduce, may have deflated mean values for measures of infection size when assessed at temporal sampling points (i.e. at 3,6,9 and 12 months following initial infection). All birds in the 3 months sample were found to be infected, though some individuals examined prior to this time were found to be free of infection. So, for the purpose of the present study it was assumed that if the technique of experimental infection failed completely in an individual bird, then that bird became infected at a time following the production of infective stages in other successfully infected birds, but prior to the 3 months sample.

A further limitation was the presence of disease unassociated with *S. tracheacolum* infection. This severely reduced the size of samples and consequently the ability for statistical analysis of results. Both control and experimentally infected birds suffered high mortality rates throughout the 1992 experiment. A repeat of the experiment was undertaken in 1993 but this experiment was plagued by similar problems.

Chapter 3. INFRAPOPULATION BIOLOGY

3.1 INTRODUCTION

In a report on the use of ecological terms in parasitology, Margolis *et al.* (1982) defined an infrapopulation as 'all individuals of a species of parasite occurring in an individual host'. In many ways the *S. tracheacolum* infrapopulation is very similar to the population concept of free living animal species with the exception that the body of the host defines the boundary of the infrapopulation rather than the more diffuse boundaries applicable to an organism interacting with its environment. Within the infrapopulation there is a natural birth and death rate that may or may not be influenced by intensity-dependent processes (analogous to the density-dependent processes of free living populations) and host immune responses, while infection and transmission are essentially equivalent to the immigration and emigration parameters of free living animal populations.

There have been many quantitative assessments of the size of endoparasitic mite infrapopulations in vertebrate host species (e.g. Amerson, 1967; Domrow, 1969; Pence, 1973; Spicer, 1987) and many exhaustive counts have been made of entire *S. tracheacolum* infrapopulations (e.g. Fain & Hyland, 1962; Murray 1966; Riffkin & McCausland, 1972; Tidemann *et al*, 1992a). However, until now little attention has been directed at the behaviour of infrapopulations over time. The difficulties involved in undertaking this type of study relate to the inability to assess the parameters of infection without sacrifice of the host. Furthermore, once the host is sacrificed, the informative value of the infrapopulation data is reduced to a single point in time and to some degree an unreferenced point without control over the time of infection. It is only recently (the present study) that our knowledge of rhinonyssid biology has enabled experimental infection of the host, and that suitable acaricidal drugs have been developed that are capable of eliminating entire rhinonyssid infections, thus ensuring infection-free subjects for parasitic manipulation experiments.

Most macroparasites of vertebrates produce a large number of eggs and consequently, a large number of transmission stages. This compensates for the very low probability that any one infective stage gains entry to a new host (Anderson & May, 1992). In contrast, *S. tracheacolum* (and observations would indicate that this phenomenon is widespread among mites inhabiting the respiratory system of vertebrates) produce only a single egg at a time. This low numerical productivity of eggs, though they are very large eggs relative to the body size of the adult female, may relate to a relatively high probability that any one infective stage (i.e. the young adult female) survives to reproduce within the host or gain entry to a new host. For this reason, the rate of *S. tracheacolum* reproduction will, in the absence of host immune responses and parasite intensity-dependent processes, determine the fundamental characteristics of infrapopulation growth.

It is well documented that the fecundity of a macroparasite may be influenced by a number of parasite and or host factors. For example, the host's nutritional status may act on a parasite's reproductive potential either directly through the nutrition of the parasite or indirectly through changes in the capacity of the host to mount an immune response to the parasite (Compton, 1991). Likewise the genetics of the host can effect not only the survival rate of established parasites but the fecundity of the parasite. This is supported by a variety of laboratory experiments (Dobson & Merenlender, 1991).

Other commonly reported influences on infrapopulation growth of macroparasites are intensity-dependent processes, whereby the rates of parasite survival, maturation and fecundity are often inversely related to the density of the parasite. Intensity-dependence acts through limitations on resources (such as space or nutrients) or as a result of host immunological or non-specific responses, where the level of the response increases disproportionately faster than the increase in parasitic burden. Intensity-dependent processes are considered to be of central importance in providing regulation of parasite infrapopulation growth (Anderson & May, 1992).

For the purposes of understanding the infrapopulation growth of *S. tracheacolum*, a knowledge of the time of initial exposure (to one or more infective stages) is of paramount importance. Once an infrapopulation is established, and growing, then further exposure to infective stages will presumably have only a marginal impact on the overall demography and pattern of growth of that infrapopulation.

The present study aims to describe the characteristics and demography of *S. tracheacolum* infrapopulation growth in captive reared Gouldian Finches. Experimental infection of previously uninfected birds provides an opportunity to investigate the infrapopulation biology of *S. tracheacolum* over time, be it only from composite infrapopulation data, and determine the factors that govern infrapopulation dynamics in Gouldian Finch hosts.

3.2 METHODS

An aviary based experiment was undertaken in 1992 and repeated in 1993. The design of the experiment is described in detail in the Experimental Design, P 61. The essential details are as follows.

Captive reared Gouldian Finches were experimentally infected with *S. tracheacolum* and maintained in an aviary environment for periods of up to one year. At intervals of 3, 6, 9 and 12 months following initial infection, samples of infected birds were removed, killed and dissected.

The host composition of these samples is shown in Table 3.1. The infrapopulation data from the birds of these samples form a dataset that is hereafter known as the '3, 6, 9 and 12 months samples'.

Table 3.1 Host sample size and composition of samples taken at 3, 6, 9 and 12 months following initial infection.

Duration following infection	Number of birds in sample	Sex and head colour of birds
3 months	5	4 male orange head, 1 female black head
6 months	6	2 male orange head, 1 male red head, 3 female black head
9 months	3	1 male orange head, 1 male black head, 1 female black head
12 months	4	1 male red head, 1 male orange head, 1 female black head, 1 female orange head

Infrapopulation data from birds sampled at 3, 6, 9 and 12 months following initial infection were combined with infrapopulation data from birds dying during the course of the aviary experiment and birds killed at various intervals following closure of the experiment. This formed a second dataset, comprising 37 birds (19M, 18F) with infrapopulations of known duration (range = 6-351 days) and is hereafter known as the 'aviary dataset'.

A third dataset was formed from the amalgamation of the 'aviary dataset' with infrapopulation data from all other birds dying or killed during the course of the overall study. This included stock birds and birds used in other experiments where the time of initial infection was known. Environmental housing conditions for the latter bird group were different from those of birds in the aviary experiment; they were held in a temperature controlled room at 24^{o}C under conditions of 12 hours light/ 12 hours dark and housed in small cages. The resultant dataset comprised infrapopulation data from 61 birds (31M, 30F) with infrapopulations of known duration (range = 6-736 days) and is hereafter known as the 'data overall'.

3.2.1 Infrapopulation growth and demography

Aspects of infrapopulation growth and demography were studied by examination of composite infrapopulation data (i.e. data assessed at a single point in time from many different host individuals carrying *S. tracheacolum* infrapopulations of known duration).

To assess the size and demography of infrapopulations, each bird was dissected and exhaustively examined for mites of all stages, both live and dead. A record was made of the site of each mite within the host. They were then removed, preserved in 70% alcohol and later cleared and mounted

on microscope slides. Mites were then examined under a compound microscope to determine their stage, sex and reproductive condition.

Statistical analyses were performed using programs in Excel 5.0 (Microsoft Corporation, 1993) Descriptive statistics (mean, standard deviation and standard error) were calculated for groups of infrapopulations. Single factor ANOVA's were used for comparisons among mean infrapopulation data. Percentage data were arcsine transformed prior to analysis.

3.2.2 Transmission

At regular intervals following experimental infection, the bill, external nares and head plumage of live infected birds were examined for *S. tracheacolum* mites. The procedure involved holding an individual bird, by hand, and examining the nares with the aid of a 10x magnification hand lens or by holding the bird under a dissecting stereo microscope. A record was made of the site and the number of mites present during an observation period of approximately 30 seconds.

3.3 RESULTS

3.3.1 Demography of *S. tracheacolum* infrapopulations and the duration of infection

3.3.1.1 Sex of mites and the duration of infection

There were no significant differences in the mean proportion of male mites within live adult infrapopulations among the '3, 6, 9 and 12 month samples' or among groups of the 'aviary dataset' (infrapopulations grouped into classes spanning 1-89 days, 90-179 days, 180-269 days and 270-359 days following initial infection). Raw percentage data for male mites was highly variable. However, the mean percentage data for male mites within infrapopulations was consistent over time, ranging from a low of 2.8% for grouped infrapopulations of 1-89 days duration (n = 6, 'aviary dataset'; Table 3.3) to 4.9% at 6 months following initial infection ('3, 6, 9 and 12 months samples', n = 6; Table 3.2).

The mean percentage of female mites within live adult infrapopulations was consistent among groups. Furthermore, there was little variation in the raw percentage data. Mean values of 97.2 (SD = 4.5), 96.7(SD = 3.3), 97.0 (SD = 4.4) and 96.9 (SD = 4.6) were recorded for grouped infrapopulations of the 'aviary dataset' from 1-89 days (n = 6), 90-179 days (n = 16), 180-269 days (n = 7) and 270-359 days (n = 8) respectively, following initial infection.

The proportion of gravid female mites, measured as a percentage of the live adult female infrapopulation, did not vary significantly among the 3, 6, 9 and 12 month samples (Table 3.2) or among groups of the 'aviary dataset' (Table 3.3).

Table 3.2 Comparisons of infrapopulation parameters among Gouldian Finches experimentally infected with *S. tracheacolum* and sampled at 3, 6, 9 and 12 months following initial infection.

Parameter	3 months (n = 5)	6 months (n = 6)	9 months (n = 3)	12 months (n =4)	*f*	*P* value
Total infrapopulation	91.4 ± 93.2	222.2 ± 37.9	38.7 ± 32.6	81.8 ± 39.1	6.9	0.004 ‡
Total number mites in live infrapopulation	85.2 ± 90.1	192.2 ± 41.1	32.0 ± 17.0	61.3 ± 55.8	5.5	0.01 ‡
Percentage of immatures in the live infrapopulation	29.6 ± 11.3	22.5 ± 8.0	17.0 ± 15.9	23.4 ± 11.4	0.86	0.49
Percentage of males in live adult infrapopulation	3.04 ± 4.7	4.9 ± 1.9	3.7 ± 3.9	3.5 ± 6.1	0.19	0.9
Percentage of mites dead in total infrapopulation	11.7 ± 6.6	14.9 ± 6.5	17.2 ± 7.0	28.1 ± 21.1	1.7	0.22
Percentage of female infrapopulation in the nasal cavity	11.2 ± 14.7	6.6 ± 5.9	2.8 ± 4.8	3.0 ± 2.0	0.82	0.5
Percentage of mites gravid in female infrapopulation	54.7 ± 13.4	38.5 ± 12.4	50.6 ± 24.2	44.4 ± 14.0	1.1	0.37

Table 3.3 Comparisons of infrapopulation parameters among Gouldian Finches experimentally infected with *S. tracheacolum* and dying or killed between 1 and 351 days following initial infection.

Parameter	1-89 days following initial infection (n = 6) mean ± SD	90-179 days following initial infection (n = 16) mean ± SD	180-269 days following initial infection (n = 7) mean ± SD	270-359 days following initial infection (n = 8) mean ± SD	*f*	*P* value
Total infrapopulation	22.5 ± 27.2	127.3 ± 101.0	122.6 ± 87.1	57.8 ± 60.2	3.1	0.04 ‡
Total number mites in live infrapopulation	21.7 ± 26.7	113.3 ± 89.2	104.4 ± 74.0	44.6 ± 43.9	3.4	0.03 ‡
Percentage of immatures in the live infrapopulation	14.5 ± 13.5	25.1 ± 12.3	15.8 ± 7.6	26.8 ± 11.0	0.95	0.43
Percentage of males in live adult infrapopulation	2.8 ± 4.5	3.3 ± 3.3	3.0 ± 4.4	3.1 ± 4.6	0.03	0.99
Percentage of mites dead in total infrapopulation	2.6 ± 5.7	9.1 ± 7.9	13.9 ± 9.6	22.4 ± 15.5	5.1	0.005 ‡
Percentage of female infrapopulation in the nasal cavity	3.4 ± 5.2	12.0 ± 14.1	3.8 ± 3.3	2.5 ± 4.3	3.5	0.03 ‡
Percentage of mites gravid in female infrapopulation	27.3 ± 24.9	39.6 ± 16.8	28.9 ± 10.3	41.1 ± 23.2	1.14	0.35

Table 3.4 Correlation coefficients between the duration of infection in Gouldian Finches and the demography of *S. tracheacolum* infrapopulations

Infrapopulation parameter	Male hosts	Female hosts	Total	*P*
Percentage of males in the live adult infrapopulation	0.02	0.05	0.08	0.63
Percentage of females in the live adult infrapopulation	-0.09	-0.22	-0.16	0.34
Percentage of immatures in the live infrapopulation	-0.1	-0.08	-0.09	0.59
Percentage of mites gravid in the female infrapopulation	0.22	0.09	0.16	0.34
Percentage of female infrapopulation in the nasal cavity	-0.3	-0.03	-0.18	0.28
Percentage of mites dead in the infrapopulation	0.67	0.47	0.57	0.0002

There was a poor correlation between the duration of infection and the proportion of male or female mites within live infrapopulations. Likewise there was a poor correlation between the duration of infection and the proportion of gravid females within the female infrapopulation. This was evident in both male and female host groups (Table 3.4).

3.3.1.2 The presence of immature mites and the duration of infection

There were no significant differences in the mean proportion of larvae, protonymphs, deutonymphs or immature mites (i.e. pooled data for larvae, protonymphs and deutonymphs) within live infrapopulations among the '3, 6, 9 and 12 month samples' (Table 3.2) or among groups of the 'aviary dataset' (Table 3.3). Raw percentage data were highly variable within and among the '3, 6, 9 and 12 month samples' and among groups of the 'aviary dataset'. The lowest recorded mean percentage for immature mites was 14.5% for the grouped infrapopulations of 1-89 days duration (n = 6, 'aviary dataset'; Table 3.3). The highest recorded mean percentage was 29.6% at 3 months following initial infection ('3, 6, 9 and 12 months samples', n = 6; Table 3.2). The raw percentages ranged from 0% to 46%, however, these extremes were found only in small infrapopulations (i.e. < 16 mites).

There was a poor correlation between the percentage of immatures within live infrapopulations and the duration of the infection. This was evident in data from both male and female host groups (Table 3.4).

3.3.1.3 The presence of dead mites and the duration of infection

A highly significant difference was found in the proportion of dead mites, measured as the percentage of mites found dead in the entire infrapopulation, within infrapopulations among groups of the 'aviary dataset' ($f = 5.1$, $P = 0.0005$). This significant difference was not shared among the smaller groups of the '3, 6, 9 and 12 month samples' ($f = 1.7$, $P = 0.22$).

For both the '3, 6, 9 and 12 month samples' (Table 3.2; Figure 3.1A) and groups of the 'aviary dataset' (Table 3.3) there was an apparent increase in the mean percentage of mites found dead with increase in the duration of infection. Correlation coefficients were uniformly positive and strong for the mean percentage of dead mites and the duration of infection which was evident in data from both male and female host groups (Table 3.4). A scatter plot of the raw percentages of mites found dead for the 'aviary dataset' against the duration of infection is shown in Figure 3.1B.

3.3.2 Infrapopulation growth of *S. tracheacolum*

Significant differences were evident in both the size of the total infrapopulation (i.e. all mites of all stages, live and dead) and the size of the live infrapopulation among the '3, 6, 9 and 12 month samples' (total infrapopulation: $f = 6.9$, $P = 0.004$; live infrapopulation: $f = 5.5$, $P = 0.01$) and

Figure 3.1A The mean percentage of mites *S. tracheacolum* found dead in the respiratory tissues of Gouldian Finches *E. gouldiae*: ■ = mean ± standard error for all birds from samples taken at 3 months (n = 5), 6 months (n = 6), 9 months (n = 3) and 12 months (n = 4) following initial infection; □ = mean for female birds only; ◆ = mean for male birds only. The solid line shows the simple linear regression fitted to the raw data for individual birds.

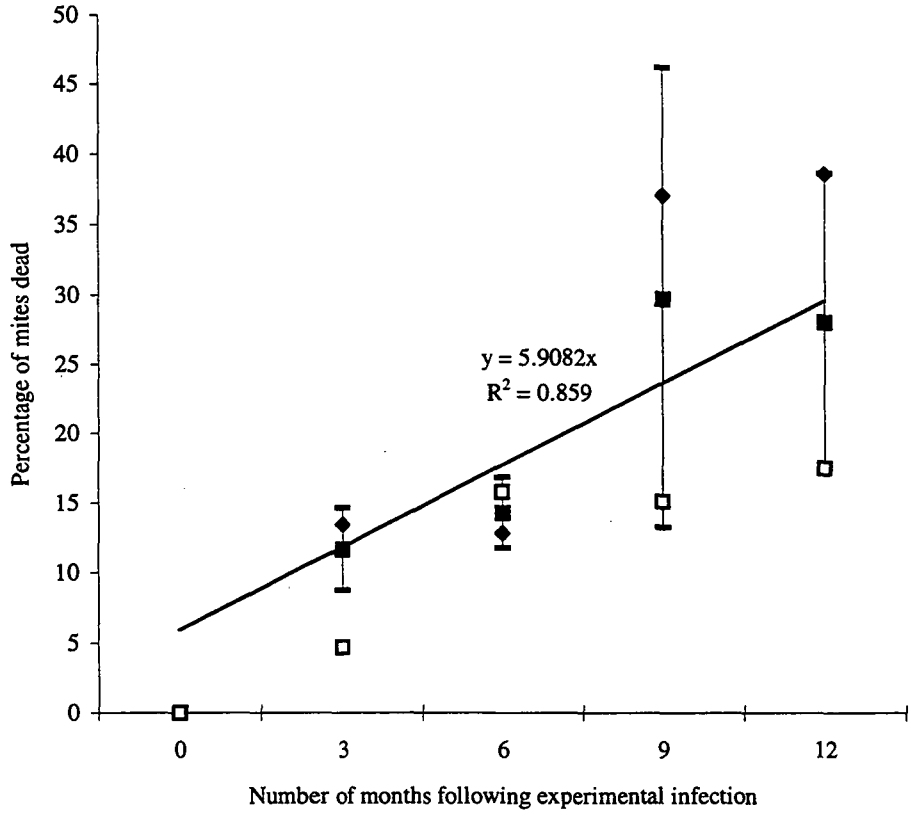
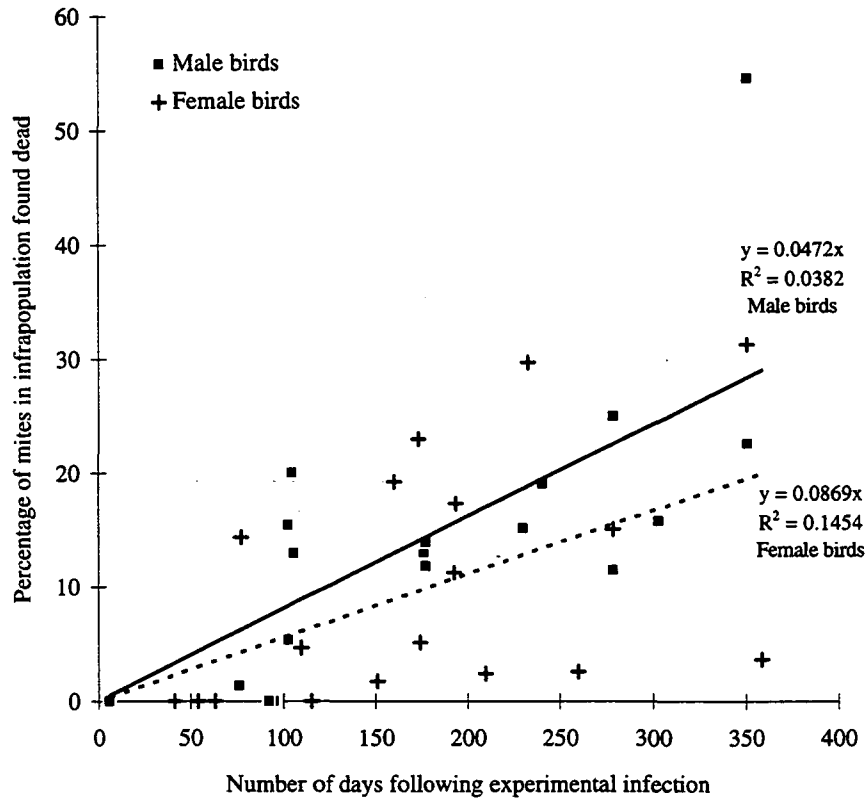


Figure 3.1B The percentage of mites *S. tracheacolum*, of the total infrapopulation, found dead in the respiratory tissues of Gouldian Finches *E. gouldiae* infected for periods ranging from 6 and 359 days: Simple linear regressions are fitted to the data for female birds (dotted line) and male birds (solid line).



among groups of the 'aviary dataset' (total infrapopulation: $f = 3.1$, $P = 0.04$; live infrapopulation: $f = 3.4$, $P = 0.03$). Figure 3.2A clearly indicates the locality of the difference.

The raw data for the size of total infrapopulations of the 'aviary dataset' (i.e. 37 infected birds) are plotted against the duration of infection in Figure 3.2B. These data suggest that, initially, there is a relatively slow rate of infrapopulation increase (slow growth phase) and this phase appears to hold until, in some cases, 90 days of infection. Following the slow growth phase there is a relatively slow rate of infrapopulation increase (rapid growth phase). This phase appears to stall at between 150 and 200 days following initial infection. Following the rapid growth phase there appears to be a gradual decline in the size of the infrapopulation (negative growth phase) until the experiment was closed at 351 days following initial infection. Raw data for live mite infrapopulations reveal a similar trend.

The raw data for total infrapopulation size from the 'data overall' (i.e. 61 infected birds) are plotted against the duration of infection in Figure 3.2C. The 'data overall' include infrapopulations examined from 6 to 736 days following initial infection. These data, which overlap the 'aviary dataset', echo the trend outlined in Figure 3.2B. That is, an initial slow growth phase which is followed by a rapid growth phase until approximately 6 months after initial infection. From 150-200 days following initial infection onwards, there is a negative growth phase until the infrapopulation is reduced to only few mites. The mean size of infrapopulations examined between 400 and 736 days (n = 4) following initial infection was a mere 17.5 mites (Range = 5-29).

3.3.3 Distribution of mites in the host respiratory system and the duration of infection

3.3.3.1 Transmission of *S. tracheacolum* and the duration of infection

All mites found within the nares of the host were infective mites (i.e. non-gravid, non-gorged adult females; see Chapter 2: Section 2.7, Transmission). The presence of mites in the nasal cavity of the host may therefore have potential use as an indicator of the timing of transmission. Furthermore, the proportion of mites within the nasal cavity, relative to the adult female infrapopulation within the entire respiratory system, may have potential use as an indicator of the abundance of infective mites within the infrapopulation over time.

The percentage of the female infrapopulation in the nasal cavity was significantly different among the grouped infrapopulations of the 'aviary dataset' ($f = 3.5$, $P = 0.03$; Figure 3.3A). The mean percentage of females in the nasal cavity was 3.4 (SD = 5.2) for 1-89 days, 3.8 (SD = 3.3) for 180-269 days and 2.5 (SD = 4.3) for 270-359 days of infection. A significantly higher mean percentage of 12.0 (SD = 14.1) was recorded for the class group of 90-179 days of infection. No differences were detected among the '3, 6, 9 and 12 months samples ($f = 0.82$, P = 0.5). However, the highest mean percentage (11.2; SD = 14.7) was recorded at 3 months following initial infection. The mean

Figure 3.2A Infrapopulation growth of *S. tracheacolum* in Gouldian Finches *E. gouldiae*: ■ = mean ± standard error for total infrapopulation size of all birds from samples taken at 3 months (n = 5), 6 months (n = 6), 9 months (n = 3) and 12 months (n = 4) following initial infection; □ = mean for female birds only; ◆ = mean for male birds only.

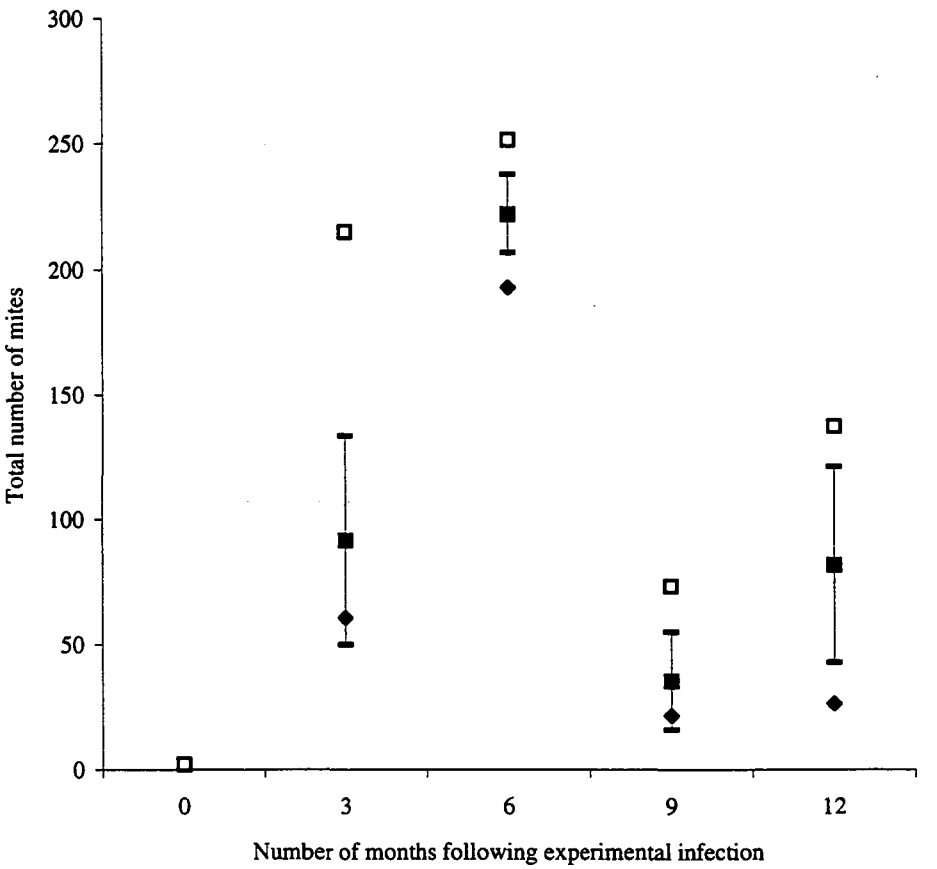


Figure 3.2B Infrapopulation growth of mites *S. tracheacolum* in captive reared Gouldian Finches *E. gouldiae*: total infrapopulation size for experimentally infected male and female birds from the 1992 and 1993 aviary experiments.

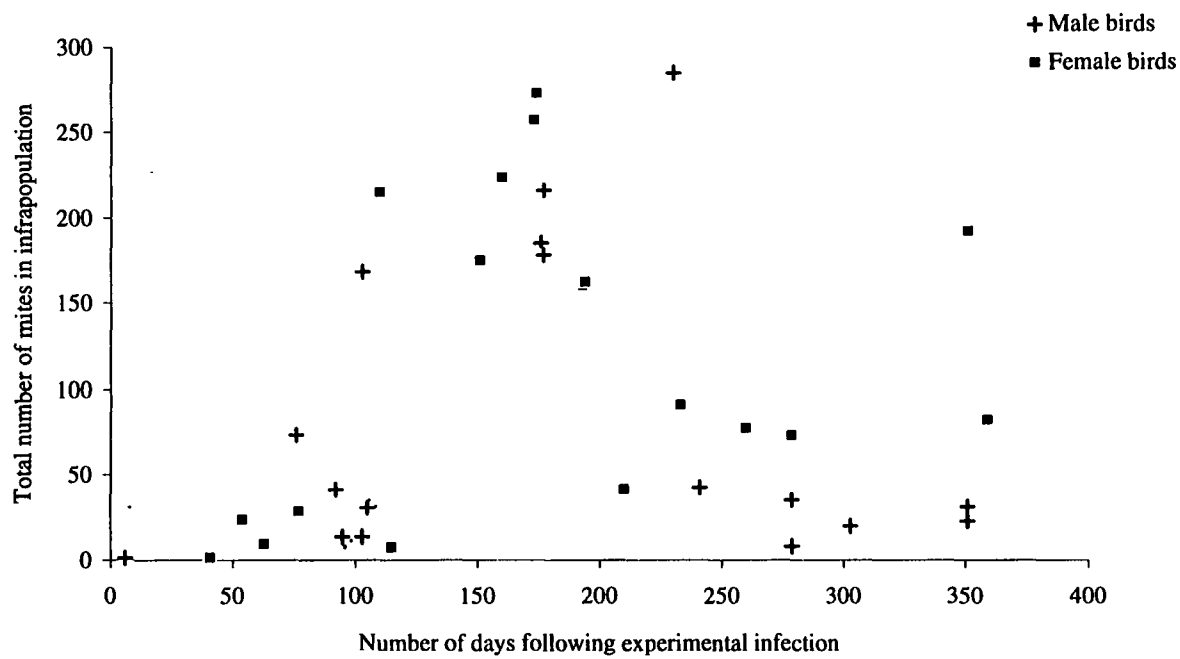


Figure 3.2C Infrapopulation growth of mites *S. tracheacolum* in captive Gouldian Finches *E. gouldiae*: total infrapopulation size for experimentally infected male and female birds from the 1992 and 1993 aviary experiment, all other birds with a known infection date and including birds maintained for more than 12 months following initial infection.

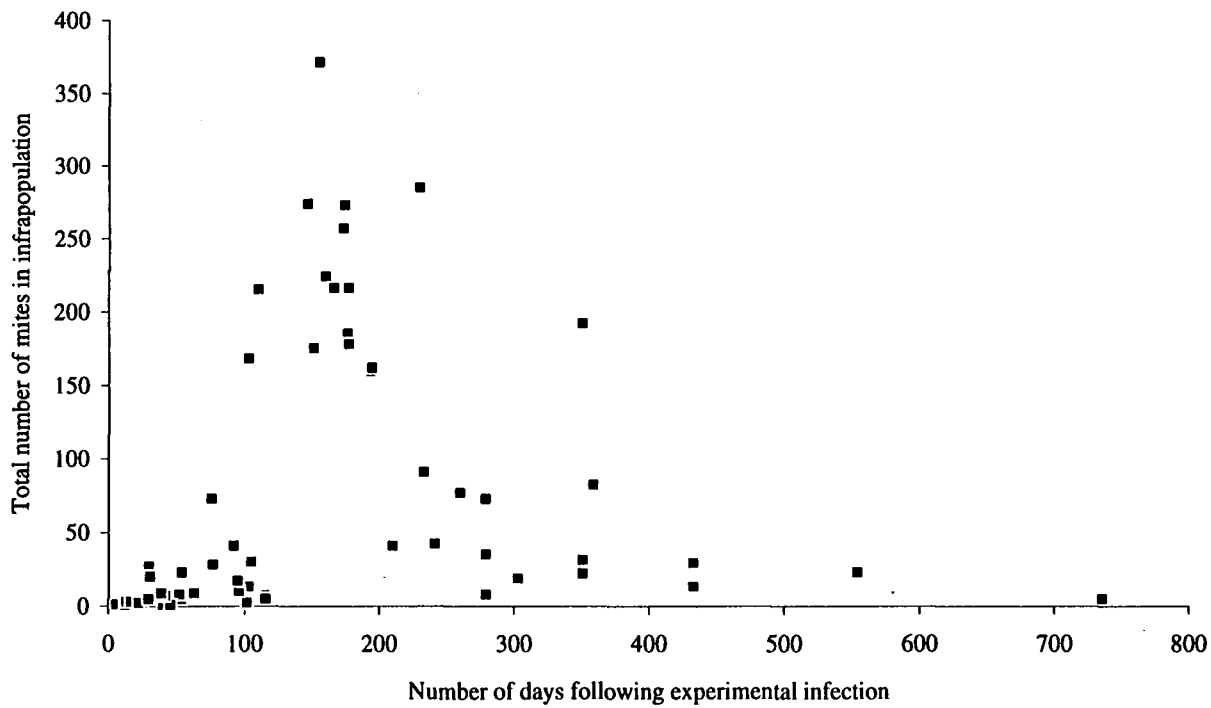


Table 3.5 Comparisons between the proportion of infrapopulations within a site in the host's respiratory system and the duration of the infection.

Locality in host respiratory system	Mean percentage of infrapopulation per locality Combined sample 3 + 6 months infected n = 11	Mean percentage of infrapopulation per locality Combined sample 9 + 12 months infected n = 7	*f*	*P*
Posterior airsacs	6.8	2.2	5.0	0.04 ‡
Thoracic airsacs	6.7	2.5	1.9	0.19
Anterior airsacs	30.1	14.9	2.5	0.13
Lungs	6.6	1.7	4.3	0.05 ‡
Bronchi	1.7	0	4.7	0.04 ‡
Syrinx	66.7	89	2.2	0.16
Trachea	30.9	61.6	11.6	0.004 ‡
Mouth and nasal cavity	9.4	2.4	1.8	0.2
Upper respiratory system	47.7	77.1	9.3	0.008 ‡

percentage for the sample taken at 6 months was 6.6 ± 5.9, 9 months, 2.8 ± 4.8 and 12 months, 3.0 ± 2.0 (Figure 3.3A).

Figure 3.3B shows the mean data for observations on the presence of live *S. tracheacolum* mites on the head plumage and bill (in particular, in and around the nares) of experimentally infected birds. For the most part the data come from examinations made on live birds on a weekly basis from 134 to 165 days following infection in 1992, and from 16 to 349 days following infection in 1993. Details of the examination regime in 1992 and 1993 are set out in Chapter 6: Table 6.1.

Figure 3.3B also shows the timing of the occurrence of *S. tracheacolum* mites in the drinking water from enclosures containing infected birds. The drinking water was examined daily from 1 to 157 days following infection in 1992, and from 1 to 359 days following infection in 1993.

In 1992, during the routine examination of infected and control (uninfected) birds at 134 days following initial infection, a mite was observed on the head plumage of one of the birds. From this time onwards, the head plumage and the bills of all infected birds were intensively examined for the presence of mites. Mites were observed on the head plumage and bills of hosts on a regular basis from the time of initial discovery until the final examination of birds at 164 days following initial infection.

In 1993, mites were first observed on the external surfaces of hosts during the examination at 83 days following initial infection. They were regularly observed in this site until 223 days following initial infection.

The timing of the presence of mites in the drinking water of infected birds was similar between 1992 and 1993. In 1992 they were regularly found from 88 days following initial infection until closure of the experiment at 164 days. During the 1993 experiment they were found less frequently during the period from 85 days until 256 following initial infection.

3.3.3.2 The proportion of mites in the upper and lower respiratory system and the duration of infection

The mean proportion of live adult female mites within each site of the host's respiratory system, measured as the percentage of the total number of live adult female mites in the entire respiratory system, is shown in Figure 3.4. These data come from the '3, 6, 9 and 12 months samples'. Notable, is a tendency for decline in the proportion of mites in sites of the lower respiratory system (i.e. posterior airsacs, thoracic airsacs, anterior airsacs, lungs and bronchi) with increase in the duration of infection. The converse relationship is evident in the upper respiratory system (i.e. syrinx, trachea and nasal cavity) with increase in the duration of the infection. Comparisons of the relative

Figure 3.3A Transmission of mites *S. tracheacolum* in Gouldian Finches *E. gouldiae*: The presence of non-gravid non-gorged mites in the mouth and nasal cavity of hosts ■ = mean ± standard error for all birds from samples taken at 3 months (n = 5), 6 months (n = 6), 9 months (n = 3) and 12 months (n = 4) following initial infection; □ = mean for female birds only; ◆ = mean for male birds.

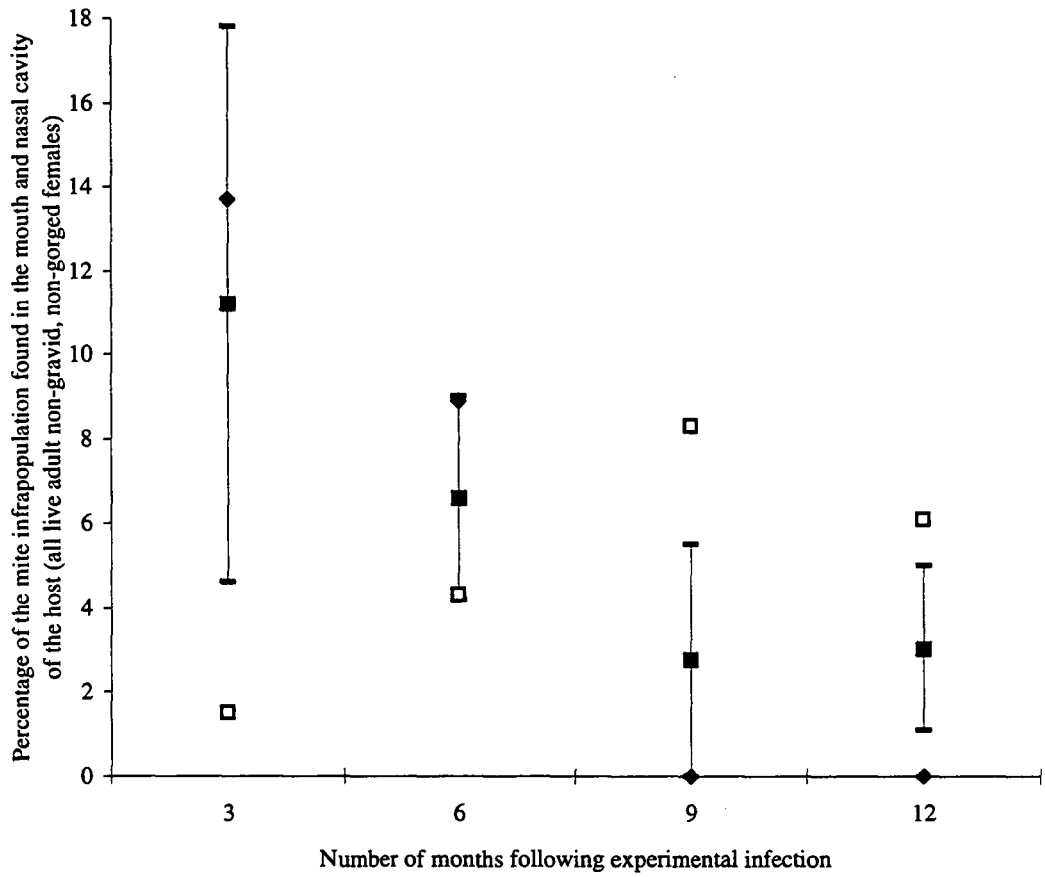


Figure 3.3B The activity of infective stage of *S. tracheacolum* in Gouldian Finches *E. gouldiae*. Observations on the presence of live mites on the head plumage and bill of experimentally infected birds: ■, Number of mites per host (mean ± standard error); □, Percentage of hosts carrying external mites; *, Presence of live non-gravid non-gorged female mites in drinking water.

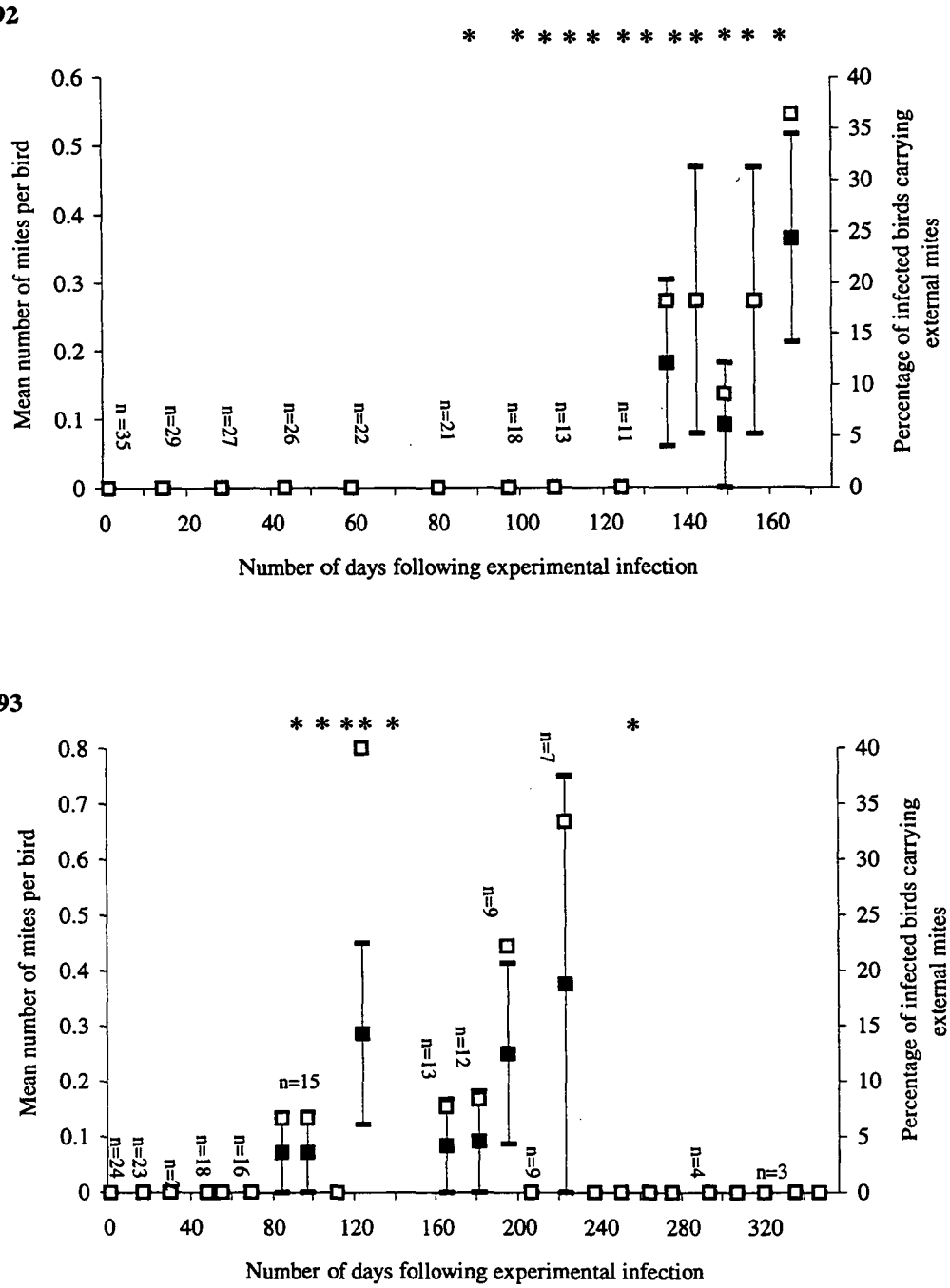
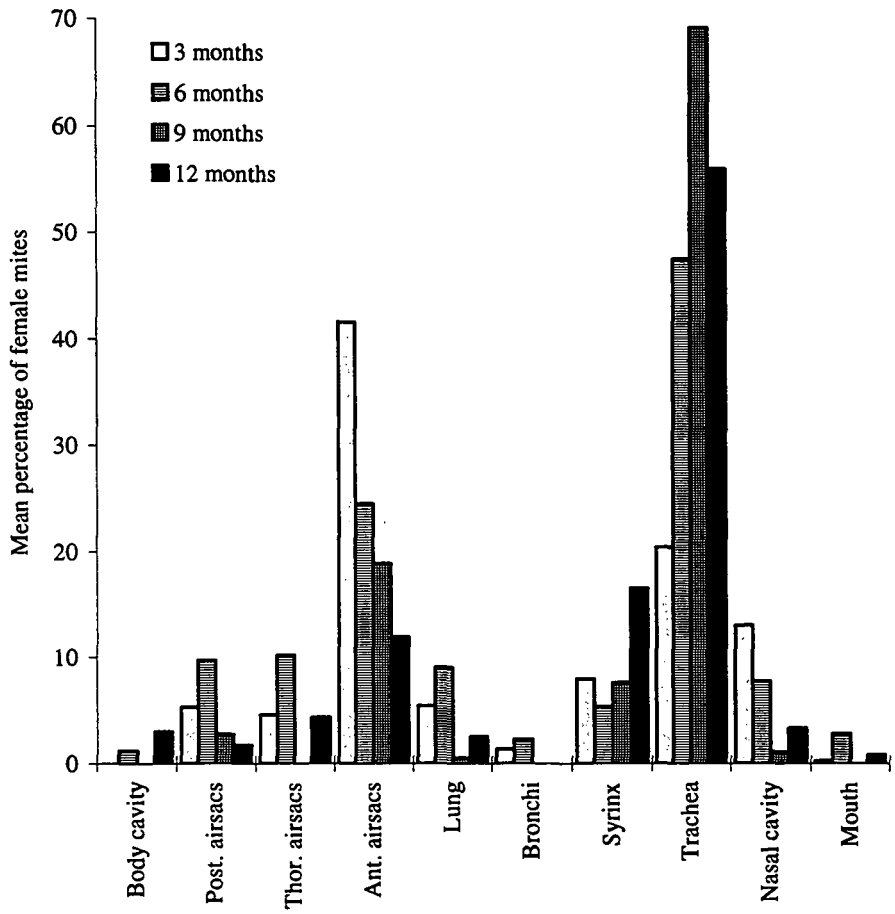


Figure 3.4 The site of live adult female mites *S. tracheacolum* within the respiratory tissues of Gouldian Finches *E. gouldiae* over a period of twelve months of infection: mean percentage of live female mites in the upper respiratory system (bronchi, syrinx, trachea, mouth and nasal cavity) and lower respiratory system (posterior airsacs, thoracic airsacs, anterior airsacs, body cavity and lung) at 3 months (n = 5), 6 months (n = 6), 9 months (n = 3) and 12 months (n = 4) following experimental infection.



percentage of adult female mites within each site of the host's respiratory system between data from the 3 and 6 months pooled samples and the 9 and 12 months pooled samples is shown in Table 3.5. Significantly higher proportions of mites were found in the posterior airsacs, lungs and bronchi in pooled samples taken at 3 and 6 months following initial infection. Conversely, significantly higher proportions of mites were found in the trachea in pooled samples taken between 9 and 12 months following initial infection. A highly significant difference was found for pooled percentage data for the entire upper respiratory system between the pooled 3 and 6 months samples and the pooled 9 and 12 month samples. The data clearly indicate a change in the distribution of mites through the hosts respiratory system with duration of infection.

3.4 DISCUSSION

3.4.1 Difficulties in the interpretation of infrapopulation growth from composite data studies

The interpretation of infrapopulation growth data from the present study was based on the assumption that all birds were successfully infected at the initiation of the experiment. This interpretation further assumes that the successful establishment of mites was similar for all hosts. Based on these assumptions, and providing that *S. tracheacolum* infrapopulation growth behaved similarly among all host individuals, the data presented in Figures 3.2B and C suggests three growth phases, firstly a slow growth phase, followed by a rapid growth phase, and finally, a negative growth phase. Reappraisal of these assumptions provides evidence for an alternative interpretation of the observed pattern of infrapopulation growth.

All hosts used in the aviary experiment were infected via a direct transfer of mites from an infected host to a recipient 'uninfected' host. Two mites were used to experimentally infect each bird, one gravid female mite (where a large egg could be clearly seen through the translucent idiosoma) and one non-gorged, non-gravid female mite. Differences in the state of fertilisation of the non-gravid female mite, and or differences in the state of embryogenesis of the gravid female mite may have lead to variations in the delay between initial exposure to infection and subsequent reproduction in the new host, and thus, may have explained some of the variation in the timing of the 'rapid infrapopulation growth phase'.

In the present study, each bird was exposed to infection by two female mites. One of three possible scenarios of infection would have followed, (1) both mites may have established and successfully reproduced in the new host, (2) only one mite may have successfully reproduced in the new host or (3) both mites may have failed to reproduce in the new host. Under the third scenario, two further outcomes are possible, (1) the host may have remained uninfected during the course of the entire experiment or (2) the host may have become infected at a later time, when exposed to infective mites coming from other successfully infected birds sharing the same enclosure.

Data from the first 100 days of the aviary experiments undertaken in 1992 and 1993 reveal that the success of initial exposure of Gouldian Finches to *S. tracheacolum* mites was 55 to 60%. In 1992, 20 birds died during the first 100 days following initial exposure. Only 11 of these birds were subsequently found to have retained infections. Over the following 259 days, the remainder of the 'infected' birds (n = 24) were examined and all were confirmed by dissection to be infected. A similar trend occurred during the 1993 experiment. Six of 10 birds examined during the first 100 days of 'infection' were found to be infected. The remainder of the 'infected' birds (n = 16) were examined over the following 636 days and were all confirmed to be infected. The peculiarity of these data suggest that, birds failing to be successfully infected at the initial exposure were subsequently infected within the following 100 days by exposure to infective mites produced by birds that were successfully infected at the time of initial exposure.

Female mites comprise the bulk of adult *S. tracheacolum* infrapopulations (i.e. approximately 97%). Male mites are therefore of little numerical significance in the assessment of infrapopulation growth. In the absence of parasite mortality and emigration (via transmission), a doubling of infrapopulation size might be expected over a period of time that is related to the successive egg laying by mature female mites (each female mite can produce only a single egg at a time) and the hatching and subsequent development of daughter mites. The proposed scenarios of mite establishment following initial infection (i.e. survival and reproduction of both mites, one mite or no mites and the re exposure of uninfected birds within the first 100 days following experimental infection) may explain the infrapopulation data pattern of Figures 3.2B and C. The interpretation of slow and rapid growth phases may, in reality, represent data points on an exponential growth curve, superimposed by variations in the timing and size of initial infection. A model of *S. tracheacolum* infrapopulation growth is further developed in Chapter 10: Population Dynamics Of The Host.

The complication produced by variation in the success rate of initial exposure to infection could be alleviated in future studies by some changes to the experimental design. Each host could be exposed to a single infective stage, directly transferred from the nasal cavity or upper trachea of an infected host. Each host could then be held in isolation to eliminate the potential for cross-infection. Thus, all subsequent infrapopulations could be assumed to have established from a single mite of known reproductive condition. The use of control birds would remain a necessity to account for the potential of pre-existing *S. tracheacolum* infections. The complete absence of mites in experimentally infected birds at subsequent examination would indicate a failure of the infective stage to have established.

Studies of the life history and biology of transmission of *S. tracheacolum* were concurrent with the study of infrapopulation biology. Furthermore, the aviary experiment was designed to return data on a range of aspects of the parasite-host relationship, not least being an assessment of the mortality

and fecundity of captive Gouldian Finch populations in the presence and absence of infection. Further investigation focusing on the infrapopulation biology of this parasite would warrant isolation studies.

Control birds, used in the aviary experiments of 1992 and 1993, were all subsequently confirmed to be free of infection. Although all birds were purchased from an aviculturist who claimed *S. tracheacolum* had not been diagnosed in his bird stock for more than 25 years, acaricide drugs were administered to all birds prior to their inclusion in the aviary experiments. Given the large number of birds involved in these aviary experiments and the known variability in the efficacy of the acaricide treatment being used (see Chapter 9: Drug Treatment) the author considers that all birds used in the aviary experiments were uninfected at the time their arrival at the laboratory of the University of Tasmania.

3.4.2 The influence of host factors on the establishment and growth of *S. tracheacolum* infrapopulations

Host genetics is a potential influence on establishment and infrapopulation growth in macroparasites. This is supported by numerous field and laboratory based experimental studies. For example, resistance to the cestode *Hymenolepis citelli* in the deermouse *Peromyscus maniculatus* is determined by a single locus that controls susceptibility or resistance. In the wild 25% of deermice are heavily infected reflecting this simple control on susceptibility (Wasson *et al.*, 1974). In other experiments, susceptibility has been found to be under polygenic control. Studies on trematode-mollusc relationships indicate that parasites may adapt to the local conditions of host populations and cross-infection experiments reveal that the parasites are most infective to host populations from which they originate. Other studies, also on trematode-mollusc relationships, suggest that the opposite may also occur, that the parasites are most infective to host populations other than those from which they originate. Resistant genes may accumulate in heavily parasitised host populations and experimental cross-infections reveal the parasites to be most infective to other host populations (Dobson & Merenlender, 1991).

Any genetic variability in the susceptibility of hosts in the present study remains unknown. Furthermore, important variations in the size and timing of initial infection would make attempts at determining the role of host genetic differences, as evidenced by obvious phenotypic differences such as head colour, in susceptibility to infection, difficult to identify.

Another potential influence on parasite infrapopulation growth is the age of the host. To some extent this may relate to a host's history of exposure to a parasite and may not be an important factor in the present study. Birds were purchased from the same avicultural breeder, though the origins of his breeding stock were not known. All birds used in the 1992 experiment were first year

birds that had not previously bred. Forty of 48 birds used in the 1993 aviary experiment were also first year birds that had not previously bred. However, the remainder were second year birds that had successfully bred during the previous breeding season (see Experimental Design: Section 3, P 63).

3.4.3 The relationship between the number of mites found dead in the respiratory system of the host and the mortality rate of *S. tracheacolum*

Significant differences were found in the mean percentage of dead mites within infrapopulations, among groups of the 'aviary dataset'. Furthermore, a high positive correlation was found between the percentage of mites found dead and the duration of infection. If the frequency or the proportion of mites found dead within the respiratory system can provide an index of mortality rate, then the results from the present study may have important implications for understanding the mechanisms that regulate *S. tracheacolum* infrapopulation growth.

When a mite dies within the respiratory system of the host, whether it dies naturally or is killed as a result of host immune responses, it is either removed from the respiratory system by mechanical means (such a the production of tenacious mucus and coughing), or it remains within the respiratory system. If the mite is not removed, and this is probably the usual situation in the airsacs, it is surrounded and broken down by host histolytic tissue. Little is known of the rate at which these mites are broken down. However, data from acaricidal drug treatment experiments (see Chapter 9: Drug Treatment) would indicate that adult mites remain readily recognisable, within the host, for at least 14 days following their death. Adult females are the most robust of all stages and presumably would be recognisable for the longest period of time following death.

A further consideration in the use of the proportion of dead mites as an indicator of relative mortality is the distribution of dead mites within the host. A significantly higher proportion of mites were found dead in the lower respiratory system (i.e. airsacs and lungs) than in the upper respiratory system (i.e. syrinx, trachea, buccal cavity and nasal cavity) (see Chapter 2: Section 2.5, Mortality). Mites dying in the upper respiratory passages are likely to be rapidly removed by host responses. The proportion of mites found dead in this locality may, in fact, more closely reflect actual mortality than the proportion in the lower respiratory system where they may accumulate over several weeks. Nonetheless, it is likely that significant changes in the proportions of dead mites in hosts infected for periods of up to two years are likely to reflect significant changes in the real mortality rates of those infrapopulations.

3.4.4 Host cues and the timing of transmission

No significant changes were detected in the proportion of immature mites (i.e. larvae, protonymphs, deutonymphs or pooled data for all immature stages) within live infrapopulations among groups of

the 'aviary dataset' or among the '3, 6, 9 and 12 months samples'. Furthermore, there was a poor correlation between the proportion of immature mites within live infrapopulations and the duration of the infection. These results would be expected from infrapopulations containing continuously reproducing females with overlapping generations. There was no evidence from the production of immatures to suspect that *S. tracheacolum* reproduction was in any way cued to the duration of infection or, more importantly, the life cycle of the host. Immature mites were commonly found in both male and female hosts of both breeding and non-breeding condition, juvenile hosts and immature hosts.

On the other hand, a significant difference was detected in the proportion of the female infrapopulation found in the host's nasal cavity among groups of the 'aviary dataset'. The proportion of females found within the host's nasal cavity, was highest during the period of greatest positive population growth (i.e. between 90 and 179 days following initial infection). Although the highest proportions of females within the nasal cavity occurred during the host's reproductive period, this was most probably coincidental with the timing of initial infection. Both juvenile and immature birds, that were naturally infected from their parents during the aviary experiment, produced large numbers of infective mites.

3.4.5 Intensity-dependent processes and the growth of *S. tracheacolum* infrapopulations

There is very little evidence to suggest a role for intensity-dependent processes in the control of *S. tracheacolum* infrapopulation growth in captive Gouldian Finches. There were no differences in the proportion of immatures or the proportion of gravid females in live infrapopulations among the '3, 6, 9 and 12 months samples' or the 'aviary dataset' and there was a poor correlation between the proportions of immature or gravid female mites and the duration of infection.

Of some interest is the strong positive correlation between the proportion of mites found dead and the duration of infection. There was an increase in the proportion of mites found dead with increase in the size of the infrapopulation. However, the number of mites found dead continued to increase with subsequent decline in the size of the infrapopulations. The latter is not consistent with a intensity-dependence process but rather with host immune responses.

3.4.6 Host immune responses and the duration of infection

The data overall support the proposition that *S. tracheacolum* growth is ultimately under the control of host immune responses. The data suggest that host responses may be elicited at very high infrapopulation levels and once they are elicited they continue to influence infrapopulation growth. As a result, birds surviving the period of heavy infection appeared able to thereafter control the size of the infrapopulation. Composite infrapopulation data suggest that there is a trend for decline in the size of the infrapopulation between 6 months and 2 years following initial infection.

3.4.7 Conclusion

Results from the present study indicate that captive reared Gouldian Finches are highly susceptible to infection by *S. tracheacolum*.

Interpretation of composite data suggests that, following initial infection, infrapopulation growth increases at an exponential rate. This rate continues until extremely large infrapopulations are reached (i.e. up to 370 mites within 155 days, from a founding infection of ≤ 2 mites). In birds surviving this period of extremely heavy infection, there is a subsequent decline in the size of the infrapopulation over the following 18 months.

The infrapopulation data also support the proposition that *S. tracheacolum* infrapopulation growth in under the control of host immune responses. These responses may be elicited by heavy infection. Host responses may influence the mortality rate of mites and once elicited the response may be maintained at the same level, unaffected by subsequent declining infrapopulation levels.

PART II THE HOST

Chapter 4. PATHOLOGY

4.1 INTRODUCTION

The pathological changes associated with *S. tracheacolum* infection has been well described for the captive Canary and Gouldian Finch (e.g. Gouldian Finch: Cumming, 1959; Murray, 1966; Riffkin & McCausland, 1972; Jolivet, 1975; Losson *et al.*, 1979. Canary: Stephan *et al.*, 1950; Baker *et al.*, 1956; Fain & Carpentier, 1958; Menchaca, 1976). Only a limited number of reports describe the pathological effects of infection in other captive species (e.g. Budgerigar: Mathey, 1967). The clinical signs of infection and the pathological changes caused by *S. tracheacolum,* as well as that for other respiratory tract inhabiting mites (e.g. Airsac mite *Kytodites nudus*) has been reviewed or summarised in several veterinary texts (e.g. Arnall & Keymer, 1975; Greve, 1978; Altman, 1979; Harrigan, 1981; Keymer, 1982). The description of *S. tracheacolum* infection in the Gouldian Finch (Tidemann *et al.*, 1992) is the only report of disease associated with this parasite in a wild host species.

Reports of the gross pathology associated with *S. tracheacolum* infection in Gouldian Finches are basically similar. Excessive tenacious mucus is usually found within the nasal cavity, trachea, syrinx and the primary bronchi. This is occasionally blood stained. Tracheitis is present varying from a slight injection of blood vessels to an acutely reddened trachea with excessive amounts of tenacious mucus (e.g. Murray, 1966; Stephan *et al.*, 1950; Baker *et al.* 1956). Riffkin and McCausland (1972) noted an association of *S. tracheacolum* infection with a low grade tracheitis in all infected birds, together with bronchial pneumonia in some cases. Lesions, together with accumulations of mucus and mites, are sometimes responsible for partial occlusion of the trachea and bronchi.

In moderate and light infections, lesions in the lungs are generally few. However, in heavy infections the lungs can become severely congested (Murray, 1966). Pneumonia may be present involving both lungs, a single lung or only a section of a lung (Stephan *et al.*, 1950). Indications of recent haemorrhage in the lung are frequently associated with the presence of mites in the smaller bronchi as well as small foci of bronchial pneumonia (Baker *et al.* 1956)

The airsacs show clear signs of the presence of infection. Thickening of the airsac membranes (airsacculitis) is commonplace and becomes particularly noticeable in the posterior airsacs. Airsacculitis varies from a slight reddening of the membrane to a chronic inflammation. Thick yellow pus is formed in the airsacs, particularly the posterior airsacs, which often contain mites in various stages of disintegration.

Riffkin and McCausland (1972) described the histopathological changes in Gouldian Finches dying from *S. tracheacolum* infection. They found that the carcases of the three infected birds examined were in good nutritional condition. In the first two birds (with *S. tracheacolum* infrapopulations of >50 mites and 96 mites respectively), the trachea showed fibrous thickening and plasma cell infiltration of segments of the lamina propria. The epithelium covering these segments was cuboidal while that covering unaffected segments was pseudostratified and columnar. In the third bird (with an *S. tracheacolum* infrapopulation of 12 mites) the tracheal mucosa was hypertrophic, forming flattened tongues which protruded into the lumen. They found that in the tertiary bronchioles, some of which contained mites, of all the infected birds, there was hypertrophy of the epithelium. Parenchyma around these bronchioles was largely replaced by mesenchyme which was infiltrated with large numbers of plasma cells, lymphocytes and a few heterophils. Again, in the third bird they found that most tertiary bronchioles had multilayered hyperplastic epithelium, which sometimes enclosed mite fragments, and severely reduced the luminal diameter. The primary bronchi had similar mucosal lesions, mucosal oedema, marked peri-bronchial lymphocytic infiltration and muscular hypertrophy. In the nasal cavity, squamous metaplasia was found adjacent to a mite.

All previous descriptions of the histopathological changes associated with infection have been made on birds dying from *S. tracheacolum* or from birds showing severe clinical signs of infection. The duration of the infection was unknown. The present study aims to describe the pathological changes in captive reared Gouldian Finches where the infection history of hosts is known and where the clinical signs of infection have been monitored over the course of the infection.

4.2 METHODS

The experimental procedure for the establishment of infected and uninfected Gouldian Finches is set out in the Experimental Design: 3 Experimental procedure, P62. Groups of experimentally infected birds and groups of birds maintained free of infection were housed under identical conditions but in separate aviary enclosures.

At intervals of 3, 6, 9 and 12 months following initial infection, samples of infected and uninfected birds were removed, euthanased and dissected. The 3 months sample comprised 5 infected (4M; 1F) and 5 uninfected birds (4M; 1F), the 6 months sample comprised 6 infected (3M; 3F) and 5 uninfected birds (2M; 3F), the 9 months sample comprised 3 infected (2M; 1F) and 3 uninfected birds (2M; 1F) and the 12 months sample comprised 3 infected (2M; 1F) and 5 uninfected birds (3M; 2F).

During the period leading up to euthanasia, records were kept on indicators of the health of birds, particularly the presence and strength of clinical signs characteristic of disease of the respiratory system (e.g. dyspnoea, sneezing, coughing, laboured breathing, and nasal and ocular discharge).

Blood samples were taken prior to the administration of a lethal anaesthetic injection (the analysis of these is presented in Chapter 5: Haematology). Birds were subsequently dissected and examined for evidence of infection by *S. tracheacolum.*

Portions of the respiratory system tissues (i.e. trachea, nasal tissue, posterior and thoracic airsac membranes, syrinx and lung), liver, kidney, spleen, intestine and gizzard were collected into a buffered solution of 10% formalin. Fixed tissues were stored and later cut in 5μm sections and stained by haematoxylin and eosin for future histopathological examination.

4.3 PATHOLOGY

4.3.1 Case reports and necropsy findings

Descriptions of the gross lesions associated with *S. tracheacolum* infection in Gouldian Finches are shown in Table 4.1 (3 months infected and control birds), Table 4.2 (6 months infected and control birds), Table 4.3 (9 months infected and control birds and Table 4.4 (12 months infected and control birds).

Plates 4.1 and 4.2 show the typical gross pathology associated with *S. tracheacolum* infection over a period of 6 months following initial infection. Plate 4.1 shows a ventral view of the viscera of a Gouldian Finch that was maintained free of infection for a period of 6 months (i.e. control bird from the 6 months sample). Plate 4.1A shows the typical clarity and fragility of airsac membranes of the anterior, thoracic and posterior regions. Plate 4.1B shows the membrane and the internal surfaces of a posterior airsac under a higher magnification. Plate 4.2A shows a ventral view of the lower respiratory system of a Gouldian Finch, 3 months after initial infection (carrying an infrapopulation of 30 mites). Of particular note is the discolouration of the airsac membranes, the occurrence of mites throughout the airsacs and a thickening of the anterior thoracic airsac (mid photo). Plate 4.2B shows a ventral view of the visceral region of a Gouldian Finch, 6 months after initial infection (carrying an infrapopulation of 273 mites). The advanced condition of the disease process is obvious. All airsacs are thickened and all contain large numbers of mites. Of particular note is the large number of mites in the interclavicular airsac adjacent to the syrinx. The thoracic airsacs have become filled with pus. Likewise, the posterior airsacs contain large amounts of pus. A white substance is present on the ventral membrane of the pericardial sac. This substance was found on mesentery throughout the thoracic region of the host and was often associated with the presence of mites outside the airsacs (i.e. freely moving between the major organs of the host). Dead mites were often associated with the presence of pus in the posterior and thoracic airsacs.

Plate 4.1 Respiratory surfaces of uninfected Gouldian Finches *Erythrura gouldiae*.

A. Ventral thoracic region of a captive reared Gouldian Finch maintained free of *S. tracheacolum* infection.

B. Airsac membrane of captive reared a Gouldian Finch maintained free of *S. tracheacolum* infection.

(Note the transparent and fragile nature of the airsac membranes of the anterior, thoracic and posterior regions)

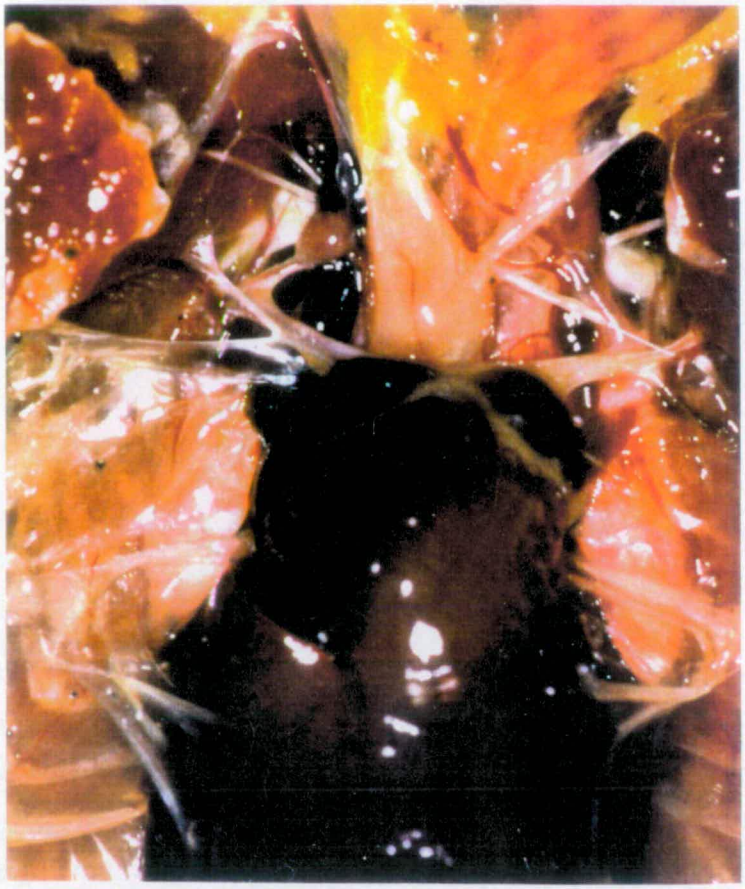
A

B

Plate 4.2 Respiratory surfaces of Gouldian Finches *Erythrura gouldiae* infected by *Sternostoma tracheacolum*.

A. Ventral thoracic region of captive reared Gouldian Finch infected by *S. tracheacolum* for a period of 3 months. Note the discolouration of the airsac membranes, the presence of mites on the airsac membranes and thickening of the anterior thoracic airsac in the mid photo.

B. Ventral thoracic region of captive reared Gouldian Finch infected by *S. tracheacolum* for a period of 6 months. The advanced condition of the pathological change is obvious. All airsacs are thickened and discoloured and contain large numbers of mites (number of mites in the infection = 273). Of particular note is the large number of mites in the interclavicular airsac adjacent to the syrinx. The thoracic airsacs have become filled with pus. Likewise, the posterior airsacs contain large amounts of pus.



A

B

Table 4.1 Gross lesions of captive Gouldian Finches *E. gouldiae* infected with *S. tracheacolum* and Gouldian Finches maintained free of infection for 3 months during the 1992 aviary experiment.

ID	Host Sex	Host weight	Number of mites	Number of days infected	External description	Internal description
Infected birds						
125	M	14.4	13	102	General appearance: alert; Plumage: perfect, orange head; Respiratory symptoms: slight wheeze; Moult: no; Nares: dry.	Nasal cavity: full of clear tenacious mucus, (mites 2); Buccal cavity: clear, (mites 2); Trachea: clear, (mites 0); Syrinx: clear, (mites 0); Lungs: normal appearance (mites 4); Airsacs: clear, (mites 5).
130	M	16.1	168	100	General appearance: alert, healthy; Plumage: perfect, orange head; Respiratory symptoms: slight click, slight wheeze; Moult: no; Nares: clean, dry.	Nasal cavity: much bloody mucus, (mites 16); Buccal cavity: clear, (mites 1); Trachea: much clear mucus, all mites surrounded by mucus, (mites 46); Syrinx: much mucus, (mites 13); Lungs: bloody during dissection, (mites 14); Airsacs: white powdery substance around anterior and thoracic airsacs, all airsacs containing yellow thickened pus, thickened airsac membrane, most thickening and pus in the posterior airsacs, (mites 78).
131	M	20.1	31	105	General appearance: alert; Plumage: perfect, orange head; Respiratory symptoms: slight wheeze; Moult: no; Nares; clean and dry.	Nasal cavity: some clear tenacious mucus, (mites 2); Trachea: clear, (mites 1); Syrinx: clear, (mites 0); Lungs: normal appearance, (mites 8); Airsacs: clear, (mites 20). Other: much fat throughout
134	F	17.8	215	107	General appearance: alert; Plumage: perfect, black head; Respiratory symptoms: slight wheeze; Moult: no; Nares: clean and dry, small lesion near left naris.	Nasal cavity: slight clear mucus, (mites 2); Buccal cavity: clear (mites 1) Trachea: much clear tenacious mucus, (mites 40); Syrinx: much clear tenacious mucus, (mites 11); Bronchi: (mites 1) Lungs: colour good, (mites 48); Airsacs containing yellow pus, (mites 112).
135	M	14.5	30	104	General appearance: slightly lethargic, slightly puffed up; Plumage: poor, some feather loss below lower mandible, orange head; Respiratory symptoms: slight wheeze; Moult: no; Nares: dry and clear; Vent: soiled.	Nasal cavity clear: (mites 0); Trachea: upper clear, some clear tenacious mucus in the lower half (mites 8); Syrinx: some tenacious mucus (mites 4); Bronchi: some clear tenacious mucus (mites 1); Lungs: clear, (mites 10); Airsacs: clear, (mites 7).

Table 4.1 Continued, Gross lesions of captive Gouldian Finches *E. gouldiae* infected with *S. tracheacolum* and Gouldian Finches maintained free of infection for 3 months during the 1992 aviary experiment.

ID	Host Sex	Host weight	Number of mites	Number of days infected	External description	Internal description
Control birds (Uninfected)						
1018	M	14.4	-	103	General appearance: bright and alert; Plumage: perfect, orange head; Respiratory symptoms: nil; Moult: no; Nares: clean and dry.	Nasal cavity: clear; Trachea: clear; Syrinx: clear; Lungs: normal appearance; Airsacs: clear.
1019	M	14.5	-	99	General appearance: alert; Plumage: perfect, orange head; Respiratory symptoms: nil; Moult: no; Nares: clean and dry.	Nasal cavity: clear; Trachea: clear; Syrinx: clear; Lungs: normal appearance; Airsacs: clear.
1020	M	18.9	-	109	General appearance: alert; Plumage: perfect, orange head; Respiratory symptoms: nil; Moult: nil; Nares: dry, clean.	Nasal cavity: clear; Trachea: clear; Syrinx: clear; Lungs: normal appearance; Airsacs: clear.
1021	F	14.2	-	104	General appearance: alert; Plumage: perfect, black head; Respiratory symptoms: nil; Moult: no; Nares: clear and dry.	Nasal cavity: clear; Trachea: clear: Syrinx: clear; Lungs: normal appearance; Airsacs: clear.
1022	M	15.5	-	106	General appearance: alert; Plumage: perfect, black head; Respiratory symptoms: nil; Moult: no; Nares: clear and dry.	Nasal cavity: clear; Trachea: clear: Syrinx: clear; Lungs: normal appearance; Airsacs: clear.

Table 4.2 Gross lesions of captive Gouldian Finches *E. gouldiae* infected with *S. tracheacolum* and Gouldian Finches maintained free of infection for 6 months during the 1992 aviary experiment.

ID	Host Sex	Host weight	Number of mites	Number of days infected	External description	Internal description
Infected birds						
160	F	14.5	257	172	General appearance: alert; Plumage: missing plumage on forehead, lores and chin, black head; Respiratory symptoms: wheeze; Moult: no; Nares: clear and dry.	Nasal cavity: clear, (mites 0); Buccal cavity: clear, (mites 3); Trachea: much clear tenacious mucus, also bloody mucus and blood patches, (mites 28); Syrinx: much tenacious mucus, (mites 3); Bronchi: much tenacious mucus; Lungs: bloodied patches, (mites 111); Airsacs: much thick white substance and thick yellow pus, (mites 109); Body cavity: (mites 3).
161	F	16.1	273	173	General appearance: alert; Plumage: perfect, black head; Respiratory symptoms: heavy wheeze; Moult: no; Nares: clear and dry.	Nasal cavity: much tenacious mucus, (mites 12); Trachea: full of tenacious mucus, (mites 79): Syrinx: full of tenacious mucus, (mites 4); Bronchi: full of tenacious mucus (mites 1); Lungs: red patches, (mites 54); Airsacs: white pussy lumps in anterior, thoracic and posterior airsacs, posterior airsacs half full of thick pus (mites 104); Body cavity: (mites 6).
162	M	16.3	185	175	General appearance: alert; Plumage: perfect, red head; Respiratory symptoms: heavy wheeze; Moult: no; Nares: clear and dry; Bill: brown; Feet: missing hind caws.	Nasal cavity: much tenacious mucus, (mites 3); Buccal cavity: clear, (mites 3); Trachea: much tenacious mucus, (mites 79): Syrinx: much tenacious mucus, (mites 8); Bronchi: much tenacious mucus, (mites 1); Lungs: reddened haemorrhaged spots, (mites 40); Airsacs: clouded and wet, (mites 46); Body cavity: (mites 5).
163	M	19.9	178	176	General appearance: alert; Plumage: perfect, orange head; Respiratory symptoms: heavy wheeze; Moult: no; Nares: clear and dry.	Nasal cavity: bloody tenacious mucus, (mites 27); Trachea: much tenacious mucus, (mites 35): Syrinx: much tenacious mucus, (mites 3); Bronchi: much tenacious mucus (mites 6); Lungs: red bloody patches, (mites 42); Airsacs: yellow pus section and whitened sections, (mites 64). Body cavity: (mites 1).

Table 4.2 Continued, Gross lesions of captive Gouldian Finches *E. gouldiae* infected with *S. tracheacolum* and Gouldian Finches maintained free of infection for 6 months during the 1992 aviary experiment.

ID	Host Sex	Host weight	Number of mites	Number of days infected	External description	Internal description
Infected birds						
164	F	13.4	224	159	General appearance: some lethargy; Plumage: good, black head; Respiratory symptoms: wheeze, bubbling; Moult: no; Nares: clear and dry; Vent: soiled and wet.	Nasal cavity: much mucus, (mites 4); Trachea: milky appearance, much clear tenacious mucus, huge congestion of mites and mucus in lower trachea, (mites 50): Syrinx: highly congested with mites and mucus, (mites 10); Bronchi (mites 6) right branch full of tenacious mucus; Lungs: reddened and whitened sections, (mites 97); Airsacs: thickened, yellow and white pus throughout, (mites 57).
165	M	14.8	216	176	General appearance: alert; Plumage: perfect, orange head; Respiratory symptoms: heavy wheeze; Moult: no; Nares: clear and dry.	Nasal cavity: much tenacious mucus, (mites 6); Buccal cavity: clear, (mites 5); Trachea: much tenacious mucus, (mites 71): Syrinx: much tenacious mucus, (mites 10); Bronchi (mites 3); Lungs: haemorrhaged in several localities, (mites 78); Airsacs: posterior airsacs containing large amounts of pus, (mites 40); Body cavity: (mites 3).
Control birds (uninfected)						
1023	M	16.3	-	172	General appearance: alert; Plumage: perfect, orange head; Respiratory symptoms: nil; Moult: no; Nares: clear and dry.	Nasal cavity: clear; Trachea: clear: Syrinx: clear; Lungs: normal appearance; Airsacs: clear.
1024	F	17.5	-	176	General appearance: alert; Plumage: perfect, black head; Respiratory symptoms: nil; Moult: no; Nares: clear and dry.	Nasal cavity: clear; Trachea: clear: Syrinx: clear; Lungs: normal appearance; Airsacs: clear.
1025	F	16.3	-	173	General appearance: alert; Plumage: missing plumage on face, orange head; Respiratory symptoms: nil; Moult: no; Nares: clear and dry..	Nasal cavity: clear; Trachea: clear: Syrinx: clear; Lungs: normal appearance; Airsacs: clear.
1026	M	13.0	-	175	General appearance: alert; Plumage: perfect, black head; Respiratory symptoms: nil; Moult: no; Nares: clear and dry.	Nasal cavity: clear; Trachea: clear: Syrinx: clear; Lungs: normal appearance; Airsacs: clear.
1027	F	15.5	-	173	General appearance: alert; Plumage: perfect, orange head; Respiratory symptoms: nil; Moult: no; Nares: clear and dry.	Nasal cavity: clear; Trachea: clear: Syrinx: clear; Lungs: normal appearance; Airsacs: clear.

Table 4.3 Gross lesions of captive Gouldian Finches *E. gouldiae* infected with *S. tracheacolum* and Gouldian Finches maintained free of infection for 9 months during the 1993 aviary experiment.

ID	Host Sex	Host weight	Number of mites	Number of days infected	External description	Internal description
Infected birds						
405	M	14.4	8	279	General appearance: alert; Plumage: perfect, black head; Respiratory symptoms: wheeze; Moult: yes; Nares: blocked with mucus.	Nasal cavity: dry, (mites 0); Trachea: clear, (mites 1): Syrinx: some mucus, (mites 0); Lungs: normal appearance, (mites 2); Airsacs: posterior airsacs heavily thickened, leathery, other airsacs slightly thickened (mites 5).
406	M	16.3	35	279	General appearance: alert; Plumage: perfect, orange head; Respiratory symptoms: wheeze; Moult: yes; Nares: clear and dry.	Nasal cavity: clear, (mites 0); Trachea: some mucus, (mites 16): Syrinx: some mucus, (mites 5), Lung: normal appearance, (mites 6); Airsacs: posterior airsacs heavily thickened, (mites 8).
407	F	13.8	73	279	General appearance: alert; Plumage: perfect, black head; Respiratory symptoms: nil; Moult: yes; Nares: clear and dry.	Nasal cavity: (mites 2); Trachea: filled with tenacious mucus, (mites 47): Syrinx: filled with tenacious mucus, (mites 1); Lungs: (mites 5); Airsacs: all airsacs thickened, particularly the posterior airsacs, much white powdery substance (mites 18).
Control birds (uninfected)						
2001	M	17.9	-	279	General appearance: alert; Plumage: perfect, orange head; Respiratory symptoms: nil; Moult: yes; Nares: clear and dry.	Nasal cavity: clear; Trachea: clear: Syrinx: clear; Lungs: normal appearance; Airsacs: clear.
2002	F	15.9	-	279	General appearance: alert; Plumage: perfect, black head; Respiratory symptoms: nil; Moult: yes; Nares: clear and dry.	Nasal cavity: clear; Trachea: clear: Syrinx: clear; Lungs: normal appearance; Airsacs: clear.
2003	M	16.1	-	279	General appearance: alert; Plumage: perfect, black head; Respiratory symptoms: nil; Moult: yes; Nares: clear and dry.	Nasal cavity: clear; Trachea: clear: Syrinx: clear; Lungs: normal appearance; Airsacs: clear.

Table 4.4 Gross lesions of captive Gouldian Finches *E. gouldiae* infected with *S. tracheacolum* and Gouldian Finches maintained free of infection for 12 months during the 1993 aviary experiment.

ID	Host Sex	Host weight	Number of mites	Number of days infected	External description	Internal description
Infected birds						
412	M	22.5	31	351	General appearance: alert; Plumage: perfect, orange head; Respiratory symptoms: slight wheeze; Moult: no; Nares: clear.	Nasal cavity: clear, (mites 0); Trachea: much tenacious mucus, (mites 10): Syrinx: much tenacious mucus, (mites 5); Lungs: normal appearance, (mites 5); Airsacs: posterior airsacs very thickened with viscous pus in dorsal portion, (mites 9).
413	M	19.6	22	351	General appearance: alert; Plumage: perfect, red head; Respiratory symptoms: slight wheeze; Moult: no; Nares: clear.	Nasal cavity: clear, (mites 0); Trachea: much tenacious mucus and blood spots, (mites 4): Syrinx: much tenacious mucus, (mites 2); Lungs: normal appearance, (mites 12); Airsacs: posterior airsacs thickened, yellow, (mites 4).
414	F	15.8	192	351	General appearance: alert; Plumage: perfect, orange head; Respiratory symptoms: slight wheeze; Moult: no; Nares: clear.	Nasal cavity: much tenacious mucus, (mites 9); Buccal cavity: much tenacious mucus around the palatine cleft, (mites 3); Trachea: much tenacious mucus, (mites 30): Syrinx: much tenacious mucus, (mites 3); Lungs: normal appearance, (mites 45); Airsacs: posterior airsacs very heavily thickened, a white powdery substance throughout the airsacs (mites 97).
Control birds (Uninfected)						
415	F	23.9	-	352	General appearance: alert; Plumage: perfect, black head; Respiratory symptoms: nil; Moult: no; Nares: clear.	Nasal cavity: clear; Trachea: clear: Syrinx: clear; Lungs: normal appearance; Airsacs: clear.
416	M	18.3	-	352	General appearance: alert; Plumage: perfect, red head; Respiratory symptoms: nil; Moult: no; Nares: clear.	Nasal cavity: clear; Trachea: clear: Syrinx: clear; Lungs: normal appearance; Airsacs: clear.
417	M	17.6	-	352	General appearance: alert; Plumage: perfect, red head; Respiratory symptoms: nil; Moult: no; Nares: clear.	Nasal cavity: clear; Trachea: clear: Syrinx: clear; Lungs: normal appearance; Airsacs: clear.
418	M	16.7	-	352	General appearance: alert; Plumage: perfect, black head; Respiratory symptoms: nil; Moult: no; Nares: clear.	Nasal cavity: clear; Trachea: clear: Syrinx: clear; Lungs: normal appearance; Airsacs: clear.
419	F	17.5	-	352	General appearance: alert; Plumage: perfect, black head; Respiratory symptoms: nil; Moult: no; Nares: clear.	Nasal cavity: clear; Trachea: clear: Syrinx: clear; Lungs: normal appearance; Airsacs: clear.

4.3.2 Gross lesions and the duration of *S. tracheacolum* infection

At 3 months of infection there is considerable variation in the presence of gross lesions (Table 4.1). This reflects a similar variation in the intensity of infection. Large quantities of tenacious mucus occur in the syrinx, trachea and nasal cavity of infected birds. The airsac membranes of most birds are clear or translucent in appearance but in more heavily infected birds there is some thickening of the airsac membranes. The respiratory tissues of birds surviving 6 months of infection are quite similar in appearance (Table 4.2). Tenacious mucus occurs throughout the upper respiratory system and may be blood tinged. The lungs are unnaturally reddened and contain bloody patches. The airsac membranes vary in appearance from clouded and wet to heavily thickened, containing large quantities of pus. Some abdominal airsacs are almost filled with this purulent substance. After 9 months of infection, copious quantities of tenacious mucus remain in the upper respiratory system, the lungs are more normal in appearance but the airsac membranes remain heavily thickened (Table 4.3). The clinical picture of gross lesions after 12 months of infection remains similar to that of 9 months (Table 4.4).

4.3.3 Gross lesions and the intensity of *S. tracheacolum* infection

The intensity of infection does not correlate well with the presence of gross lesions. Small infections of short duration (measured in terms of the number of live or dead mites present) may be associated with little or no observable lesions while small infections of long duration (i.e. after 6 months) may be associated with the presence of considerable tenacious mucus, as well as heavily thickened and discoloured airsac membranes, a legacy from a history of heavy infection. In birds infected for more than 12 months (and up to 2 years) the infection may comprise only a few mites but the airsac membranes remain considerably thickened and yellow in colour (at least in the cases observed in the present study), particularly the posterior airsacs.

4.4 DISCUSSION

There is a recognisable pattern of gross pathological change with duration of infection. However, the number of mites found within an infection does not correlate with the sequence of lesions. The appearance of the respiratory tissues, particularly the state of the posterior airsacs provides a good index of the duration of infection.

Many of the birds dying of *S. tracheacolum* infection showed signs of secondary infection. Others showed occlusion of the syrinx and/ or the lower trachea by large agglomerations of mucus and mites and some showed haemorrhaged regions of the lungs. These factors may have contributed to the death of birds and all are associated with the presence of *S. tracheacolum* infection. The course of histopathological change associated with *S. tracheacolum* infection was not described as part of the present study but will be published elsewhere as part of a collaborative study.

Chapter 5. HAEMATOLOGY

5.1 INTRODUCTION

Haematology can provide a valuable contribution to the diagnosis of disease and the monitoring of disease processes in birds (Riddell, 1987; Campbell, 1988; Black, 1978). Routine analyses include tests that evaluate the erythrocytes such as haematocrit, total erythrocyte count, haemoglobin concentration and mean corpuscular values, tests that evaluate the leucocytes such as the total white blood cell count and differential leucocyte count, and tests that evaluate the thrombocytes and blood coagulation (Campbell, 1988).

Whereas the presence of microparasites such as viruses, bacteria and protozoa may often be indicated from quantitative changes in the haematological values it is less understood what changes take place in the presence of haematophagous macroparasites such as mites and ticks. Chapman and George (1991) in a study of the effects of blood-feeding ectoparasites on the growth and survival of Cliff Swallows *Hirundo pyrrhonota* (Vieillot), found that the concentration of haemoglobin in the blood of nestlings from colonies exposed to ectoparasites was significantly less than that from colonies treated with an acaricidal spray. Significantly higher haematocrit values were recorded from non-parasitised nestlings and furthermore, the blood of non-parasitised nestlings carried more erythrocytes and less of each leucocyte than parasitised nestlings. Chapman and George concluded that high densities of ectoparasites create changes in the blood composition of young Cliff Swallows, however, in the absence of an adequate information base on the blood-cellular systems of these birds they were unable to assess what these changes mean in relation to the physiological condition of the nestling hosts.

Tidemann, Calley and Burgoyne (in press) investigated blood smears of 8 wild finch species in Northern Australia including 81 Long-tailed Finches *Poephila acuticauda*, 30 Masked Finches *P. personata*, 19 Pictorella Mannikins *Heteromunia pectoralis*, 19 Chestnut-breasted Mannikins *Lonchura castaneothorax*, 141 Zebra Finches *Taeniopygia guttata*, 77 Star Finches *Neochmia ruficauda* (Gould), 411 Double-barred Finches *T. bichenovii* and 77 Gouldian Finches. As far as Gouldian Finches were concerned they did not find blood parasites (i.e. protozoa such as *Plasmodium, Leucocytzoon* and *Haemoproteus*, microfilariae or trypanosomes) and the haematological values for leucocytes and erythrocytes fell within the range recorded for other finch species examined. Tidemann and her associates provided mean values and standard deviations for leucocytes and thrombocytes in wild populations, and relative percentage estimates for erythrocytes in these species.

The aim of the present study is to investigate whether the presence, size or duration of *S. tracheacolum* infection produces a recognisable quantitative change in the haemoglobin and or the cellular elements of the host's blood. Comparisons are made between haematological values obtained from *S. tracheacolum* infected birds with corresponding values from uninfected birds.

5.2 METHODS

Blood samples were taken from captive reared Gouldian Finches, Canaries and Budgerigars. Canaries and Budgerigars were sampled at 6 months following experimental infection. Gouldian Finches were sampled at 3, 6, 9 and 12 months following experimental infection. Within 2 days of the collection of blood samples, birds were killed by a lethal anaesthetic injection and examined. Both infected and uninfected birds were maintained under similar housing and dietary conditions.

During the period leading up to euthanasia, records were kept on indicators of the health of birds, particularly the presence and strength of clinical signs characteristic of disease of the respiratory system (e.g. dyspnoea, sneezing, coughing, laboured breathing, and nasal and ocular discharge). These data and observations are described in Chapter 6: Behaviour/ Clinical Signs. Following death, samples of respiratory tissues (i.e. nasal tissue, trachea, syrinx, lung and airsacs), heart, liver, kidney, intestine, spleen and ovary or testes were fixed in 10% buffered formalin and stored for later histopathological study (Chapter 4: Pathology). Additional observations were made on the locality and abundance of mucus and purulent substances within the respiratory system at the time of host dissection. These data and observations are also described in Chapter 4.

5.2.1 Blood Collection

Quantities between 100 and 300 µl of blood were collected from the cutaneous ulnar vein of birds (between 0900 and 1200 hours). The vein was punctured with a 27 gauge syringe needle and as blood formed a drop on the skin it was collected into 100 µl capillary tubes and transferred to small tubes containing EDTA (an anticoagulant containing ethylenediaminetetraacetic). Samples were stored in a refrigerator at 4^{o} C prior to testing at the Haematology Unit at the Royal Hobart Hospital, Tasmania.

During the collection of the 3 months and 6 months samples, blood smears were prepared from fresh blood (i.e. not containing anticoagulant) using the standard two-slide wedge technique commonly used for preparing mammalian blood slides (Campbell, 1988).

5.2.2 Haematological parameters

Haemoglobin concentration was determined by Drabkin's method, as modified for nucleated red cells by Melrose (in press). Triton x100 was added to a commercial Drabkin's solution (Sigma Chemicals) to a concentration of 5%. Twenty microlitres of blood was added to 5 ml of the

modified Drabkin's, left to stand for 30 minutes, then centrifuged at 3500 rpm to remove nuclear and cell debris. The absorbence was measured by a spectrophotometer at 540 nm and the concentration of haemoglobin was obtained from a standard curve prepared by serial dilutions of a commercial cyanmethaemoglobin standard in modified Drabkin's.

Packed Cell Volume (PCV), Mean Corpuscular Values (MCV) and **Red Blood Cell counts (RBC)** were measured with a Coulter S Plus haematology analyser. **Mean Corpuscular Haemoglobin (MCH)** and the **Mean Corpuscular Haemoglobin Concentration (MCHC)** were calculated using the manual haemoglobin method because the Coulter haemoglobin reading is falsely high due to the turbidity induced by the nuclear debris (Melrose, in press).

The total **White Blood Cell Count** and **Thrombocyte** count were measured by diluting whole blood in Natt and Herrick's Solution (Natt & Herrick, 1952) and counting in a haemocytometer.

For differential leucocyte counts (**Heterophils, Lymphocytes, Monocytes, Eosinophils** and **Basophils**), blood films were stained in an Ames Haematek slide stainer using a 50-50 mixture of Leishman and Wright's stain buffered to pH 6.8 with a phosphate buffer. Leucocytes were classified under oil immersion using a x10 eyepiece and a x100 objective.

5.23 Statistical analysis

Descriptive statistics (means and standard deviations) and t-Tests were performed using Excel 4.0 (Microsoft Corporation, 1993). Two sample t-Tests, assuming equal variances, were used to compare mean haematological values of uninfected (control) and infected birds (experimentally infected with *S. tracheacolum*). Percentage data were arcsine transformed prior to analysis.

5.3 RESULTS

5. 3.1 Comparisons between *S. tracheacolum* infected and uninfected hosts

No signs of haematozoa were found in blood samples taken from infected and uninfected birds at 3 months and 6 months following experimental infection (confirmed at the International Reference Centre for Avian Haematozoa, Memorial University of Newfoundland).

The raw values for evaluation of Gouldian Finch erythrocytes, haemoglobin, leucocytes, leucocyte differential and thrombocytes are presented in Table 5.1 (for 3 months and 6 months samples only). The mean values for infected birds at 3 months and combined 3 months and 6 months samples were not significantly different from mean values obtained from uninfected birds at 3 months and combined 3 months and 6 months samples. Three birds showed distinctive signs of anaemia (indicated by an asterisk in Table 5.1). One uninfected female from the 3 months sample, and one uninfected male and one uninfected female from the 6 months sample had low haemoglobin values

Table 5.1 Haematological values, PCV, MCV, RBC, MCH and MCHC for captive reared Gouldian Finches uninfected and infected with *S. tracheacolum* for 3 and 6 months following experimental infection. Individuals considered to be anaemic are marked with an asterisk.

Identity	Sex	PCV (%)	RBC ($x10^{12}/l$)	MCV (fl)	MCH (pg)	MCHC (%)
3 months infected						
Z/LB 130	Male	52.2	4.19	135.8	35.5	28.6
Y/Z 125	Male	42.7	3.76	136.6	36.9	32.5
G/R 135	Male	44.0	3.80	123.2	36.3	31.3
Y/B 131	Male	58.0	4.49	131.8	35.1	27.7
Y/M 134	Female	56.6	4.68	135.5	35.4	29.3
Mean ± SD		**50.7±7.1**	**4.2±0.4**	**132.6±5.6**	**35.8±0.7**	**29.9±2.0**
Uninfected						
B/LG 1018	Male	57.5	5.12	120.4	31.6	28.2
Y/W 1022	Male	48.9	4.72	153.1	33.6	32.5
W/LG 1020	Male	48.8	4.86	137.1	33.3	33.1
LG/B 1019	Male	56.3	4.26	134.4	37.3	28.3
*B/P 1021	Female	41.5	3.82	109.5	32.9	30.3
Mean ± SD		**50.6±6.5**	**4.6±0.2**	**130.9±16.7**	**33.7±2.1**	**30.5±2.3**
t-Test 3 months infected vs 3 months uninfected		$t = 0.03$, $P = 0.98$	$t = 1.264$, $P = 0.24$	$t = 0.21$, $P = 0.84$	$t = 2.08$, $P = 0.07$	$t = 0.444$, $P = 0.67$
6 months Infected						
G/P 163	Male	43.6	4.15	145.5	36.6	36.6
LG/W 162	Male	48.3	4.05	131.7	31.1	30.9
Z/R 160	Female	58.8	4.56	128.7	33.1	26.6
Mean ± SD		**50.2±7.8**	**4.3±0.3**	**135.3±9.0**	**33.6±2.8**	**31.4±5.0**
Uninfected						
*R/LB 1026	Male	43.8	3.25	146.6	39.3	29.2
W/O 1028	Male	47.7	4.0	129.0	31.4	31.4
R/P 1023	Male	54.4	4.67	142.2	29.4	29.4
*W/W 1024	Female	36.2	3.25	142.2	39.4	35.5
R/Z 1027	Female	58.8	4.56	128.7	33.1	26.6
Mean ± SD		**48.2±8.9**	**3.9±0.7**	**137.7±8.3**	**34.5±4.6**	**30.4±3.3**
t-Test 3+6 months infected vs 3+6 months uninfected		$t = 0.33$, $P = 0.74$	$t = 0.16$, $P = 0.88$	$t = 0.14$, $P = 0.89$	$t = 0.64$, $P = 0.53$	$t = 0.01$, $P = 0.99$

Table 5.1 Continued, Haematological values, Haemoglobin, White Blood Cell Count, Thrombocytes and differential leucocyte counts for captive reared Gouldian Finches uninfected and infected with *S. tracheacolum* for 3 and 6 months following experimental infection.

Identity	Sex	Weight (grams)	Haemoglobin (g/dl)	White Blood Cell Count ($x10^9/l$)	Heterophils (%)	Lymphocytes (%)	Monocytes (%)	Eosinophils (%)	Basophils (%)	Thrombocytes ($x10^9/l$)	Number of mites present
3 months infected											
Z/LB 130	Male	16.1	14.9	21.2	43	43	6	4	4	27.8	168
Y/Z 125	Male	14.4	13.9	19.2	54	33	7	3	3	32.2	13
G/R 135	Male	14.5	13.8	19.0	48	39	5	4	4	19.6	30
Y/B 131	Male	20.1	16.1	22.5	42	40	9	6	3	17.0	31
Y/M 134	Female	17.8	16.6	23.3	42	46	6	4	2	31.5	215
Uninfected											
B/LG 1018	Male	14.4	16.2	19.2	50	33	8	6	3	28.8	0
Y/W 1022	Male	15.5	15.9	29.1	32	46	14	4	4	26.1	0
W/LG 1020	Male	18.9	16.2	30.8	26	52	18	2	2	29.9	0
LG/B 1019	Male	14.5	15.9	26.0	45	59	8	4	2	29.9	0
*B/P 1021	Female	14.2	12.6	19.8	45	37	9	3	6	34.4	
6 months infected											
G/P 163	Male	19.9	16.0	8.6	56	31	4	0	9	27.7	178
LG/W 162	Male	16.3	15.0	10.9	54	35	6	2	3	36.5	185
Z/R 160	Female	14.5	15.1	15.5	42	47	6	1	5	clumped	257
Uninfected											
*R/LB 1026	Male	13.0	12.8	11.9	36	53	7	0	4	25.2	0
W/O 1028	Male	15.9	15.0	19.7	48	41	3	2	6	36.9	0
R/P 1023	Male	16.3	16.0	10.2	32	49	10	0	7	30.5	0
*W/W 1024	Female	17.5	12.8	13.9	52	31	9	2	4	clumped	0
R/Z 1027	Female	15.5	15.1	15.5	42	47	6	1	5	clumped	0

Table 5.2 Haematological values, Haemoglobin, White Blood Cell Count, Thrombocytes and differential leucocyte counts for captive reared Gouldian Finches uninfected and infected with *S. tracheacolum* for 9 and 12 months following experimental infection.

Identity	Sex	Weight (grams)	Haemoglobin (g/dl)	White Blood Cell Count ($x10^9$/l)	Heterophils (%)	Lymphocytes (%)	Monocytes (%)	Eosinophils (%)	Basophils (%)	Thrombocytes ($x10^9$/l)	Number of mites present
9 months infected											
R/R 406	Male	16.3	19.5	24.1	51	41	4	2	2	32.0	35
LG/LG 405	Male	14.3	14.8	15.7	46	47	6	1	0	39.1	8
W/R 407	Female	14.4	19.2	17.3	64	32	1	2	1	43.0	73
Uninfected											
B/R 2001	Male	17.85	16.0	17.9	51	43	1	4	1	45.2	0
Y/R 2003	Male	16.1	17.9	25.9	77	19	3	1	0	34.9	0
O/O 2002	Female	15.9	15.8	27.7	81	18	1	0	0	33.9	0
12 months infected											
R/L 412	Male	22.5	16.8	22.0	24	75	0	0	1	24.7	31
B/B 413	Male	19.6	13.5	31.6	54	45	0	1	0	36.1	22
W/W 414	Female	15.8	13.3	24.1	41	59	0	0	0	34.0	192
Uninfected											
0/R 416	Male	18.3	15.8	25.9	64	33	2	1	0	26.4	0
B/R 417	Male	17.6	17.2	19.2	64	33	1	2	0	21.4	0
*B/R 418	Male	16.7	7.7	85.3	16	83	0	0	0	29.3	0
W/R 419	Female	17.5	15.1	27.7	45	55	0	0	0	19.8	0
Z/R 415	Female	23.9	16.1	33.4	67	30	1	2	0	27.0	0

Table 5.3 Descriptive statistics (mean ± SD) and comparisons between the mean haematological values of infected and uninfected captive reared Gouldian Finches.

Period of infection	Haemoglobin (g/dl)	White Blood Cell Count ($x10^9$/l)	Heterophils (%)	Lymphocytes (%)	Monocytes (%)	Eosinophils (%)	Basophils (%)	Thrombocytes ($x10^9$/l)
3 months infected	15.1±1.3	21.0±1.9	45.8±5.2	40.2±4.9	6.6±1.5	4.2±1.1	3.2±0.8	25.6±7.0
3 months uninfected	15.4±0.7	25.0±5.3	39.6±10.1	45.4±10.7	11.4±4.4	3.8±1.5	3.4±1.7	29.8±3.0
t-Test	t = -0.34, P = 0.75	t = -1.56, P = 0.16	t = 1.22, P = 0.26	t = -0.99, P = 0.35	t = -2.28, P = 0.05	t = 0.49, P = 0.64	t = -0.24, P = 0.82	t = -1.24, P = 0.25
6 months infected	15.4±0.6	11.7±3.5	50.7±7.5	37.7±8.3	5.3±1.2	1.5±0.7	5.7±3.1	32.1±6.2
6 months uninfected	14.3±1.5	14.2±3.7	42.0±8.2	44.2±8.6	7.0±2.7	1.7±0.6	5.2±1.3	30.9±5.9
t-Test 3+6 months infected vs 3+6 months uninfected	t = 0.52, P = 0.61	t = -1.56, P = 0.16	t = 1.85, P = 0.08	t = -1.48, P = 0.16	t = -1.97, P = 0.07	t = 0.51, P = 0.62	t = -0.19, P = 0.85	t = -0.96, P = 0.36
9 months infected	17.8±2.6	19.0±4.5	53.7±9.3	40.0±7.6	3.7±2.5	1.7±0.6	1.0±1.0	38.0±5.6
9 month uninfected	16.6±1.2	23.8±5.2	69.7±16.3	26.7±14.2	1.7±1.2	1.7±2.1	0.3±0.6	38.0±6.3

Table 5.3 Continued, Descriptive statistics (mean ± SD) and comparisons between the mean haematological values of infected and uninfected captive reared Gouldian Finches.

Period of infection	Haemoglobin (g/dl)	White Blood Cell Count ($x10^9$/l)	Heterophils (%)	Lymphocytes (%)	Monocytes (%)	Eosinophils (%)	Basophils (%)	Thrombocytes ($x10^9$/l)
12 months infected	14.5±2.0	25.9±5.0	39.7±15.0	59.7±15.0	0.0	0.3±0.6	0.3±0.6	31.6±6.1
12 months uninfected	14.4±3.8	38.3±26.8	51.2±21.5	46.8±22.6	0.8±0.8	1.0±1.0	0.0	24.8±4.0
t-Test 9+12 months infected vs 9+12 months uninfected	t = 0.61, P = 0.55	t = -1.13, P = 0.28	t = -1.17, P = 0.27	t = 1.03, P = 0.32	t = 0.72, P = 0.49	t = -0.38, P = 0.71	t = 1.69, P = 0.12	t = 1.26, P = 0.23
Total infected	15.6±1.9	19.6±5.9	47.21±9.6	43.8±11.7	4.3±2.9	2.31±1.8	2.6±2.4	30.9±7.4
Total uninfected	15.0±2.3	25.5±16.4	48.5±17.2	42.3±15.5	5.6±5.2	2.1±1.7	2.4±2.5	30.0±6.2
t-Test All infected vs All uninfected	t = 0.78, P = 0.44	t = -1.28, P = 0.21	t = -0.25, P = 0.80	t = 0.29, P = 0.77	t = -0.86, P = 0.40	t = 0.27, P = 0.78	t = 0.23, P = 0.82	t = 0.35, P = 0.73

Table 5.4 Haematological values for captive reared Budgerigars and Canaries uninfected and infected with *S. tracheacolum* for 6 months following experimental infection.

Identity	Sex	Mean Weight (grams)	Haemoglobin (g/dl)	White Blood Cell Count ($x10^9/l$)	Heterophils (%)	Lymphocytes (%)	Monocytes (%)	Eosinophils (%)	Basophils (%)	Thrombocytes ($x10^9/l$)	Mean number of mites present
Budgerigar infected	4 M, 1 F	52.1	17.3±0.6	17.2±3.9	42.2±5.4	43.6±5.4	2.6±1.1	5.6±3.7	1.0±1.0	30.0±4.2	0
Budgerigar uninfected	2 M, 3 F	65.2	14.7±2.0	15.0±2.9	43.6±15.1	47.0±15.5	2.4±0.6	5.8±3.6	1±0.7	25.5±7.0	0
Canary infected	4 M, 3 F	16.5	14.6±2.1	23.2±5.8	50.0±10.8	42.0±11.6	3.6±1.3	2.7±1.1	1.6±0.5	35.4±3.7	42
Canary uninfected	3 F	17.2	13.6±2.1	23.1±3.6	57.3±6.1	34.0±4.4	4.3±2.5	2.3±0.6	2.0±1.7	37.5±5.7	0

(i.e. 12.6, 12.8 and 12.8 g/dl respectively) and low PCV values (i.e. 41.5, 43.8 and 36.2% respectively).

Raw values for haemoglobin, leucocytes, leucocyte differential and thrombocytes for infected and uninfected birds at 9 months and 12 months samples are shown in Table 5.2 . Mean values and standard deviations for each of these samples is presented in Table 5.3.

The t-values from comparisons between the mean haematological values for 3 months infected versus 3 months uninfected, pooled 3 months and 6 months infected versus pooled 3 months and 6 months uninfected, pooled 9 months and 12 months infected versus pooled 9 months and 12 months uninfected samples, and all infected versus all uninfected birds are also shown in Table 5.3. Mean haematological values for all infected samples and pooled infected samples were not significantly different from their uninfected counterparts.

There were no significant trends between haematological values and the duration, or the size of *S. tracheacolum* infection. Raw data for each of these relationships are presented in Figures 5.1 (size of infection) and Figure 5.2 (duration of infection).

Table 5.4 shows means and standard deviations for haematological values of captive reared Budgerigars and Canaries examined at 6 months following experimental infection. No mites were found in Budgerigars (6 months following experimental infection) and there were no obvious signs that these birds had experienced *S. tracheacolum* infection during the previous 6 months. Nonetheless, the mean blood-cellular values for 'infected' birds were not statistically different (t-Tests, $P > 0.05$) from those of 'uninfected' birds. Canaries infected for 6 months have similar haematological values to Canaries kept free of infection over the same period.

5.3.2 Normal haematological values

As no significant differences could be found between mean haematological values of infected and uninfected birds, values obtained from *S. tracheacolum* infected birds are included in an assessment of 'normal' haematological values (mean values and standard deviations) of captive reared Gouldian Finches (Table 5.5). Excluded from the calculations are 4 uninfected birds that showed obvious signs of anaemia (indicated with an asterisk in Tables 5.1 and 5.2).

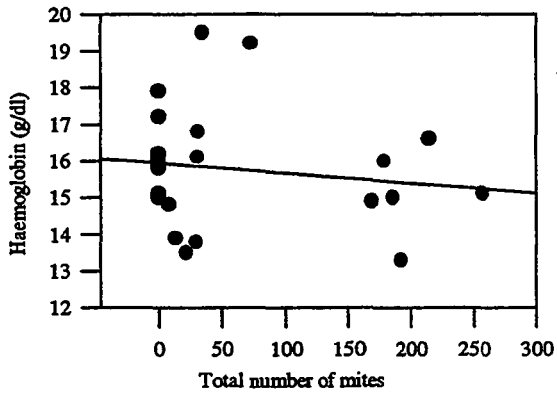
5.4 DISCUSSION

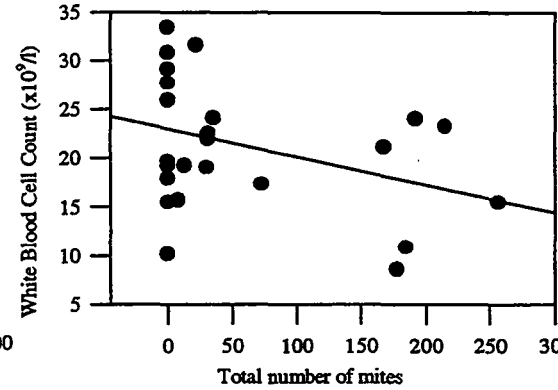
Infection by *S. tracheacolum* over a period of 12 months does not appear to have a recognisable impact on the cellular haematology of captive reared Gouldian Finches. Although both low haemoglobin and erythrocyte values, and elevated leucocyte values were found in some birds, all

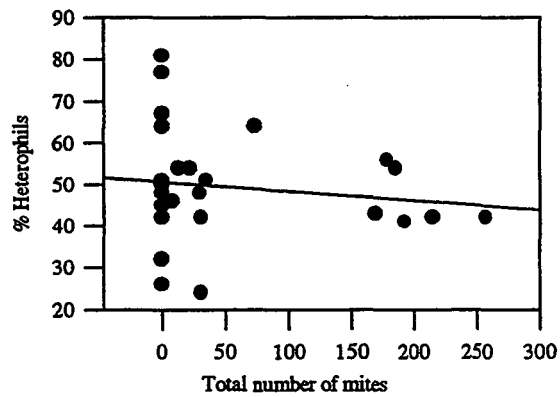
Table 5.5 'Normal' haematological values for captive reared male and female Gouldian Finches aged between 6 and 18 months (infected and uninfected by *S. tracheacolum*).

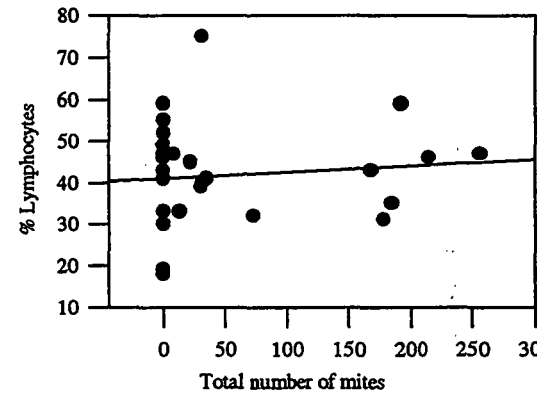
Measurement	Number of birds	Mean ± SD	Range
Hb (g/dl)	20 male	15.8±1.4	13.5-19.5
	8 female	15.8±1.7	13.3-19.2
PCV (%)	12 male	50.2±5.4	42.7-58.0
	3 female	58.1±1.3	56.6-58.8
RBC ($x10^{12}$/l)	12 male	4.3±0.4	3.8-5.1
	3 female	4.6±0.07	4.6-4.7
MCV (fl)	12 male	135.1±9.1	120.4-153.1
	3 female	131.0±3.9	128.7-135.5
MCH (pg)	12 male	34.0±2.7	29.4-37.3
	3 female	33.9±1.3	33.1-35.4
MCHC (%)	12 male	30.9±2.6	27.7-36.6
	3 female	27.5±1.6	26.6-29.3
WBC ($x10^{9}$/l)	20 male	15.8±1.4	13.5-19.5
	8 female	15.8±1.7	13.3-19.2
Heterophils (%)	20 male	48.0±13	24-77
	8 female	53.0±15.5	41-81
Lymphocytes (%)	20 male	41.9±11.7	19-75
	8 female	41.8±13.9	18-59
Monocytes (%)	20 male	5.8±4.6	0-18
	8 female	2.6±2.8	0-6
Eosinophils (%)	20 male	2.5±1.9	0-6
	8 female	1.3±1.4	0-4
Basophils (%)	20 male	2.7±2.5	0-9
	8 female	1.6±2.2	0-5
Thrombocytes ($x10^{9}$/l)	20 male	30.1±6.9	17-45.2
	6 female	31.5±7.8	19.8-43

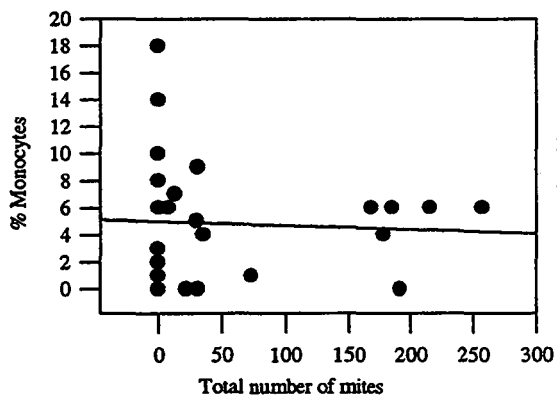
Figure 5.1 The relationship between haematological values and the size of *S. tracheacolum* mite infrapopulations in experimentally infected Gouldian Finches *E. gouldiae*. Linear regressions are superimposed on scatter plots of raw values for all individuals examined but excluding 4 uninfected birds that showed extreme haemoglobin and white blood cell counts (n = 29). Correlation coefficients: Haemoglobin, r = -0.15, $P = 0.44$; White Blood Cell Count, r = -0.36, $P = 0.053$; Heterophils, r = -0.35, $P = 0.06$; Lymphocytes, r = 0.1, $P = 0.61$; Monocytes, r = -0.06, $P = 0.76$; Eosinophils, r = -0.07, $P = 0.72$; Basophils, r = 0.29, $P = 0.13$; Thrombocytes, r = 0.09, $P = 0.64$.

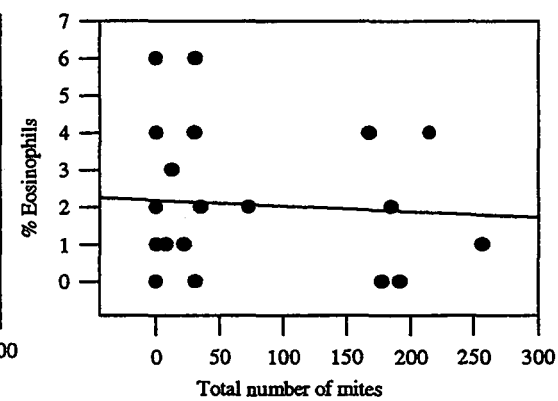

Haemoglobin (g/dl)
20
19
18
17
16
15
14
13
12
0 50 100 150 200 250 300
Total number of mites

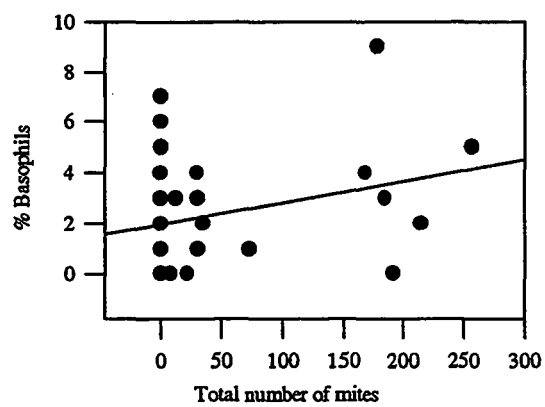

White Blood Cell Count (x10⁹/l)
35
30
25
20
15
10
5
0 50 100 150 200 250 300
Total number of mites


% Heterophils
90
80
70
60
50
40
30
20
0 50 100 150 200 250 300
Total number of mites


% Lymphocytes
80
70
60
50
40
30
20
10
0 50 100 150 200 250 300
Total number of mites


% Monocytes
20
18
16
14
12
10
8
6
4
2
0
0 50 100 150 200 250 300
Total number of mites


% Eosinophils
7
6
5
4
3
2
1
0
0 50 100 150 200 250 300
Total number of mites


% Basophils
10
8
6
4
2
0
0 50 100 150 200 250 300
Total number of mites

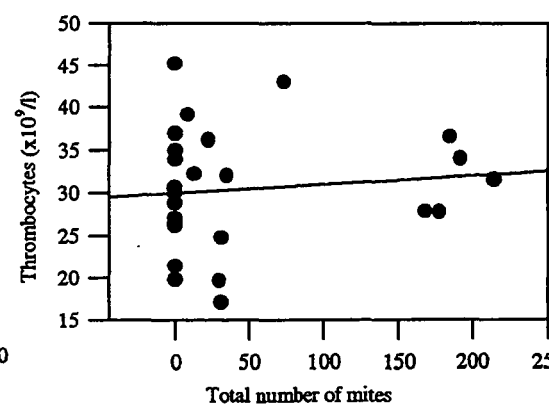
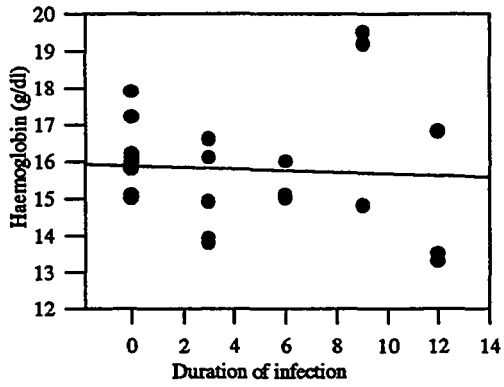
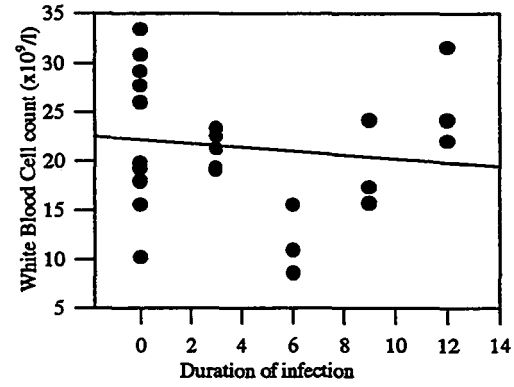
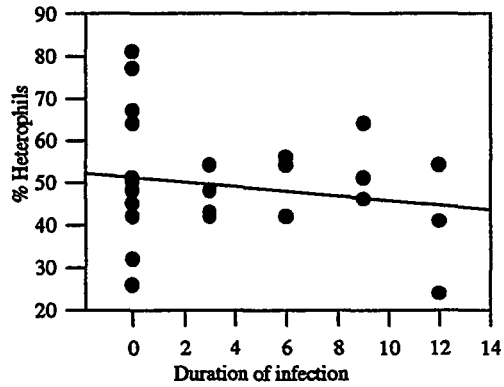
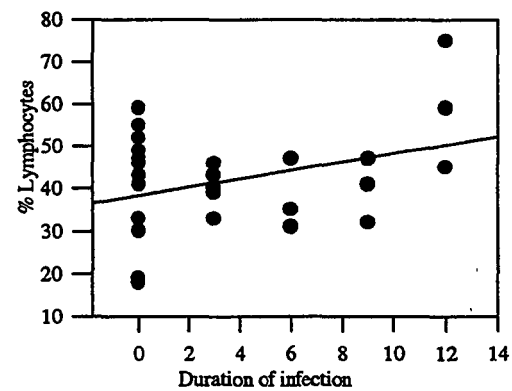

Thrombocytes (x10⁹/l)
50
45
40
35
30
25
20
15
0 50 100 150 200 250
Total number of mites

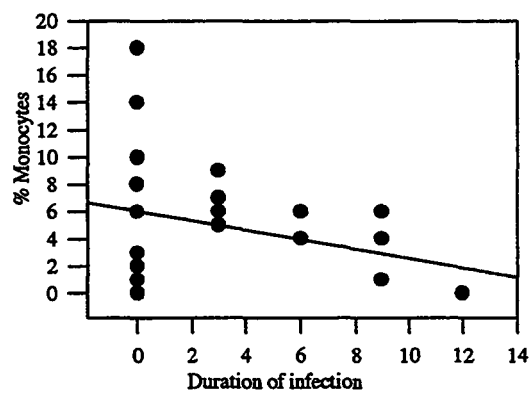
Figure 5.2 The relationship between haematological values and the duration of infection in experimentally infected Gouldian Finches *E. gouldiae*. Linear regressions are superimposed on scatter plots of raw values for all individuals examined but excluding 4 uninfected birds that showed extreme haemoglobin and white blood cell counts (n = 29). Correlation coefficients: Haemoglobin, r = -0.06, $P = 0.76$; White Blood Cell Count, r = -0.13, $P = 0.53$; Heterophils, r = --0.17, $P = 0.38$; Lymphocytes, r = 0.35, $P = 0.06$; Monocytes, r = -0.34, $P = 0.07$; Eosinophils, r = -0.31, $P = 0.1$; Basophils, r = -0.14, $P = 0.47$; Thrombocytes, r = 0.25, $P = 0.19$.

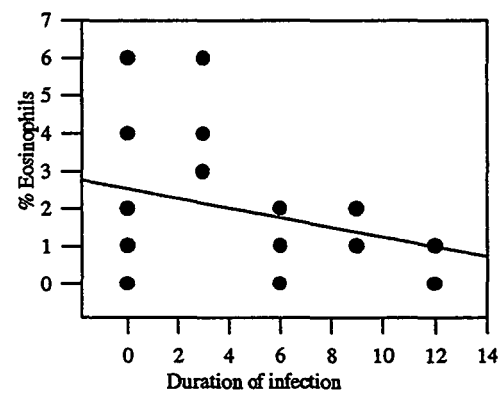

Haemoglobin (g/dl)
Duration of infection

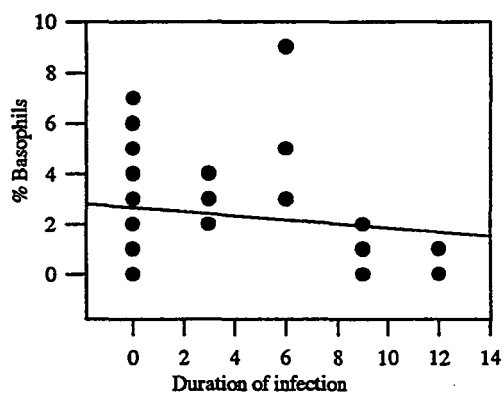

White Blood Cell count (x10⁹/l)
Duration of infection

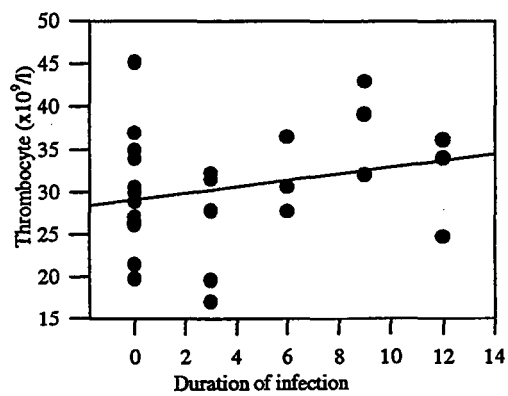

% Heterophils
Duration of infection


% Lymphocytes
Duration of infection


% Monocytes
Duration of infection


% Eosinophils
Duration of infection


% Basophils
Duration of infection


Thrombocyte (x10⁹/l)
Duration of infection

exceptional values were found in uninfected birds and could not be attributed to the presence of *S. tracheacolum*. The same conclusion is apparent for Canaries infected over a period of 6 months.

No mites were found in Budgerigars, experimentally infected and examined after a 6 month period, and therefore no comment can be made regarding the similarity of haematology between infected and uninfected birds. However, it is worthy of note that Mathey (1967) examined the blood of a heavily infected captive reared Budgerigar and did not detect any abnormalities in the haematology.

The results of the present study are in accord with haematological findings for wild Gouldian Finches. Wild populations are known to be infected by *S. tracheacolum* at both a high prevalence and a high intensity (Tidemann *et al.*, 1992; Chapter 7: Section 7.3.2 - 7.3.3, Prevalence and intensity of infection). However, Tidemann *et al.* (in press) found that as far as blood smears could indicate Gouldian Finches showed no gross abnormalities in comparison to other finches. It is therefore unlikely that disease known to be associated with *S. tracheacolum* infection could have been indicated from a survey of blood smears.

Elsewhere, heavy infections by blood-feeding arthropods have been known to induce hyperaemia in birds (Feare, 1976). Increased heterophil levels have also been associated with some ecto-parasitic infections (Olson, 1965). Clark (1991) argues that even under relatively homogeneous conditions ectoparasites may have variable effects on their hosts, thus complicating haematological studies. For example, very heavy infections of the Northern Fowl Mite *Ornithonyssus sylviarum* (i.e. 1000-10,000 mites per bird) were found by Matthysse *et al.* (1974) and Devaney (1979) to cause anaemia in domestic hens with an associated decrease in egg production. Previous studies did not detect haematological change (Loomis *et al.*, 1970). Furthermore, anaemia has not been detected in similarly infected roosters although it has been known to cause a reduction in weight, seminal fluid, sperm concentration and plasma testosterone levels (Clark, 1991).

In mammals it is not uncommon to have severe respiratory disease with little or no change in the haematology. Diseases such as tuberculosis, legionella and human psittacosis seldom cause an elevation of the white cell count unless in the presence of a secondary pyrogenic infection (Melrose, pers. comm.). It is therefore probable that *S. tracheacolum* only influences haematological values at an experimentally detectable level when associated with a secondary infection such as bacterial pneumonia. In the present study large variations were evident in haematological values of both infected and uninfected birds at all sample points. If consistent haematological changes occur in the presence of *S. tracheacolum* infection, and if trends exist over time or in relation to the size of infection, then these changes are likely to be small and overshadowed by individual variations and further complicated by the presence of other unidentified disease agents.

In conclusion, it appears unlikely that routine blood-cellular tests would provide informative data on either the presence, duration, or the size of infection in the Gouldian Finch. As a tool for the study of *S. tracheacolum* in wild host populations or in laboratory based experiments cellular haematology is therefore considered to be of limited value.

PART III THE HOST-PARASITE RELATIONSHIP

Chapter 6. BEHAVIOUR/ CLINICAL SIGNS

6.1 INTRODUCTION

In general, the clinical signs associated with respiratory disease in captive birds tend to follow a similar course. The first detectable sign is usually impaired or restricted flight. Birds show a reluctance to fly or may be unable to maintain flight for any length of time. Following exercise, laboured breathing becomes obvious and may continue even after rest. Sneezing, coughing and nasal discharge may also occur. Dyspnoea (characterised by open-mouthed breathing or panting) may be present and as the condition progresses tail bobbing (associated with increased thoracic movement) occurs. With excessive respiratory secretions, bubbling or gurgling sounds can be heard on both inspiration and expiration. Wheezing birds usually emit a high pitched whining sound on inspiration (Altman, 1979).

Prior to the present study, confident diagnosis of *S. tracheacolum* infection could only be made by post-mortem examination (see Chapter 2: Section 2.7, Transmission) though very occasional diagnosis has been made by examination of tracheal swabs or coughed up tracheal mucus. In future, examination of the external nares for mites may prove to be the simplest means of accurately diagnosing infection in live birds. However, it remains that many of the clinical signs associated with the presence of *S. tracheacolum* infection are non-specific and associated with a variety of other respiratory illnesses including bacterial, fungal and viral infections, macroparasitic infections such as gapeworms and irritations of the respiratory surfaces by chemicals or particles (Madill, 1987; Kummerfeld & Hinz, 1982; Harrigan, 1981; Arnall & Petrak, 1982).

The clinical signs of infection by *S. tracheacolum* were first described by Stephan *et al.* (1950). Stephan and his associates described the course of the infection in captive reared Canaries as follows: "The clinical signs shown are essentially respiratory in character. The affected bird appears to be puffed up and shows slight heavy breathing while sitting quietly on the perch in a sleeping position. As the intensity of the clinical signs increases the bird shows a degree of irritation of the trachea, which is characterised by a peculiar sucking or smacking sound usually made twice in succession followed by quietness. The males refuse to sing. Eventually the bird squats on the floor and marked respiratory distress is shown by sneezing, frequent opening of the beak and repeated attempts to clear the throat, together with gasping respirations. The condition of the bird rapidly deteriorates. Towards the end, it selects a corner of the cage in which to die. There is a discharge from the mouth and nose and, after slight struggling, it falls over with its beak in the sawdust at the bottom of the cage".

Since the first report of *S. tracheacolum* infection there have been numerous additional descriptions of the clinical signs associated with infection in captive reared birds, particularly the Canary (eg. Torres *et al.*, 1951; Aeckerlein, 1974; Blasco-Sabio & Portús-Vinyeta, 1974; Menchaca, 1976; Zwart, 1976; Losson *et al.*, 1979; Kummerfeld & Hinz, 1982) and the Gouldian Finch (eg. Cumming, 1959; Murray, 1966; Riffkin & McCausland, 1972; Jolivet, 1975; Kummerfeld & Hinz, 1982; Szeleszczuk & Kruszewicz, 1987).

Cumming (1959) was the first to identify *S. tracheacolum* infection in captive reared Gouldian Finches. He noted that "once established" in the host the infection was "far more rapidly fatal" than in the Canary and "once respiratory distress was noticed the disease terminated fatally in about three weeks".

Murray (1966) described the course of the clinical signs in a group of Gouldian Finches as follows: "The feathers of infected birds were ruffled and respiratory movements of the body were most apparent, particularly in the evening. The bill was wiped frequently on the perch and the beak was opened widely, as in gasps. The noise of air rushing up and down the obstructed trachea could be heard clearly when an infested bird was held near to the ear. Mature birds ceased to breed. The birds gradually became lethargic, and eventually remained hunched on the floor of the cage with their eyes closed until they died".

Kummerfeld and Hinz (1982), from extensive observations in veterinary practise, summarised the clinical signs of infection by *S. tracheacolum* in captive reared birds as loss of voice (particularly noticeable in male birds), breathing through the bill rather than the nares, bill wiping, shaking of the head, sneezing, rattled breathing, wheezing and loss of weight (particularly in the pectoral muscles). Ruffled plumage, lethargy and sleepiness are also commonly observed (Arnall & Keymer, 1975). Aeckerlein (1974) describes sudden movements of the head in infected birds as if regurgitating. This symptom has also been noted by other authors. For example, Riffkin and McCausland (1972) describe it as "constantly extending the neck, coughing and making respiratory sounds as if trying to clear the throat". Many authors (eg. Cumming, 1959; Aeckerlein, 1974) report an increase in the severity of wheezing and other audible respiratory clinical signs at night.

All previous descriptions of *S. tracheacolum* infection have been made in the absence of a knowledge of either the size or the duration of the infection. The present study describes the course of clinical signs in experimentally infected Gouldian Finches. As the time and the size of the initial infection is known, both the severity and frequency of *S. tracheacolum* clinical signs can be quantitatively assessed through a direct comparison of the parameters of infected and uninfected birds. Of particular interest is the duration of the infection prior to the onset of clinical signs and the duration of clinical signs prior to either the remission of the infection, or the death of the host.

6.2 METHODS

The experimental procedure for the establishment of infected and uninfected Gouldian Finches is set out in the Experimental Design: 3 Experimental procedure, P62. Groups of experimentally infected birds and groups of birds maintained free of infection were housed under identical conditions but in separate aviary enclosures. In the 1992 experiment, the clinical signs of infection and the general behaviour of birds were monitored over the first 157 days of infection and again between 367 and 736 days of infection. In the 1993 experiment, birds were monitored over the first 349 days of infection.

Table 6.1 Examination of infected and uninfected Gouldian Finches during the 1992 and 1993 aviary experiments.

1992				1993			
Date and time of examination		Number of days following experimental infection	Number and sex of birds examined infected/ uninfected	Date and time of examination		Number of days following experimental infection	Number and sex of birds examined infected/ uninfected
12 February	initial infection		18M 18F/ 18M/18F	3 March	initial infection		12M 12F/ 12M 12F
20 February	1300 hr	8	17M 17F/ 18M/12F	19 March	1300 hr	16	12M 11F/ 10M 12F
5 March	1300 hr	21	16M 12F/ 17M 12F	1 April	1300 hr	29	12M 11F/ 11M 12F
20 March	1400 hr	37	16M 10F/ 17M 10F	19 April	1200 hr	47	11M 10F/ 11M 11F
3 April	1400 hr	50	14M 9F/ 14M 8F	26 April	1300 hr	54	9M 9F/ 11M 11F
24 April	1500 hr	71	14M 8F/ 11M 6F	10 May	1400 hr	68	8M 8F/ 10M 9F
11 May	1400 hr	88	11M 8F/ 10M 6F	25 May	1100 hr	83	7M 8F/ 10M 9F
22 May	1300 hr	99	7M 7F/ 5M 5F	7 June	1200 hr	96	6M 8F/ 9M 9F
7 June	1200 hr	115	6M 6F/ 4M 5F	21 June	1200 hr	110	6M 8F/ 9M 8F
19 June	1300 hr	127	6M 6F/ 4M 5F	4 July	1400 hr	123	6M 8F/ 8M 7F
26 June	1400 hr	134	6M 6F/ 4M 5F	14 August	1400 hr	165	6M 7F/ 6M 8F
3 July	1300 hr	141	6M 6F/ 4M 5F	30 August	1000 hr	181	6M 6F/ 7M 7F
10 July	1400 hr	148	6M 6F/ 4M 5F	13 September	1100 hr	195	6M 3F/ 7M 7F
19 July	1400 hr	157	6M 5F/ 4M 5F	26 September	900 hr	208	6M 3F/ 7M 7F
				11 October	900 hr	223	6M 3F/ 6M 6F
				25 October	1100 hr	237	5M 2F/ 4M 6F
				7 November	1100 hr	250	5M 2F/ 5M 5F
				22 November	1100 hr	265	5M 2F/ 5M 5F
				2 December	1400 hr	275	5M 2F/ 5M 5F
				20 December	1400 hr	293	3M 1F/ 2M 3F
				3 January	1500 hr	307	2M 1F/ 3M 3F
				16 January	1400 hr	320	2M 1F/ 3M 3F
				31 January	1700 hr	335	2M 1F/ 3M 3F
				14 February	1900 hr	349	2M 1F/ 3M 3F

At various intervals following initial infection, infected and uninfected birds were examined and weighed to 0.1g (Table 6.1). The severity of audible respiratory clinical signs (wheezing, clicking

and gurgling) were recorded immediately following capture of the bird (i.e. following exercise) then again following a period of rest. An index of the severity of clinical signs (i.e. mild or slight = 1, moderate = 2 and heavy or severe = 3) was used to facilitate quantitative comparisons between infected and uninfected birds. The moult condition (presence or absence of wing feather moult or body moult), the presence of external parasites (arthropods such as lice, mites and ticks) and obvious abnormalities such as missing plumage, soiled plumage, and lesions were also recorded.

In the 1992 experiment, remote observations were made on both infected and uninfected birds at intervals between 106 and 165 days following initial infection (between 29 May and 17 July) (Table 6.2). Each bird was observed for a period of 5 minutes during which a record was made of the frequency of (a) flight events, (b) audible respiratory sounds (sneezing and coughing), (c) general vocalisations (chirping and male singing), (d) bill wiping (associated or unassociated with drinking or feeding), (e) preening events, (f) head shaking, (g) fluffing up of plumage, (h) head scratching and (i) 'regurgitation action' (i.e. extension of the neck associated with attempts to clear the throat); the period of time involved in (a) eating, (b) drinking, (c) preening and (d) male singing and the distance covered in each flight event. The use of a cassette tape recorder enabled the time duration and the frequency of behavioural events to be recorded while maintaining a continuous observation on an individual bird. Birds were observed from outside the enclosures and appeared to be undisturbed by the observers presence.

Table 6.2 Observations on infected and uninfected Gouldian Finches during the 1992 aviary experiment.

Date and time of observation		Number of days following experimental infection	Number of birds examined
12 February	Initial infection		
29 May	1300 - 1500 hr	106	4M 4F/ 4M 4F
5 June	1300 - 1500 hr	113	4M 3F/ 3M 4F
12 June	1145 - 1320 hr	120	" "
19 June	1430 - 1530 hr	127	" "
26 June	1110 - 1250 hr	134	" "
3 July	1320 - 1540 hr	151	" "
13 July	1130 - 1310 hr	161	" "
17 July	1145 - 1340 hr	165	3M 2F/ 3M 4F

Birds sampled at 3 months and 6 months following initial infection were exercised prior to euthanasia. Each bird was encouraged to fly continuously in a large room containing only a limited number of perching sites. The time between initial release and apparent respiratory exhaustion (i.e. when the bird remained on the floor and could not be coaxed to fly) was recorded for several trials on each bird.

Programs in the Statistical Analysis System (SAS Institute INC., 1988) were employed for data manipulations and statistics. Descriptive statistics, means and standard deviations, were calculated using PROC MEANS. Comparisons were made between infected and uninfected bird groups using ANOVA (PROC GLM). A multivariate analysis of repeated-measures design REPEATED (PROC: GLM) was used to determine the effect of time within and between infected and uninfected bird groups.

6.3 RESULTS

6.3.1 Weight

6.3.1.1 Weight of infected birds

Loss of weight was evident in individual birds heavily infected by *S. tracheacolum*. However, the overall mean weight of infected birds did not significantly differ from that of uninfected birds over the first 88 days of infection in the 1992 aviary experiment and 223 days of infection in the 1993 aviary experiment (ANOVA's > 0.05; Tables 6.3 and 6.4).

In 1992, the mean weight of infected males did not differ significantly from that of uninfected males over the first 157 days of infection. However, the mean weight of infected females was significantly less than that of uninfected females from 99 to 157 days.

In 1993, the mean weight of infected males was not significantly different from uninfected males for the first 223 days of infection. A significantly lower weight was recorded for males at 223 days after which a lower but not significantly lower mean weight was recorded for infected males until 265 days.

The results from multivariate tests on weight data for the 1992 aviary experiment using 17 observations from 14 repeated measurements indicate that time has a clear effect (Time: f = 20.11, df = 13, 3, $P = 0.02$) and there is a clear interaction between time and infection (Time*Infection: f = 36.59, df = 13, 3, $P = 0.006$).

Weight data for individual birds indicate that loss of weight is not rapid following infection but occurs over a period of between 50 and 100 days prior to the eventual death of the host. Birds that survived infection showed an initial steady loss of weight followed by an increase in weight associated with their apparent recovery.

6.3.1.2 Offspring from infected parents

The mean weight of offspring from experimentally infected parents tended to be lower than that of offspring from uninfected parents (Table 6.5). The mean weight of 6 immature control birds (3M;

Table 6.3 Comparisons between mean weights of *S. tracheacolum* infected and uninfected Gouldian Finches *E. gouldiae* from 1 to 157 days following experimental infection during the 1992 aviary experiment.

Number of days following initial infection	Date	Mean weight of uninfected birds	(n)	Mean weight of infected birds	(n)	*f*	*P* value
1	12 February	F 15.4	18	F 15.9	18	-1.22	>0.1
		M 15.9	18	M 15.7	18	0.36	>0.1
8	20 February	F 16.9	16	F 16.5	13	0.49	>0.1
		M 16.8	18	M 16.3	16	0.82	>0.1
21	5 March	F 16.0	12	F 15.6	12	0.4	>0.1
		M 15.7	17	M 16.1	14	-0.61	>0.1
37	20 March	F 16.7	10	F 17.4	10	-0.88	>0.1
		M 16.4	16	M 16.2	14	0.72	>0.1
50	3 April	F 16.4	8	F 15.8	9	0.81	>0.1
		M 15.8	14	M 16.4	12	-0.76	>0.1
71	24 April	F 16.4	7	F 16.3	8	0.11	>0.1
		M 16.1	13	M 16.5	12	-0.58	>0.1
88	11 May	F 16.8	6	F 16.4	8	0.36	>0.1
		M 15.7	10	M 16.7	9	-1.25	>0.1
99	22 May	F 16.8	4	F 15.5	7	1.86	0.047 ‡
		M 15.3	5	M 16.3	6	-1.4	0.09
115	7 June	F 17.4	4	F 15.7	6	2.54	0.017 ‡
		M 16.0	4	M 17.0	7	-0.9	0.1
127	19 June	F 18.4	4	F 15.7	6	2.35	0.02 ‡
		M 15.8	4	M 16.5	5	-0.65	>0.1
134	26 June	F 18.1	4	F 15.9	6	2.6	0.06
		M 15.8	4	M 16.7	5	-0.82	>0.1
141	3 July	F 17.1	4	F 15.3	6	2.22	0.03 ‡
		M 15.3	4	M 16.4	5	-0.85	>0.1
148	10 July	F 18.1	4	F 15.5	6	2.65	0.01 ‡
		M 15.8	4	M 16.3	5	-0.39	>0.1
157	19 July	F 18.9	4	F 15.9	5	4.41	0.002 ‡
		M 18.9	3	M 16.4	5	1.86	0.06

‡, Significant differences; F, Female; M, Male.

Table 6.4 Comparisons between mean weights of *S. tracheacolum* infected and uninfected Gouldian Finches *E. gouldiae* from 1 to 208 days following experimental infection during the 1993 aviary experiment.

Number of days following initial infection	Date	Mean weight of uninfected birds	(n)	Mean weight of infected birds	(n)	*f*	*P* value
1	3 March	F 16.0	12	F 16.0	12	0.12	>0.1
		M 16.0	12	M 16.1	12	-0.06	>0.1
16	19 March	F 16.5	12	F 16.7	12	-0.32	>0.1
		M 16.6	11	M 17.1	12	-0.67	>0.1
29	1 April	F 16.5	12	F 16.9	11	-0.61	>0.1
		M 16.5	11	M 16.5	12	0.003	>0.1
47	19 April	F 17.0	11	F 16.9	10	0.08	>0.1
		M 16.4	11	M 16.9	11	-0.84	>0.1
54	26 April	F 17.1	11	F 17.2	9	-0.16	>0.1
		M 16.4	11	M 16.5	9	-0.41	>0.1
68	10 May	F 16.9	9	F 17.1	8	-0.25	>0.1
		M 16.8	10	M 17.1	8	-0.29	>0.1
83	25 May	F 16.6	9	F 17.2	8	-0.7	>0.1
		M 16.1	9	M 17.1	7	-1.69	0.06
96	7 June	F 17.1	9	F 16.9	8	0.18	>0.1
		M 16.1	9	M 16.9	6	-0.73	>0.1
110	21 June	F 16.4	8	F 16.7	8	-0.45	>0.1
		M 15.5	9	M 16.8	6	-1.07	>0.1
123	4 July	F 16.8	8	F 16.8	8	-0.04	>0.1
		M 16.3	8	M 16.9	6	-0.74	>0.1
165	14 August	F 16.7	7	F 17.1	6	-0.36	>0.1
		M 16.7	7	M 16.4	6	0.24	>0.1
181	30 August	F 16.8	7	F 16.4	6	0.34	>0.1
		M 16.5	7	M 15.8	6	0.81	>0.1
195	13 September	F 16.8	7	F 16.7	3	0.05	>0.1
		M 16.4	7	M 16.3	6	0.13	>0.1
208	26 September	F 15.8	7	F 15.5	3	0.42	>0.1
		M 16.6	7	M 15.8	6	0.75	>0.1

‡, Significant differences; F, Female; M, Male.

Table 6.4 Continued, Comparisons between mean weights of *S. tracheacolum* infected and uninfected Gouldian Finches *E. gouldiae* from 223 to 265 days following experimental infection during the 1993 aviary experiment.

Number of days following initial infection	Date	Mean weight of uninfected birds	(n)	Mean weight of infected birds	(n)	*f*	*P* value
223	11 October	F 16.1	5	F 15.5	3	0.56	**>0.1**
		M 17.2	5	M 15.8	5	2.17	**0.03 ‡**
237	25 October	F 17.6	5	F 15.3	2	1.49	**>0.1**
		M 17.5	5	M 16.4	5	1.5	**0.08**
250	7 November	F 17.5	5	F 15.6	2	1.49	**>0.1**
		M 17.4	5	M 16.2	5	1.48	**0.09**
265	22 November	F 17.6	5	F 15.6	2	1.54	**>0.1**
		M 17.4	5	M 16.2	5	1.65	**0.06**

‡, Significant differences; F, Female; M, Male.

Table 6.5 Details of juvenile and immature Gouldian Finches *E. gouldiae* from infected parents and immature Gouldian Finches from parents maintained free of infection during the 1993 aviary experiment.

Identity	Sex	Number of days after fledging	Moult condition	Head/bill length (mm)	Tarsus length (mm)	Wing length (mm)	Tail length (mm)	Weight (g)	Size of infrapopulation (i.e. number of mites)
Infected									
170	Male	104	body moult in progress	27.5	14.3	-	-	15.5	57
456 (LG/L)	"	219	"	24.9	13.6	66	43	14.4	117
455 (O/L)	Female	306	retains juvenile plumage	24.7	14.8	65	30	16.7	91
457	"	175	"	25.2	12.9	64	32	14.4	135
454 (LB/L)	Male	281	body moult in progress	24.6	13.1	66	32	16.6	51
Control									
R/R	Female	311	complete adult plumage	25.2	15.2	68	43	18.2	-
M/R	"	270	"	25.5	13.7	66	46	20.0	-
B/R	Male	306	"	25.0	13.0	70	53	15.9	-
O/R	"	300	"	24.3	14.4	67	46	16.1	-
W/R	Female	219	"	24.3	12.9	66	45	17.1	-
Y/R	Male	219	"	24.9	13.0	68	47	16.9	-

3F) was 15.8g (SD = 0.6) 100 days after fledging and 17.0g (SD = 1.09) 200 days after fledging. The mean weight of 4 infected birds was 14.9g (SD = 1.0) 100 days after fledging and 14.9g (SD = 0.5) 200 days after fledging. The lower mean weight of infected immature birds was associated with a slower development rate (measured in terms of the time taken to complete the first moult). Infected immature birds had not completed the first plumage moult by 104, 175, 219, 281 and 306 days respectively, following fledging. However, all immature uninfected birds had completed the first plumage moult by 219, 219, 270, 300, 306 and 311 days respectively following fledging. One infected immature female bird at 175 days and another at 306 days after fledging still retained their juvenile plumage.

6.3.2 Audible respiratory clinical signs

6.3.2.1 Types of clinical signs

Respiratory sounds were detected in both infected and uninfected birds in both the 1992 and 1993 aviary experiments. Wheezing was the only 'respiratory symptom' recorded from uninfected birds. The frequency in uninfected birds was low and the severity did not exceed a 'slight wheeze'.

A slight audible wheeze was the first detectable sign of infection by *S. tracheacolum* in experimentally infected birds. As the infection progressed the severity of wheezing increased and was occasionally accompanied by a 'clicking' sound. Heavy wheezing was often accompanied by gurgling and bubbling sounds. These clinical signs were particularly noticeable following exercise. In heavily infected birds the respiratory sounds were audible from outside the enclosures.

6.3.2.2 Severity of clinical signs and the duration of infection

Figure 6.1 shows the mean severity of audible respiratory clinical signs (wheezing, clicking and gurgling) for male (Figure 6.1B, 6.2D) and female birds (Figure 6.1A, 6.2C) over 157 days in the 1992 aviary experiment (Figure 6.1A, 6.1B) and 349 days in the 1993 aviary experiment (Figure 6.1C, 6.1D). The mean time to the onset of clinical signs was similar for both male and female birds, and between years. Clinical signs were first detectable between 40 and 60 days following initial infection. From this point onwards in 1992 there was a steady increase in the mean severity until termination of the experiment after 157 days. The mean severity followed a similar course in 1993 and reached a maximum mean severity by 180 days. The severity remained high until between 250 and 300 days following which there appeared to be a gradual subsidence of clinical signs until conclusion of the experiment at 349 days.

Figure 6.2 shows the mean severity of audible respiratory clinical signs for birds maintained longer than 12 months following initial infection. The mean severity represents measurements taken on 4 birds originally infected on 12 February 1992. These include an orange headed male, killed after 736 days of infection; a black headed female and an orange headed male, killed after 433 days of

Figure 6.1 The mean severity of respiratory clinical signs (i.e. wheezing, clicking and gurgling) in Gouldian Finches *E. gouldiae* infected by *S. tracheacolum*: index of severity; 1 = mild or slight, 2 = moderate, 3 = heavy or severe.

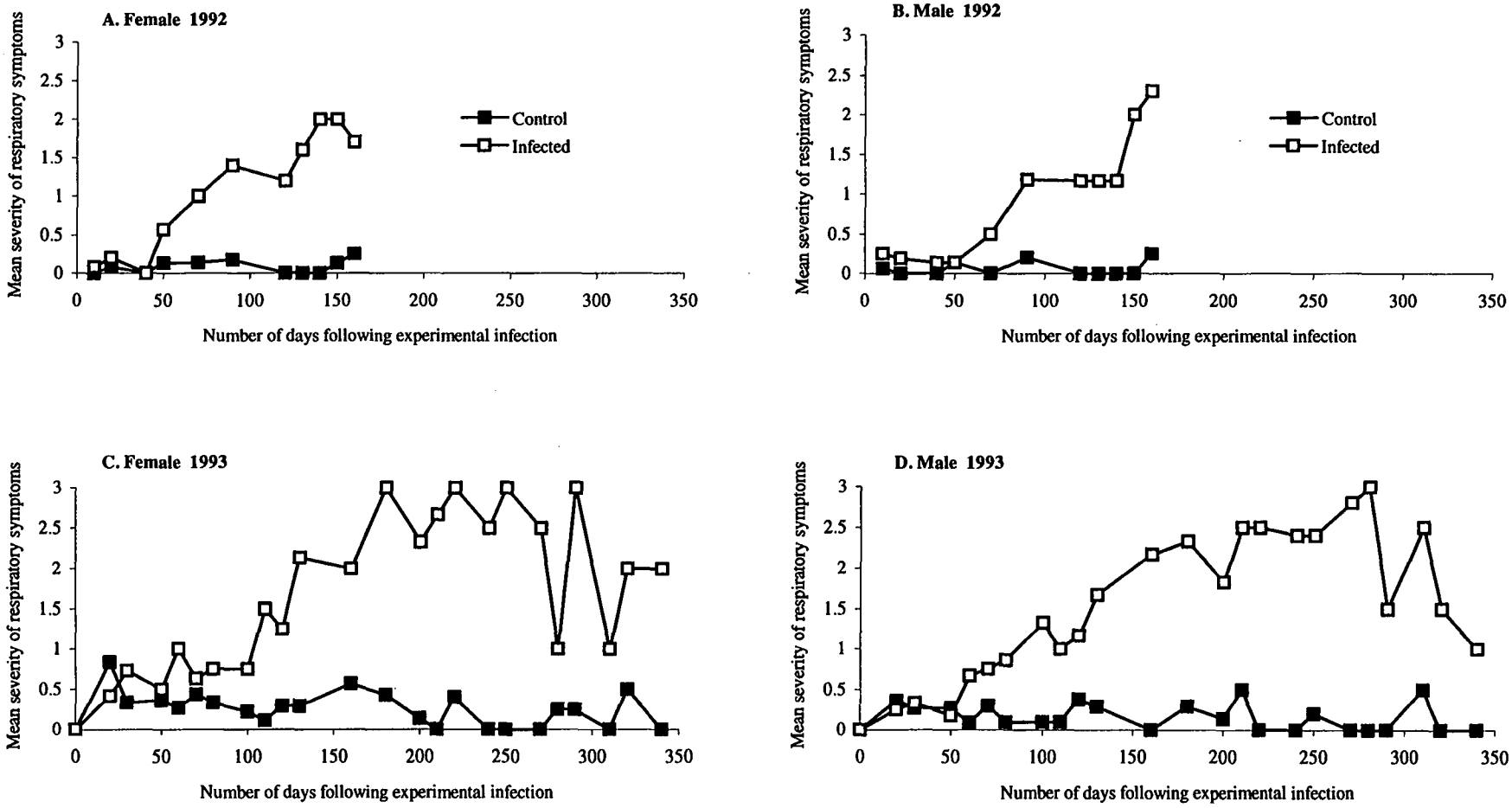
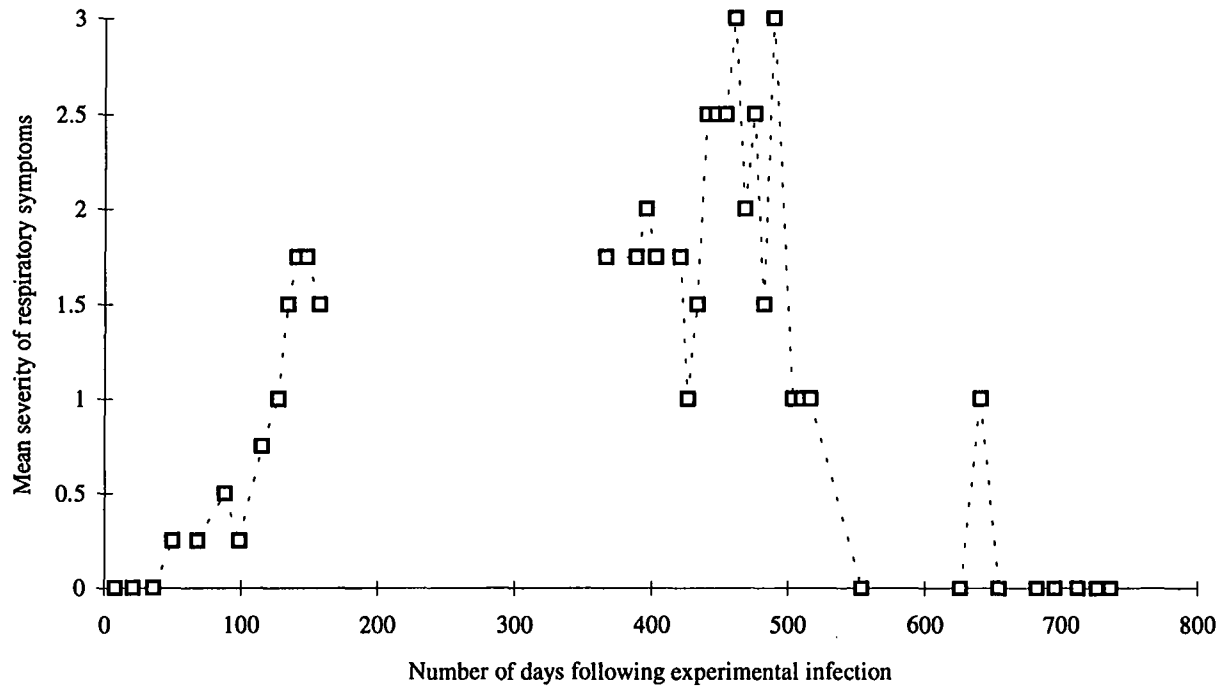


Figure 6.2 Mean severity of respiratory clinical signs (wheezing, clicking and gurgling) in Gouldian Finches *E. gouldiae* infected by *S. tracheacolum* and maintained longer than 12 months after initial infection: index of severity; 1 = mild or slight, 2 = moderate, 3 = heavy or severe.



infection and a black headed male, killed after 554 days of infection. Regular observations were made between 1 and 157 days (12 February to 19 July 1992) and between 367 and 736 days (15 February 1993 to 24 February 1994) following initial infection. The data indicate a similar trend to that of the 1992 and 1993 experiments for the first 157 days. No observations were made between 157 and 367 days (19 July 1992 to 15 February 1993). From 367 days to 500 days (15 February 1993 to the end of June) the mean severity of clinical signs was high. The severity of clinical signs then subsided to a complete absence of clinical signs after 654 days (note that between 433 and 554 days mean severity is calculated from measurements on only 2 birds and between 554 and 736 days all measurements come from a single bird).

Table 6.6 presents data from 47 birds known to be free of infection at the time of experimental infection. Using indices of the severity of infection the total infrapopulation size is positively correlated with the mean severity of clinical signs ($r = 0.6$, $P = 0.0001$). However, the correlation between the duration of infection and the severity of clinical signs is poor ($r = 0.24$, $P = 0.11$).

6.3.3 Activity level and respiratory ability

Observations on infected and uninfected birds in 1992 over the period 106 to 165 days following initial infection suggests that uninfected birds are more active than infected birds. Figure 6.3C shows the mean distance flown spontaneously by infected and uninfected birds at 106, 113, 120, 127, 134, 151, 161 and 165 days following initial infection. There was a high variation in the mean values at each observation point. This is a result of high variance both among birds at each observation point and between observation points. However, the data suggest that infected birds are less active (measured in terms of the total distance flown) than their uninfected counterparts. The mean distance flown over a 5 minute observation period by 7 infected birds (3 female and 4 male) and 7 uninfected birds (4 female and 3 male) is shown in Figure 6.5D. The mean value is calculated from 8 observations each of 5 minute duration between 106 and 165 days following initial infection. The data suggest a higher activity level among uninfected than infected birds.

The mean exercise ability of birds at 3 months following initial infection (measured as the length of time birds are able to maintain flight) was not significantly different from uninfected birds (ANOVA: $f = 0.22$, $P = 0.65$). However, after 6 months of infection the mean exercise ability of infected birds (3 male and 3 female) was significantly less than that of uninfected birds (3 male and 3 female) (ANOVA: $f = 31.27$, $P = 0.00023$). Table 6.7 shows details of individual birds, their flight time scores, severity of respiratory clinical signs and the size of their respective mite infections. Both the severity of audible respiratory clinical signs ($r = -0.87$, $P = 0.0002$) and the size of the mite infrapopulation ($r = -0.83$, $P = 0.0008$) correlate with the time of sustained flight. The most heavily infected bird carrying 273 mites and showing the highest severity of audible respiratory clinical signs showed the least ability for sustained flight whereas the least heavily

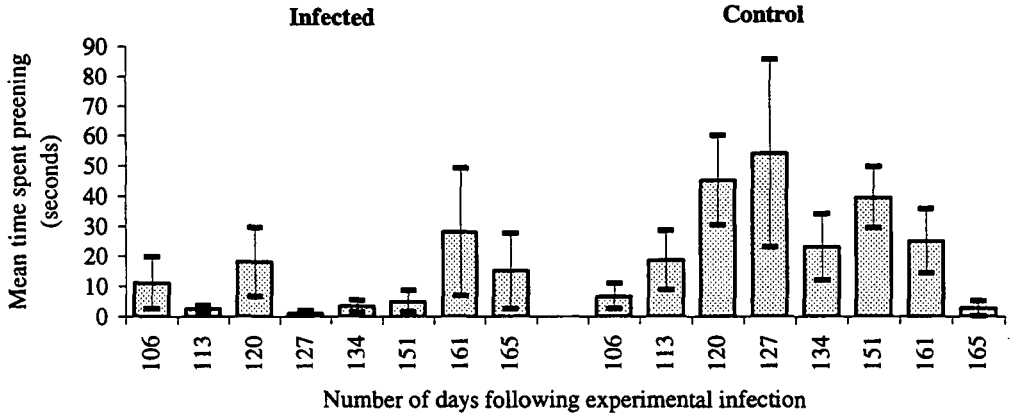
Table 6.6 The relationship between the duration and size of *S. tracheacolum* infection and the severity of audible respiratory clinical signs in Gouldian Finches.

Number of days infected	Sex of host	Head colour of host	Weight of host	Severity of audible respiratory clinical signs	Size of mite infrapopulation (total number of mites)
41 D	F	B	12.5	nil	1
6 D	M	O	16.7	nil	1
13 D	F	B	NR	nil	1
14 D	M	O	NR	nil	3
129 D	F	O	17.4	nil	5
736 K	M	O	18.8	nil	5
110 D	F	B	12.9	nil	7
279 K	M	B	14.4	wheeze	8
9 D	F	B	12.5	nil	9
96 D	M	O	17.1	nil	11
95 D	M	O	12.9	nil	13
433 K	F	B	13.9	nil (ns)	13
102 K	M	O	14.4	wheeze	13
95 D	F	B	16.0	nil	17
303 D	M	O	13.3	heavy wheeze	19
351 K	M	R	19.6	slight wheeze	22
54 D	F	B	14.2	nil (ns)	23
554 K	M	B	16.0	wheeze	23
189 D	F	B	13.7	wheeze	25
166 D	F	B	15.8	heavy wheeze/ gurgle (ns)	27
77 D	F	B	14.4	nil	28
433 K	M	O	18.7	wheeze	29
104 K	M	O	14.5	slight wheeze	30
105 K	M	O	20.1	slight wheeze	31
351 K	M	O	22.5	slight wheeze	31
279 K	M	O	16.3	heavy wheeze/ gurgle	35
92 D	M	R	13.0	slight wheeze (ns)	41
210 D	F	R	NR	wheeze (ns)	41
241 D	M	R	17.0	wheeze	42
279 K	F	B	14.4	heavy wheeze/ gurgle	73
76 D	M	B	14.7	nil (ns)	73
260 D	F	B	15.2	heavy wheeze	77
359 K	F	B	16.2	wheeze	82
233 D	F	B	15.0	heavy wheeze/ gurgle	91
193 D	F	B	14.9	heavy wheeze/ gurgle (ns)	160
194 D	F	R	14.0	wheeze	162
100 K	M	O	16.1	heavy wheeze	168
150 D	F	B	13.5	slight wheeze	175
176 K	M	O	19.9	wheeze	178
162 K	M	R	16.3	wheeze	185
351 K	F	O	15.8	heavy wheeze/ gurgle	192
107 K	F	B	17.8	slight wheeze	215
176 K	M	O	14.8	heavy wheeze/ gurgle	216
159 D	F	B	13.4	heavy wheeze/ gurgle	224
172 K	F	B	14.5	heavy wheeze/ gurgle	257
173 K	F	B	16.1	heavy wheeze/ gurgle	273
230 D	M	O	13.0	wheeze (ns)	285

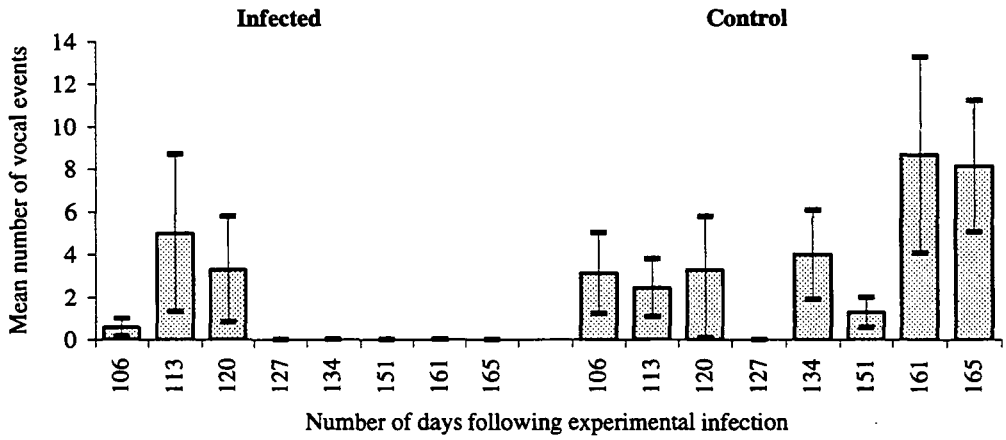
ns = nasal discharge; K = bird killed; D = bird died; NR = not recorded; B = black head; O = Orange head; R = red head.

Figure 6.3 Behaviour of Gouldian Finches *E. gouldiae* infected by *S. tracheacolum*: between 106 and 165 days following initial infection. Mean values ± SE for all birds, male and female; **Infected** 106 days (n = 8), 113 days (n = 7), 120 days (n = 7), 127 days (n = 7), 134 days (n = 7), 151 days (n = 7), 161 days (n = 7), 165 days (n = 5); **Uninfected** 106 days (n = 8), 113 days (n = 7), 120 days (n = 7), 127 days (n = 7), 134 days (n = 7), 151 days (n = 7), 161 days (n = 7), 165 days (n = 7).

A. Preening



B. Vocal events



C. Distance of flight

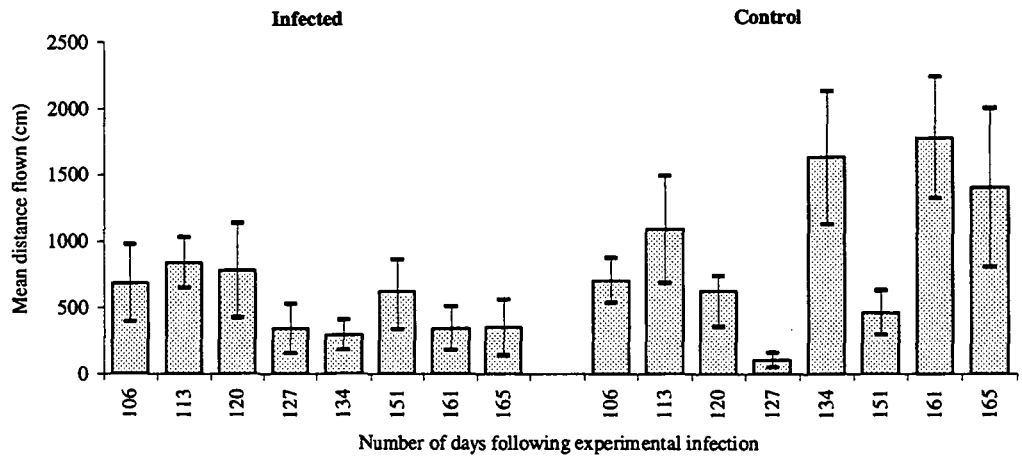


Table 6.7 Exercise ability of Gouldian Finches *E. gouldiae* infected with *S. tracheacolum* and Gouldian Finches maintained free of infection for 6 months during the 1992 aviary experiment.

Identity	Sex of host	Weight of host	17/7 Clinical signs at rest	17/7 Clinical signs following exercise	17/7 1500h Duration of maintained flight A (seconds)	17/7 1600h Duration of maintained flight B (seconds)	24/7 Clinical signs at rest	24/7 Clinical signs following exercise	24/7 Duration of maintained flight A (seconds)	Total number of mites in infrapopulation
Infected										
G/P 163	Male	19.9	nil	wheeze	76	82	heavy wheeze	heavy wheeze	56	178 (31/7/92)
LG/W 162	"	16.3	wheeze	"	41	25	slight wheeze	"	38	185 (30/7/92)
LB/R 165	"	14.8	heavy wheeze	heavy wheeze/ gurgling	22	40	wheeze	"	24	216 (31/7/92)
Z/R 160	Female	14.4	wheeze/ gurgling	wheeze	36	39	slight click	heavy click	55	257 (27/7/92)
R/W 167	"	14.7	nil	click	84	89	nil	slight wheeze	133	41 (2/9/92)
O/R 161	"	16.1	heavy wheeze/ gurgling	heavy wheeze	23	31	wheeze	heavy wheeze/ gurgling	14	273 (28/7/92)
Uninfected										
W/O 1028	Male	15.9	slight wheeze	nil	346	-	nil	nil	173	-
R/P 1023	"	16.3	nil	"	318	-	"	"	292	-
R/LB 1026	"	13.0	"	"	274	-	"	"	610	-
B/B 1025	Female	16.3	"	"	267	-	"	"	234	-
R/Z 1027	"	15.5	"	"	178	-	"	"	260	-
W/W 1024	"	17.5	"	"	105	-	"	"	211	-
				"						

Table 6.8 Comparisons of the mean measurements of the duration or frequency of a behaviour between infected and uninfected birds during the 1992 aviary experiment.

Description of behaviour (measured over a 5 minute observation period)	Infected (n=7) Mean ± SE	Uninfected (n=7) Mean ± SE	f	*P*
Distance flown (total distance flown in cm)	552.9 ± 102.4	994.8 ± 169.4	3.96	0.07
Male singing (frequency)	0 (n =3)	0.32 ± 0.19 (n =3)		
Male singing (mean time duration in seconds)	0 (n = 3)	1.75 ± 1.5 (n =3)		
Vocalisations (frequency of events)	0.9 ± 0.67	2.99 ± 0.88	3.55	0.09
Bill wiping (frequency of events)	1.86 ± 0.46	0.62 ± 0.16	6.56	0.02 ‡
Preening (frequency of events)	1.94 ± 0.35	4.58 ± 0.64	13.19	0.03 ‡
Preening (mean time duration in seconds)	10.41 ± 3.33	26.74 ± 4.07	9.63	0.009 ‡
Bill gaping (frequency)	0.61 ± 0.18	0.22 ± 0.09	3.94	0.07
Head shaking (frequency)	1.04 ± 0.24	0.24 ± 0.05	15.10	0.002 ‡
Sneezing (frequency)	3.05 ± 1.41	0	5.4	0.04 ‡
Sleeping (mean time duration in seconds)	8.22 ± 4.69	0	3.8	0.07
Throat clearing (frequency)	2.39 ± 1.5	0.04 ± 0.03	4.41	0.05 ‡

Mean values presented represent the average values for 8 observations each of 5 minutes taken at 106, 113, 120, 127 134 151 161 and 165 days following experimental infection; ‡, significant differences.

infected bird carrying 41 mites and showing no or only slight audible respiratory clinical signs showed the longest period of sustained flight.

6.3.4 Other clinical signs of *S. tracheacolum* infection

A number of the clinical signs previously described by other authors were evident in captive reared Gouldian Finches in the present study.

Figure 6.3 presents mean group values for observations taken between 106 and 165 days following initial infection. Infected birds appeared to spend less time preening (Figure 6.4A), a trend also evident from the examination of mean values for individual birds over the entire observation period (Figure 6.5A, 6B). Individual infected birds spend less time preening than their uninfected counterparts (Figure 6.5A) and this would appear to be accounted for by a reduction in the number of preening events rather than a reduction in the duration of each preening event (Figure 6.5B).

Infected birds cease to vocalise as a result of infection (Figure 6.3B). Only uninfected birds vocalised throughout the entire period of observations (between 106 and 165 days followings initial infection). Infected birds vocalised during observations taken at 106, 113 and 120 days following infection but no vocalisations were recorded during observations at 127, 134, 151, 161 and 165 days following infection.

Figures 6.4 and 6.5 summarise mean observational data for infected and uninfected bird groups at the observation points, 106, 113, 120, 127, 134, 151, 161 and 165 days (Figure 6.4) and mean observational data for individual birds for the entire period between 106 and 165 days following initial infection (Figure 6.5). Comparisons between data obtained from infected and uninfected birds is summarised in Table 6.8. Infected birds sleep during the day (particularly after 127 days of infection), and clear their throats and sneeze frequently. These clinical signs probably increase with severity and duration of infection (Figure 6.4A, 6.4B, and 6.4C) and were not present in uninfected birds. Head shaking, bill gaping and bill wiping were more common in infected birds than uninfected birds though there was no apparent trend with duration or severity of infection (Figure 6.4D, 6.4E, 6.4F). Infected birds vocalise less frequently than their uninfected counterparts (Figure 6.4F) and only uninfected male birds were observed to sing at observation points throughout the observation period 29 May to 17 July (Figure 6.4E).

6.4 DISCUSSION

Clinical signs associated with *S. tracheacolum* infection in the Gouldian Finch and other avicultural species have been adequately described by previous authors (eg. Murray, 1966; Riffkin & McCausland, 1972; Jolivet, 1975; Szeleszczuk & Kruszewicz, 1987). However, the relationship

Figure 6.4 The presence of respiratory signs of *S. tracheacolum* infection in Gouldian Finches *E. gouldiae*: for observations made between 106 and 165 days following experimental infection (Infected and control: 1 = 106 days; 2 = 113 days; 3 = 120 days; 4 = 127 days; 5 = 134 days; 6 = 151 days; 7 = 161 days; 8 = 165 days following experimental infection). Mean values for all birds, male and female; **Infected** 106 days (n = 8), 113 days (n = 7), 120 days (n = 7), 127 days (n = 7), 134 days (n = 7), 151 days (n = 7), 161 days (n = 7), 165 days (n = 5); **Uninfected** 106 days (n = 8), 113 days (n = 7), 120 days (n = 7), 127 days (n = 7), 134 days (n = 7), 151 days (n = 7), 161 days (n = 7), 165 days (n = 7).

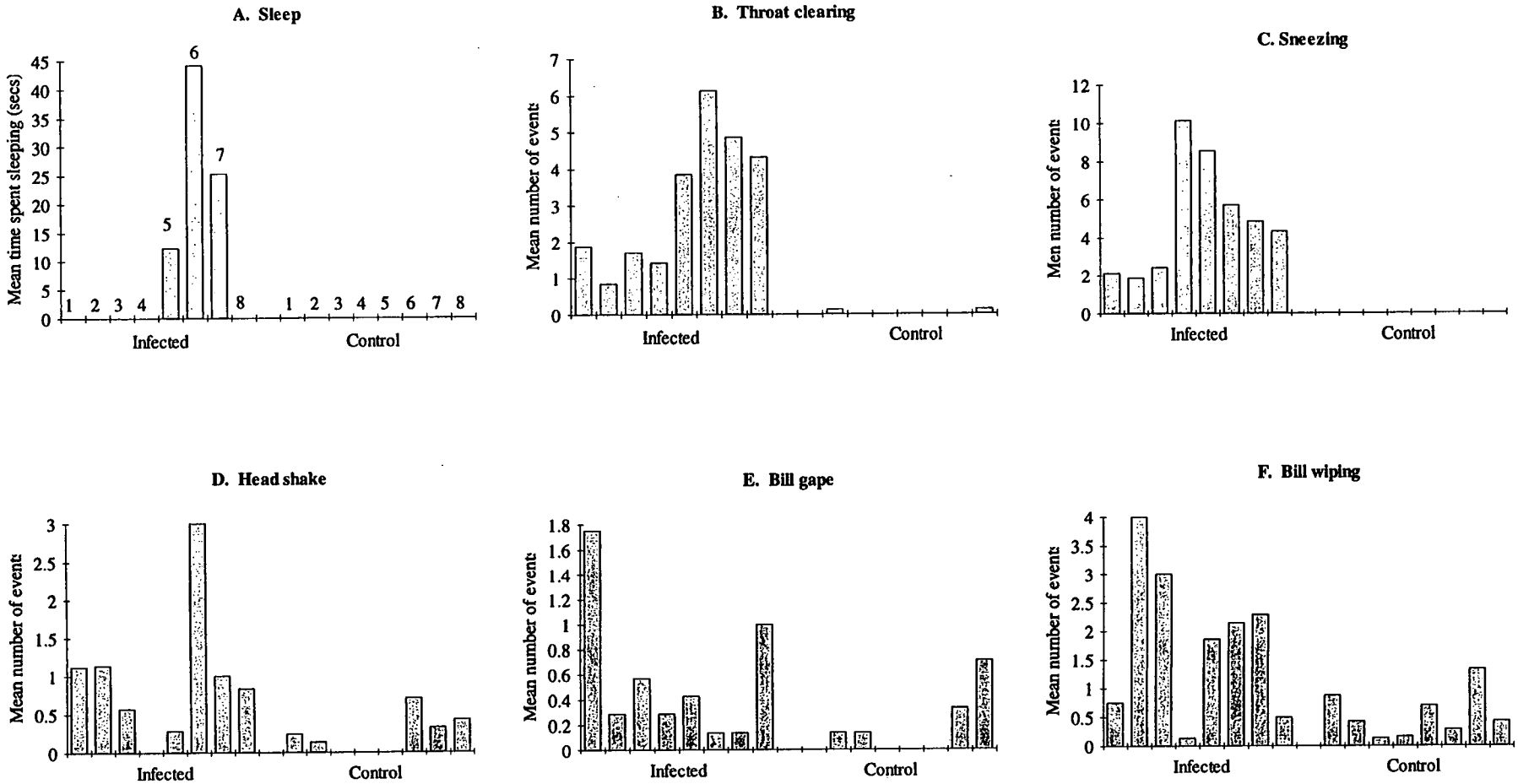
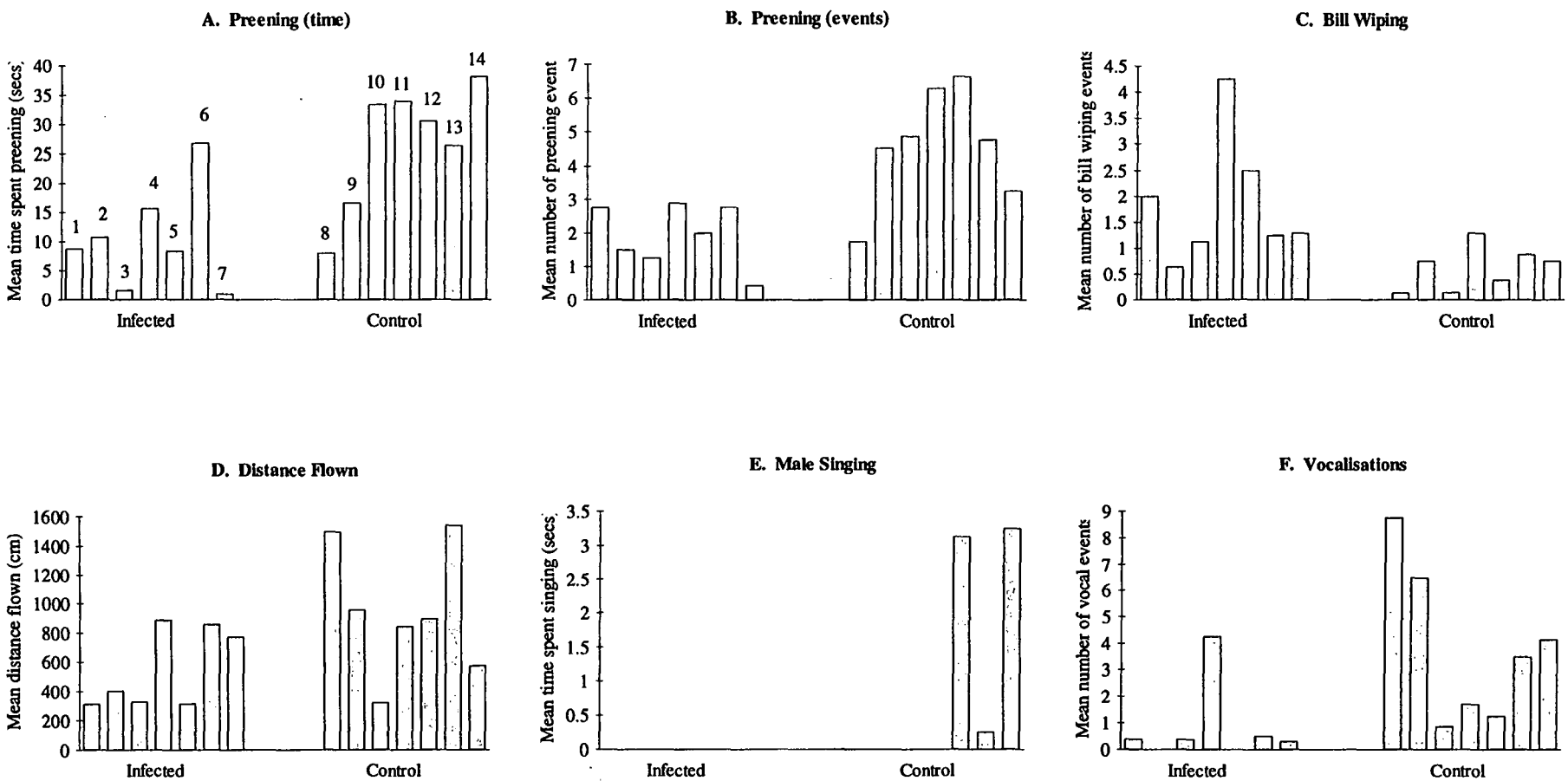


Figure 6.5 The presence of clinical signs of *S. tracheacolum* infection in individual Gouldian Finches *E. gouldiae*: for observations made between 106 and 165 days following experimental infection (Infected: 1 = Female, Orange head; 2 = Female, Black head; 3 = Female, Orange head; 4 = Male, Orange head; 5 = Male, Orange head; 6 = Male, Red head; 7 = Male, Black head. Control: 8 = Female, Black head; 9 = Female, Black head; 10 = Female, Black head; 11 = Female, Orange head; 12 = Male, Black head; 13 = Male, Orange head; 14 = Male, Black head).



between audible respiratory clinical signs and (a) the duration of the infection and (b) the size of the infection, has not previously been addressed.

Audible respiratory clinical signs (i.e. wheezing, clicking and gurgling) provide the most useful indicators of the size of the infection. However, as the relationship between severity of clinical signs and duration of infection is not linear, (Chapter 3: Section 3.3.2, Infrapopulation growth of *S. tracheacolum*) infections of long standing may be easily confused with those of recent origin, particularly where the history of the bird is not known. Wheezing or heavy wheezing (± clicking and gurgling) is generally indicative of a large *S. tracheacolum* mite infection.

The clinical signs of birds carrying small numbers of mites in long standing infections (i.e. longer than 12 months duration) may mimic those from birds infected by large numbers of mites of only short duration (i.e. less than 3 months duration). This may to some extent be explained by differences in the locality of mites within the respiratory system rather than the total number of mites present. Audible respiratory clinical signs result from the presence of excess mucus and associated agglomerations of mites within the upper respiratory system, particularly in the bronchus, syrinx and trachea. In the early stages of infection, the greater proportion of a mite infrapopulation is located in the lower respiratory system (i.e. lungs and airsacs). As the course of the infection progresses, in time, the greater proportion of the mites occur in the upper respiratory system (i.e. bronchus syrinx and trachea; see Chapter 3: Section 3.3.3.2, The proportion of mites in the upper and lower respiratory system and the duration of infection). Mites in the trachea rather than the airsacs have the potential to elicit mucus production and themselves cause obstruction, thus creating a recipe for audible respiratory clinical signs.

The clinical signs of *S. tracheacolum* infection in captive reared Gouldian Finches may have implications for the survival and reproductive potential of wild Gouldian Finches. However, prior to speculation it is first necessary to establish that the parameters of infection in captive populations are similar to those of wild populations. Between 33 and 100% of wild Gouldian Finches are infected by *S. tracheacolum* (overall prevalence = 47.4%, see Chapter 7: Section 7.3.2, Prevalence of infection) at an intensity of between 20.5 and 33 mites per infected host (overall intensity = 26.7 mites per infected host, see Chapter 7: Section 7.3.3, Intensity of infection). Heavy infections are common in wild birds and infections containing up to 267 mites have been found in immature wild caught Gouldian Finches. These figures clearly indicate that intensities of infection found in captive birds are comparable with by those in wild caught birds. Infections of this magnitude, in wild birds, are likely to have significant impacts on the ability of their hosts to maintain flight for prolonged periods and to communicate with other individuals. For male birds, the ability to successfully court females may be severely hampered. It is therefore reasonable to

anticipate that life history parameters of the infected population will differ markedly from the uninfected population.

Chapter 7. HOST SPECIFICITY

7.1 INTRODUCTION

The Rhinonyssidae exhibit a varying degree of host specificity (Domrow, 1987). Some species are restricted to one host species, while others are reported from many different families of hosts (Pence, 1973).

The genus *Sternostoma* is a large and cosmopolitan group that has been found in many bird species, genera, families and orders. Most species are host specific at or above the familial level except for *S. tracheacolum* which occurs in numerous families of the Passeriformes as well as the Psittaciformes. Unlike all other rhinonyssids, *S. tracheacolum* is the only species that occurs primarily in the trachea, lungs and airsacs (Domrow, 1969). This movement into the lower respiratory system may be of recent origin and may to some extent explain the apparent lack of host specificity exhibited by this parasite (Radovsky, 1969).

Several authors have reviewed host specificity and phylogeny of the nasal mite groups (e.g. Hyland, 1963; Domrow, 1969). Bregetova (1967) noted that in the Macronissidae (a group closely allied to the Rhinonyssidae) that parasitise bats, more primitive parasites tend to be associated with the more primitive hosts and that the evolution of the parasites appears to have occurred in parallel with that of the hosts. In contrast, there is a lack of relationship between the evolution of birds and that of the Rhinonyssidae which suggests that the radiation of the rhinonyssids (all endoparasitic in birds) probably took place recently and subsequent to the divergence of the major avian groups (Radovsky, 1969).

Large studies on the prevalence of rhinonyssids and other nasal mites (e.g. Maa & Kuo, 1965; Domrow, 1969; Pence, 1973; Spicer, 1987) have indicated that between 35 and 50% of bird species are suitable hosts and to some extent the proportion of species acting as hosts varies among families. There is consistent evidence of geographic variation in prevalence of rhinonyssids within host species (Maa & Kuo, 1965; Spicer, 1987).

Few studies have investigated changes in the parameters of nasal mite infection over time (e.g. Vaccari and Ballarini, 1963; Domrow, 1967; Hood and Welch, 1980; Amerson, 1967) and no studies have surveyed the prevalence within host species over more than a year. Domrow (1967) found no difference in the prevalence and the intensity of rhinonyssid infection between the 'wet' and the 'dry' season of Australia's tropics and considered that the stability in the parameters of infection was probably a reflection of the consistency of the nasal cavity microclimate in contrast to the extreme climatic changes that occur between the seasons. Amerson (1967) detected variations

in both the prevalence and intensity of infection during the breeding season of the Sooty Tern and attributed these to aspects of the timing and mechanism of rhinonyssid transmission.

Some authors have noted differences in the intensity of infection and the age and sex of host individuals (e.g. Murray, 1966; Tidemann *et al.*, 1992a). Murray (1966) noted that in captive Gouldian Finches infected with *S. tracheacolum* juveniles were more heavily infected than adults. Tidemann *et al.* (1992a) found the converse in wild Gouldian Finches and also detected differences in the intensity of infection and the sex of host birds.

The investigation of prevalence and intensity of infection, mean parasite burden and or measures of the distribution of parasites in the host population (i.e. measures of dispersal), do not provide useful indicators of the state of the parasite-host relationship at the population level unless also tracked through time and supplemented by other studies. This is particularly true for the Rhinonyssidae where the parasite-host relationship remains poorly understood. Such descriptive parameters alone cannot indicate whether a particular parasite-host relationship is aberrant or whether infections are in anyway different from a putative normal pattern and hence whether the relationship is likely to have a strong or weak influence on the demography of the host population. The parameters of infection, however, become more meaningful when comparisons can be made between host individuals and host groups, and over space and time. Tidemann *et al.* (1992a) examined some 380 individuals of eight finch and mannikin species and a further 240 individuals from 78 genera and 32 families of birds in northern Australia and found *S. tracheacolum* in only three species, the Gouldian Finch, Masked Finch and Pictorella Mannikin. By comparison with the Masked Finch and the Pictorella Mannikin they considered that both the prevalence and the intensity of the infection in the Gouldian Finch appeared high.

The present study extends the work of Tidemann and her associates to a comparison of the prevalence and intensity of *S. tracheacolum* infection and other rhinonyssid infections between geographic localities, between taxonomic host groups and between successive years. Additional comparisons are also made between the measures of infection reported here and those reported by other authors, both for *S. tracheacolum* and other nasal mite infections. The primary aim of this investigation is to determine whether the measures of infection observed for *S. tracheacolum* infection in the Gouldian Finch are aberrant in comparison to the corresponding measures in other host species parasitised by *S. tracheacolum* and or other rhinonyssid mites.

7.2 METHODS

7.2.1 Wild Hosts

Gouldian Finches, Long-tailed Finches, Masked Finches, Pictorella Mannikins, Zebra Finches, Double-barred Finches and Budgerigars were collected by mist netting or by shooting at Newry Station, Northern Territory in August 1992, July 1993 and August 1994. These samples were supplemented by collections of Long-tailed Finches, Masked Finches and Gouldian Finches from Yinberrie Hills, Northern Territory between 1992 and 1994 which died accidentally during banding/netting operations (Table 7.1). To supplement the major sampling effort at Newry Station it was intended that a sample of 10 Gouldian Finches be taken at Newry Station in 1993. However, following considerable difficulty in capturing birds they were subsequently taken at Yinberrie Hills. The localities where birds were captures is shown in Figure 8.1.

Some birds were examined fresh, others were frozen and examined within a month following collection. The sex, age and weight were recorded for each bird. These data are listed in Appendix IV. The nasal cavity, lower respiratory system and the general body cavity of all birds were then dissected and examined for nasal mites.

Table 7.1 Locality and number of birds examined.

Birds examined	Locality and date of collection		
	Newry Station August 1992	**Newry Station July 1993**	**Newry Station August 1994**
Gouldian Finch	-	4 4I, 2M 2F	-
Long-tailed Finch	9 9A, 4M 4F 1U	29 28A 1I, 17M 12F	33 32A 1I, 15M 18F
Masked Finch	29 29A, 16M 13F	23 22A 1I, 14M 9F	20 19A 1I, 12M 8F
Pictorella Mannikin	30 26A 4I, 17M 13F	15 11A 4I 7M 8F	29 12A 17I, 17M 11F
Zebra Finch	-	11 11A, 5M 6F	13 12A 1I, 7M 6F
Double-barred Finch	1 1A, 1F	1 1A, 1F	4 4A, 1M 3F
Budgerigar	27 26A 1I, 13M 14F	26 22A 4I, 18M 8F	33 21A 12I, 21M 12F
	Yinberrie Hills August 1992	**Yinberrie Hills July 1993**	**Yinberrie Hills August 1994**
Gouldian Finch	3 1A 2I, 2M 1F	12 12I, 9M 2F 1U	-
Long-tailed Finch	6 6A, 3M 3F	14 12A 2I, 7M 7F	3 3A, 2M 1F
Masked Finch	2 1A 1I, 2M	9 7A 2I, 7M 4F	1 1A, 1M

(A = Adult; I = Immature; M = Male; F = Female; Sex undetermined)

A record was made of the site in the host where each mite was found and whether the mite was live or dead at the time of host death (see Chapter 9: Section 9.2.2, Post-mortem examination of birds). Following initial storage in 70% alcohol, all mites were cleared and mounted on microscope slides. The species, sex and stage was determined for each specimen. Keys for 'Mesostigmata parasitic on

Australian vertebrates' (Domrow, 1987), 'Astigmata parasitic on Australian vertebrates' (Domrow, 1992), 'Cytoditidae' (Fain & Bafort, 1964) and '.....nasal mites of North American Birds (Acarina: Rhinonyssidae, Turbinoptinae, Speleognathinae and Cytoditidae)' (Pence, 1975), were used to identify mites.

7.2.2 Parameters of infection

Within population **prevalence of infection** was calculated as the percentage of a sample of hosts that were infected. Prevalence of infection, at the species level, was calculated as the percentage of species in a sample that were infected. The within population **intensity of infection** was calculated as the total number of mites from all infections in a host sample, divided by the total number of hosts infected. The total number of mites in an **infrapopulation** included all mites (live or dead) of both sexes and all stages (larval, nymphal and adult) found within one host. The **mean parasite burden** was calculated as the total number of mites from all infrapopulations in a host sample divided by the sum of the infected and non-infected individuals in that sample.

7.2.3 Analysis

Statistical Analysis System programs (SAS Institute INC., 1988) were used in the analysis of data. Continuity-adjusted chi-square (χ^2) tests were performed on prevalence (frequency) data using PROC FREQ with the CHISQ option; the CMH option, requesting Cochran-Mantel-Haenszel statistics, was used on 3-way contingency tables to analyse the relationship between host sex and age, and the presence of infection. PROC NPAR1WAY was used to perform Wilcoxon 2-Sample Tests and Kruskal-Wallis Tests on comparisons of intensity of infection between host species; Kolmogorov-Smirnov 2-Sample Tests were used to compare the frequency distribution of mites in host samples between host species.

7.3 AUSTRALIAN WILD HOSTS

7.3.1 Occurrence of rhinonyssid mites

Table 7.2 lists the 6 species of rhinonyssid and the 2 species of kytoditid mites found in the respiratory system of the 7 bird species surveyed.

7.3.1.1 *Sternostoma*

S. tracheacolum was previously recorded in Australia by Tidemann *et al.* (1992a) from the Gouldian Finch, Masked Finch and Pictorella Mannikin, and from the same localities as those reported here (i.e. Newry Station and Yinberrie Hills, Northern Territory). Tidemann *et al.* (1993) also found *S. tracheacolum* in the wild Gouldian Finch taken in Queensland. Whereas *S. tracheacolum* has been previously recorded from captive reared Budgerigars (e.g. Fain & Hyland (1962) in Belgium; Mathey (1967) in the USA and Amaral (1968) in Brazil), this is the first record from the wild Budgerigar.

Table 7.2 The occurrence of rhinonyssid and kytoditid mites in the Gouldian Finch and six co-occurring species at Yinberrie Hills and Newry Station, NT in August 1992, July 1993 and August 1994.

Host	Parasite	Remarks
PSITTACIDAE		
Melopsittacus undulatus (n = 86) Budgerigar	*Sternostoma tracheacolum*	New host record
PASSERIFORMES		
Erythrura gouldiae (n = 19) Gouldian Finch	*Sternostoma tracheacolum*	Recorded by Tidemann *et al.* (1992)
	Sternostoma paddae	New host and Australian record
Heteromunia pectoralis (n = 74) Pictorella Mannikin	*Sternostoma tracheacolum*	Recorded by Tidemann *et al.* (1992)
	Ptilonyssus emberizae	New host record
Poephila acuticauda (n = 94) Long-tailed Finch	*Sternostoma paddae*	New host and Australian record
	Ptilonyssus astridae	New host record
	Ptilonyssus neochmiae	New host record
	Kytonyssus andrei	New host and Australian record
Poephila personata (n = 85) Masked Finch	*Sternostoma tracheacolum*	Recorded by Tidemann *et al.* (1992)
	Sternostoma paddae	New host and Australian record
	Ptilonyssus astridae	New host record
	Kytodites amandavae	New host and Australian record
Taeniopygia bichenovii (n = 6) Double-barred Finch	*Ptilonyssus emberizae*	Recorded by Domrow (1987)
Taeniopygia guttata (n = 24) Zebra Finch	*Ptilonyssus astridae*	New host record
	Sternostoma sp.	New host record

The morphology of *S. tracheacolum* specimens from the wild Budgerigar is identical to that reported by Fain and Hyland (1962) for specimens coming from Budgerigars found dead at the Antwerp Zoo, Belgium in 1958 (Chapter 1: Morphology). This morphological similarity suggests that infection was probably brought with host specimens from the wild and was not contracted during their captivity. Overseas, *S. tracheacolum* has been recorded from a large number of passeriform and psittaciform species from both wild and captive hosts (Tables 7.6 and 7.7).

Sternostoma paddae Fain 1958 has been recorded only from the Java Sparrow *Padda oryzivora* (L.) (Estrildidae) a native of Java, Bali and Sumatra (Fain, 1958). *S. paddae* has been associated with conjunctivitis in captive hosts (Domrow, 1969). The original description is of specimens from the respiratory system of a captive bird that died at the Antwerp Zoo in Belgium. *S. paddae* is a new species record for Australia, and the Gouldian Finch, Long-tailed Finch and Masked Finch are all new host records.

A single specimen of *Sternostoma* sp. (not *S. tracheacolum*) was found in the nasal cavity of the Zebra Finch at Newry Station. Insufficient characters were discernible to identify the specimen to species level; nonetheless the Zebra Finch represents a new host record for this genus.

7.3.1.2 *Ptilonyssus*

Ptilonyssus astridae Fain 1956 was found in the nasal cavity of the Zebra Finch, Long-tailed Finch and Masked Finch. Previous host records include the Red-billed Firefinch *Lagonosticta rubricata congica* Sharpe (Estrildidae) from Africa (Fain, 1956) and the Chestnut-breasted Mannikin *Lonchura castaneothorax* (Gould) (Estrildidae) from 'The Kimberley', Western Australia (Fain & Lukoschus, 1979). The Zebra Finch, Long-tailed Finch and the Masked Finch are all new host records.

Ptilonyssus emberizae Fain 1956 was described from the emberizid *Emberiza flaviventris* Stephens in Africa. It has been recorded from wild emberizids, fringillids and hirundinids (Kadosaka, Kaneko & Asanuma, 1983; Guewara-Benitez, Ubeda-Ontiveros & Morillas-Marquez, 1986) and the captive reared Gouldian Finch overseas (Domrow, 1969). In Australia *P. emberizae* has been found in the Double-barred Finch *Taeniopygia bichenovii* (Vigors & Horsfield) in 'The Kimberley', Western Australia (Domrow, 1987). The Pictorella Mannikin is a new host record.

Ptilonyssus neochmiae Domrow 1969 was found in the nasal cavity of the Long-tailed Finch. This species was described from the Crimson Finch *Neochmia phaeton* (Hombron & Jacquinot) in Queensland, Australia (Domrow, 1969). It has also been recorded from the captive reared Gouldian

Finch, in Darwin by the author (Appendix II: *Ptilonyssus neochmiae* Domrow 1969 in the captive reared Gouldian Finch). The Long-tailed Finch is a new host record.

7.3.1.3 *Kytonyssus*

Two species of Kytoditidae were found in the respiratory system of the birds surveyed. *Kytonyssus andrei* Fain 1960 was present in the nasal cavity of the Long-tailed Finch. A single mite was found in 1 of 11 birds collected at Newry Station. Previous host records include estrildids and emberizids from Africa and Asia. Host species records include *Munia punctulata* (L.) from Malaysia and the Java Sparrow *P. oryzivora* from Indonesia (Fain & Bafort, 1964). *K. andrei* is a new genus record for Australia and the Long-tailed Finch is a new host record.

7.3.1.4 *Kytodites*

Kytodites amandavae Fain & Bafort (1964) was found in the airsacs and the trachea of the Masked Finch at a prevalence of 12% (n = 25) in 1993 and 10% (n = 20) in 1994 at Newry Station only. The mean intensity was 3 mites per infected host in 1993 and 8 mites per infected host in 1994. This species has previously been reported from the Red Avadavat *Amandava amandava* (L.), Estrildidae (Fain & Bafort, 1964) which has a distribution from southern to south-eastern Asia, as far east as Timor (Long, 1981) and *Sporopipes frontalis* Daudin (Passeridae) from north Africa. Two species of *Kytodites* are known from wild birds in Australia. *K. geopeliae* Fain & Lukoschus, is known from the trachea of the Bar-shouldered Dove *Geopelia humeralis* (Temminck) in the Kimberley region of Western Australia (Fain & Lukoschus, 1979). *Kytodites* sp, an undescribed species and similar to *K. nudus* (Vizioli) is known from the White-browed Babbler *Pomatostomus superciliosus* (Timaliidae) in South Australia (Domrow, 1992). *K. amandavae* is a new species record for Australia and the Masked Finch is a new host record.

7.3.2 Prevalence of infection

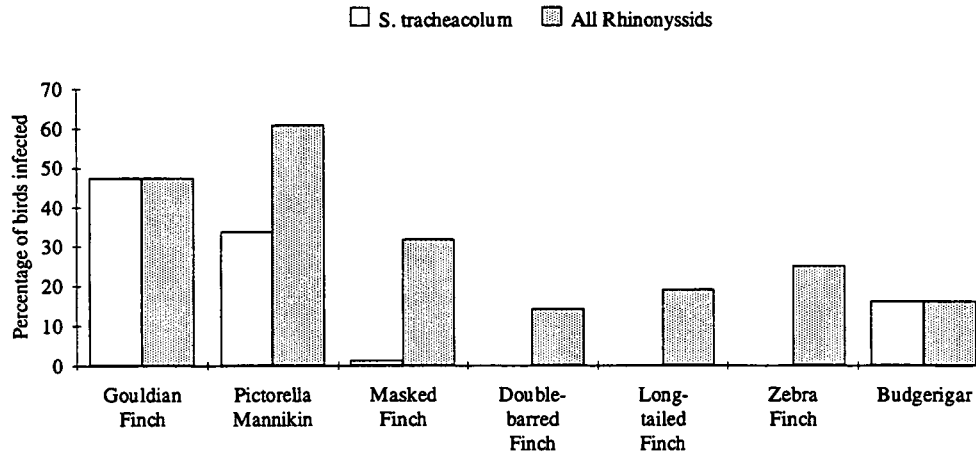
The prevalence of rhinonyssids at Yinberrie Hills and Newry Station between 1992 and 1994 is shown in Table 7.3. The prevalence overall (i.e. pooled data for Yinberrie Hills and Newry Station in all years) for *S. tracheacolum* and 'all rhinonyssids' is shown in Figure 7.1A. All of 7 bird species examined were infected by nasal mites: Budgerigar 1, Gouldian Finch 2, Pictorella Mannikin 2, Long-tailed Finch 4, Masked Finch 4, Zebra Finch 2 and Double-barred Finch 1. The prevalence of nasal mite infection overall for all individual birds examined was 33% (n = 388).

7.3.2.1 Prevalence of infection by *S. tracheacolum*

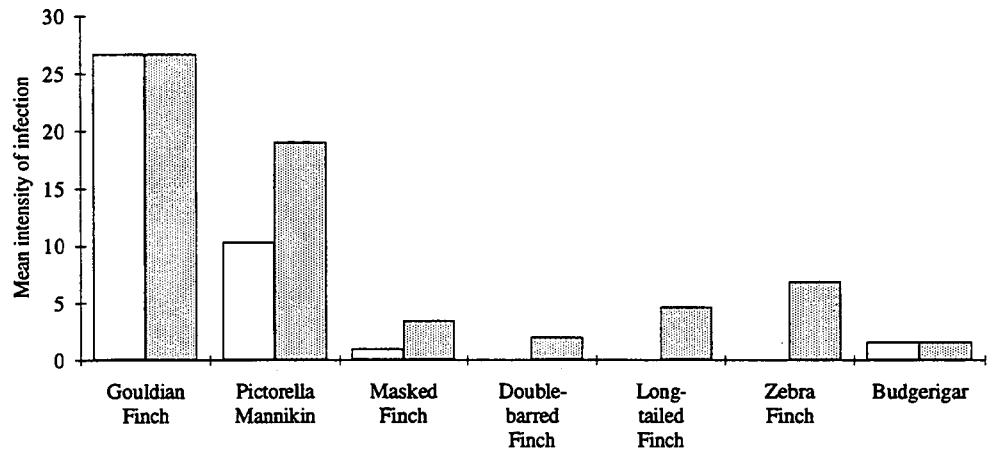
The prevalence of infection in the Gouldian Finch was similar between sites. Overall, the prevalence was 47.4%. For ethical reasons juvenile birds were taken in preference to breeding adults. Therefore, prevalence figures for this species are primarily for juvenile (n = 6) and immature

Figure 7.1 Parameters of rhinonyssid infection in the Gouldian Finch and six co-occurring species: A, Prevalence; B, Intensity; C, Mean parasite burden. Data is pooled from both sites (i.e. Yinberrie Hills and Newry Station, NT) and from all sample years (ie. 1992, 1993 and 1994).

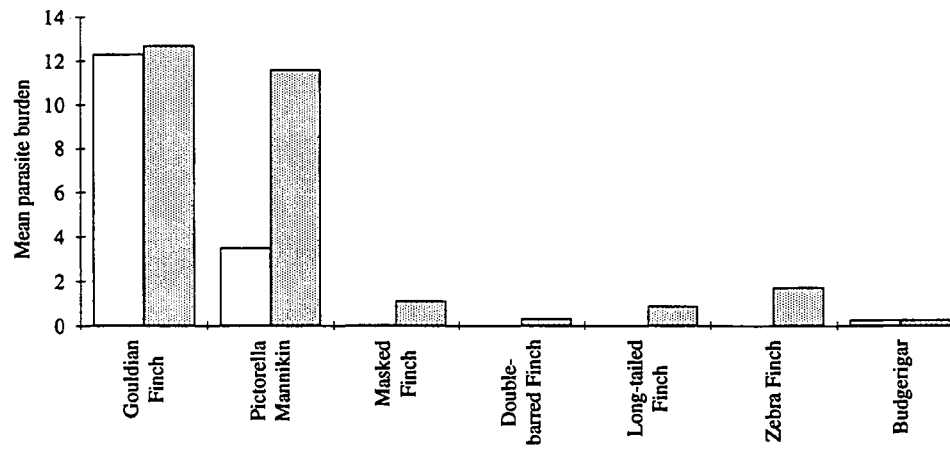
A.



B.



C.



birds (n = 12) and not adult birds (n = 1). Sixty percent of females (n = 5) and 50% of males (n = 12) were infected though sex was not determined for two juvenile birds taken at Yinberrie Hills.

The prevalence of infection in the Pictorella Mannikin at Newry Station did not vary significantly between 1992 (20%), 1993 (47%) and 1994 (41%) ($\chi^2 = 4.4$, df = 2, $P = 0.11$). Tidemann *et al.* (1992a) reported a prevalence of 12.5% from 8 Pictorella Mannikins collected in 1987. This was not significantly different from the prevalences recorded at Newry Station between 1992 and 1994 ($\chi^2 = 6.7$, df =3 $P = 0.08$).

The prevalence of infection in the Budgerigar at Newry Station did not vary significantly between 1992 (22%), 1993 (15%) and 1994 (12%) ($\chi^2 = 1.1$, df = 2, $P = 0.56$).

Only at Newry Station in 1992 was a Masked Finch found to be infected. The prevalence of 3% was not significantly different from that found by Tidemann *et al.* (1992a) from the examination of 118 Masked Finch specimens taken between 1987 and 1991 (Prevalence = 0.8%; Fisher exact test; $P = 0.81$).

Considering overall figures, the prevalence of infection was significantly higher in the Gouldian Finch and the Pictorella Mannikin than the Budgerigar and the Masked Finch ($\chi^2 = 38.1$, df = 1, $P < 0.0001$) however, the prevalence of infection in the Gouldian Finch was not significantly different from the Pictorella Mannikin ($\chi^2 = 1.2$, df = 1, $P = 0.27$).

7.3.2.2 Prevalence of infection by other rhinonyssids

The prevalence of *P. emberizae* infection in the Pictorella Mannikin differed significantly between years at Newry Station ($\chi^2 = 6.8$, df = 2, $P = 0.03$) rising dramatically from a prevalence of 20% in 1992 and 13% in 1993 to 72% in 1994. The prevalence of *P. astridae* infection in the Masked Finch did not differ significantly between 1992 and 1994 at Newry Station ($\chi^2 = 1.163$, df = 2, $P = 0.56$). The prevalence of *S. paddae* in the Gouldian Finch (Fisher Exact Test; $P = 0.81$), Long-tailed Finch (Fisher Exact Test; $P = 0.3$) and the Masked Finch (Fisher Exact Test; $P = 0.18$) and the prevalence of *P. neochmiae* in the Long-tailed Finch (Fisher Exact Test; $P = 0.52$) did not differ significantly between years at Yinberrie Hills .

7.3.2.3 Prevalence of infection by all rhinonyssids

Prevalence of infection in the Gouldian Finch was significantly higher than that found in the Budgerigar, Long-tailed Finch, Masked Finch and the Double-barred Finch ($\chi^2 = 12.96$, df = 5, $P = 0.02$) (see Figure 7.1A). Likewise the prevalence of infection was significantly higher in the Pictorella Mannikin than the Budgerigar, Long-tailed Finch, Masked Finch and the Double-barred

Table 7.3 The prevalence of rhinonyssid mites in Gouldian Finches and six co-occurring species at Yinberrie Hills and Newry Station, NT.

Parasite/Host	Locality and date of collection					
	Yinberrie Hills August 1992	Yinberrie Hills July 1993	Yinberrie Hills August 1994	Newry Station August 1992	Newry Station July 1993	Newry Station August 1994
Sternostoma tracheacolum						
Gouldian Finch	3/3 (100)	4/12 (33)	-	-	2/4 (50)	-
Pictorella Mannikin	-	-	-	6/30 (20)	7/15 (47)	12/29 (41)
Masked Finch	0/2	0/9	0/1	1/29 (3)	0/23	0/20
Budgerigar	-	-	-	6/27 (22)	4/26 (15)	4/33 (12)
Sternostoma paddae						
Gouldian Finch	0/3	1/12 (8)	-	-	0/4	-
Long-tailed Finch	1/6 (17)	0/14	0/3	0/9	0/29	0/33
Masked Finch	1/2 (50)	0/9	0/1	0/29	0/24	0/20
Sternostoma sp.						
Zebra Finch	-	-	-	-	1/11 (9)	0/13
Ptilonyssus astridae						
Long-tailed Finch	0/6	1/14 (7)	0/3	0/9	4/29 (14)	5/33 (15)
Masked Finch	1/2 (50)	0/9	0/1	8/29 (28)	10/23 (43)	7/20 (35)
Zebra Finch	-	-	-	-	3/11 (27)	2/13 (15)
Ptilonyssus neochmiae						
Long-tailed Finch	3/6 (50)	4/14 (29)	0/3	0/9	0/23	0/33
Ptilonyssus emberizae						
Pictorella Mannikin	-	-	-	6/30 (20)	2/15 (13)	21/29 (72)
Double-barred Finch	-	-	-	0/1	0/1	1/4 (25)

(Number of individuals infected/Number of individuals examined (percentage prevalence))

Finch. However, there was no significant difference in the prevalence between the Gouldian Finch and the Pictorella Mannikin.

7.3.2.4 Prevalence of rhinonyssid mite infections and the age of hosts

Data were available on sex and age and the presence or absence of host infection for 19 Gouldian Finches, 99 Long-tailed Finches, 85 Masked Finches, 24 Zebra Finches, 9 Double-barred Finches and 86 Budgerigars. One Gouldian Finch, 3 Double-barred Finches, 2 Long-tailed Finches and a Masked Finch from Timber Creek, NT (15° 39' S 129° 29' E) were also added to the data set for analysis.

For pooled data from all seven host species from the 3 collection sites (i.e. Yinberrie Hills, Newry Station and Timber Creek) no interaction was detected between the sex and age of the host and the presence or absence of rhinonyssid infection (Cochran-Mantel-Haenszel Statistic = 0.42, df = 1, P = 0.52). There was no difference between the sex of the host and the prevalence of infection (χ^2 = 0.04, df = 1, P = 0.84) but a highly significant difference was detected between the age of the host and the prevalence of infection (χ^2 = 12.56, df = 1, P = 0.001). Pooling juvenile and immature host data to form the group 'subadult', a significantly higher proportion of subadult birds were infected than adult birds. Within species the prevalence of infected subadult birds was not significantly different from adult infected birds (i.e. Gouldian Finch (χ^2 = 1.059, df = 1, P = 0.3), Pictorella Mannikin (χ^2 = 2.76, df = 1, P = 0.10), Long-tailed Finch (χ^2 = 1.47, df = 1, P = 0.23), Masked Finch (χ^2 = 0.43, df = 1, P = 0.5) and Zebra Finch (χ^2 = 0.42, df = 1, P = 0.52) and the Budgerigar (χ^2 = 0.82, df = 1, P = 0.37).

7.3.2.5 Parasite species presence between sites

Parasite species presence varied between Newry Station and Yinberrie Hills. *S. paddae* infecting the Gouldian Finch, Long-tailed Finch and Masked Finch at prevalences of 8% (n = 12), 17% (n = 6) and 50% (n = 2) respectively, was found only at Yinberrie Hills. Likewise, *P. neochmiae* infecting the Long-tailed Finch at Yinberrie Hills at a prevalence of 35% (n = 20) was not found at Newry Station (n = 32).

7.3.2.6 Prevalence of double infections

No multiple infections were found in the present study, however, 11 double infections were found: *S. tracheacolum* and *S. paddae* in a juvenile female Gouldian Finch at Yinberrie Hills, *P. astridae* and *K. amandavae* in an adult male Masked Finch at Newry Station and *S. tracheacolum* and *P. emberizae* in 9 Pictorella Mannikins (3 immature females, 4 immature males, 1 juvenile male and 1 unsexed immature bird) at Newry Station. For all species and all birds examined this represents a double infection prevalence of 2.8% (n = 388) and a within host species prevalence of 5.3%, 1.2% and 12.2% for the Gouldian Finch, Masked Finch and the Pictorella Mannikin respectively. A

Table 7.4 The mean intensity of infection by rhinonyssids in Gouldian Finches and six co-occurring species at Yinberrie Hills and Newry Station, NT.

Parasite/Host	Locality and date of collection					
	Yinberrie Hills August 1992	Yinberrie Hills July 1993	Yinberrie Hills August 1994	Newry Station August 1992	Newry Station July 1993	Newry Station August 1994
Sternostoma tracheacolum						
Gouldian Finch	99/3 (33) 2-51	82/4 (20.5) 2-56	-	-	59/2 (29.5) 6-53	-
Pictorella Mannikin	-	-	-	11/6 (1.8) 1-4	80/7 (11.4) 2-22	167/12 (13.9) 1-84
Masked Finch				1/1 (1)		
Budgerigar	-	-	-	7/6 (1.2) 1	8/4 (2) 1-3	7/4 (1.8) 1-2
Sternostoma paddae						
Gouldian Finch		1/1 (1)	-	-		-
Long-tailed Finch	1/1 (1)					
Masked Finch	3/1 (3)					
Sternostoma sp.						
Zebra Finch	-	-	-	-	1/1 (1)	
Ptilonyssus astridae						
Long-tailed Finch		4/1 (4)			25/4 (6.3) 2-12	40/5 (8) 1-20
Masked Finch	1/1 (1)			35/8 (4.4) 2-11	36/10 (3.6) 1-8	18/7 (2.6) 1-5
Zebra Finch	-	-	-	-	13/3 (2.3) 1-9	28/2 (14) 1-27
Ptilonyssus neochmiae						
Long-tailed Finch	5/3 (1.7) 1-4	8/4 (2) 1-4		-	-	
Ptilonyssus emberizae						
Pictorella Mannikin	-	-	-	34/6 (5.7) 1-22	13/2 (6.5) 6-7	551/21 (26.2) 1-143
Double-barred Finch	-	-	-			2/1 (2)

(Total number of mites from all infected hosts/Number of infected hosts **(mean intensity of infection)** Range)

significantly higher proportion of 'subadult' birds carried double infections than adult birds (examined for Pictorella Mannikins only; $\chi^2 = 21.35$, df = 1, $P < 0.0001$) though there was no difference in the double infection prevalence between male and female birds (Fisher Exact Test; $P = 0.37$).

7.3.3 Intensity of infection

The intensity of rhinonyssid infection in birds at Yinberrie Hills and Newry Station between 1992 and 1994 is shown in Table 7.4. The overall intensity (i.e. pooled data for Yinberrie Hills and Newry Station in all years) for *S. tracheacolum* and 'all rhinonyssids' is shown in Figure 7.1B. The intensity of nasal mite infection overall for all infected individual birds examined was 10.2 (n = 388).

7.3.3.1 Intensity of infection by *S. tracheacolum*

The overall intensity of infection ranged between 26.7 mites per host for the Gouldian Finch, 10.3 for the Pictorella Mannikin, 1.6 for the Budgerigar and 1 for the Masked Finch. The mean intensity of infection differed significantly between host species, though the Masked Finch was excluded from analysis due to a lack of infected individuals in the sample (Kruskal-Wallis Test; $\chi^2 = 15.32$, df = 2, $P = 0.0005$). The intensity of *S. tracheacolum* infection in the Gouldian Finch was not significantly higher than the intensity of infection in the Pictorella Mannikin (Wilcoxon 2-Sample Test; Z = 1.58, $P = 0.11$). However, both the Gouldian Finch and the Pictorella Mannikin carried significantly larger infections than the Budgerigar (Gouldian Finch/Budgerigar: Wilcoxon 2-Sample Test; Z = 1.87, $P = 0.06$, Pictorella Mannikin/Budgerigar: Z = -2.82, $P = 0.005$).

Highest recorded mean intensities were 33 for the Gouldian Finch (n = 3) at Yinberrie Hills in 1992, 13.9 for the Pictorella Mannikin (n = 12) at Newry Station in 1994, 2 for the Budgerigar (n = 4) at Newry Station in 1993 and 1 for the Masked Finch (n = 1) at Newry Station in 1992. The highest recorded individual intensities were 84 mites for a Pictorella Mannikin from Newry Station in 1994, 56 mites for a Gouldian Finch from Yinberrie Hills in 1993, 3 mites for a Budgerigar from Newry Station in 1993 and a single mite for a Masked Finch from Newry Station in 1992.

7.3.3.2 Intensity of infection by other rhinonyssids

The overall intensity of infection in host species for *S. paddae* was 1.7 mites per host; *Sternostoma* sp., 1; *P. astridae*, 4.9; *P. neochmiae*, 1.9 and *P. emberizae*, 20.

7.3.3.3 Intensity of infection over time

Intensity of infection at Newry Station within host species and within parasite species was similar throughout the period 1992 to 1994 except for *S. tracheacolum* infection in the Pictorella Mannikin

Table 7.5 The mean parasite burden of rhinonyssids in Gouldian Finches and six co-occurring species at Yinberrie Hills and Newry Station, NT.

Parasite/Host	Locality and date of collection					
	Yinberrie Hills August 1992	Yinberrie Hills July 1993	Yinberrie Hills August 1994	Newry Station August 1992	Newry Station July 1993	Newry Station August 1994
Sternostoma tracheacolum						
Gouldian Finch	**33** (3)	**6.83** (12)	-	-	**14.75** 4	-
Pictorella Mannikin	-	-	-	**0.37** (30)	**5.33** (15)	**5.76** (29)
Masked Finch	**0** (2)	**0** (9)	**0** (1)	**0.03** (29)	**0** (24)	**0** (20)
Budgerigar	-	-	-	**0.26** (27)	**0.31** (26)	**0.21** (33)
Sternostoma paddae						
Gouldian Finch	**0** (3)	**0.08** (12)	-	-	**0** (4)	-
Long-tailed Finch	**0.17** (6)	**0** (14)	**0** (3)	**0** (9)	**0** (29)	**0** (33)
Masked Finch	**1.5** (2)	**0** (9)	**0** (1)	**0** (29)	**0** (24)	**0** (20)
Sternostoma sp.						
Zebra Finch	-	-	-	-	**0.09** (11)	**0** (13)
Ptilonyssus astridae						
Long-tailed Finch	**0** (6)	**0.29** (14)	**0** (3)	**0** (9)	**0.86** (29)	**1.21** (33)
Masked Finch	**0.5** (2)	**0** (9)	**0** (1)	**1.21** (29)	**1.5** (23)	**0.9** (20)
Zebra Finch	-	-	-	-	**1.18** (11)	**2.15** (13)
Ptilonyssus neochmiae						
Long-tailed Finch	**0.83** (6)	**0.57** (14)	**0** (3)	**0** (9)	**0** (29)	**0** (33)
Ptilonyssus emberizae						
Pictorella Mannikin	-	-		**1.13** (30)	**0.87** (15)	**19** (29)
Double-barred Finch	-	-	-	**0** (1)	**0** (1)	**0.5** (4)

(Mean parasite burden (Total number of birds in sample))

which showed a significant increase between 1992 and 1994 (Kruskal-Wallis Test; $\chi^2 = 15.32$, df = 2, $P = 0.0005$). The intensity of *S. tracheacolum* infection in the Pictorella Mannikin in 1987 was 1 mite per host, for one of 8 birds examined from the Northern Territory by Tidemann, *et al.* (1992a). At Newry Station in 1992 the intensity was 1.83 for 6 birds from a sample of 30, in 1993 the intensity was 11.4 for 7 birds from a sample of 15 and in 1994, 13.9 for 12 birds from a sample of 29.

7.3.4 Mean parasite burden

The mean parasite burden of rhinonyssid infection in birds at Yinberrie Hills and Newry Station between 1992 and 1994 is shown in Table 7.5. The overall mean parasite burden (i.e. pooled data for Yinberrie Hills and Newry Station in all years) for *S. tracheacolum* and 'all rhinonyssids' infections is shown in Figure 7.1C. The mean parasite burden of nasal mites overall for all individual birds examined was 3.5 (n = 388).

7.3.4.1 Mean parasite burden of *S. tracheacolum*

The mean parasite burden in the Gouldian Finch (12.6) was extremely high in relation to other host species infected with the same parasite (i.e. Pictorella Mannikin, 3.5; Masked Finch, 0.012 and Budgerigar, 0.26). Significant differences were detected in the mean parasite burden between species (Kruskal-Wallis Test; $\chi^2 = 47.34$, df = 3, $P < 0.0001$). The mite burden was significantly higher in the Gouldian Finch than the Budgerigar (Wilcoxon 2-Sample Test; Z = 3.56, $P = 0.0004$) and the Masked Finch (Wilcoxon 2-Sample Test; Z = 6.2, $P < 0.0001$) but not the Pictorella Mannikin (Wilcoxon 2-Sample Test; Z = 1.58, $P = 0.11$). The mite burden was significantly higher in the Pictorella Mannikin than the Budgerigar (Wilcoxon 2-Sample Test; Z = 2.96, $P = 0.003$) and the Masked Finch (Wilcoxon 2-Sample Test; Z= 5.79, $P = 0.0001$).

7.3.4.2 Mean parasite burden of all rhinonyssids

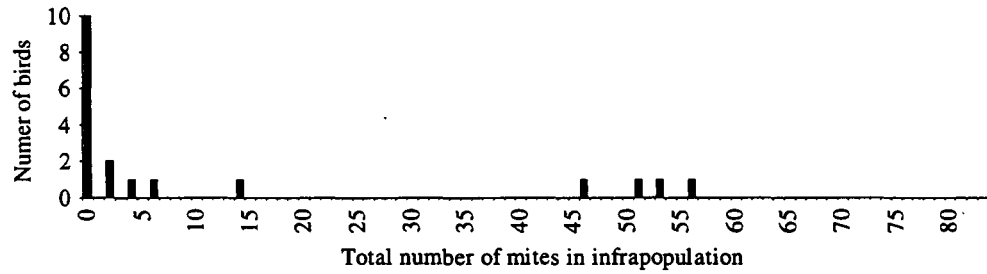
Viewed in the context of rhinonyssid infections generally the mean burden in both the Gouldian Finch and the Pictorella Mannikin were extremely high in relation to the Budgerigar, Long-tailed Finch, Zebra Finch, Double-barred Finch and the Masked Finch (Figure 7.1C).

7.3.4.3 Mean parasite burden over time

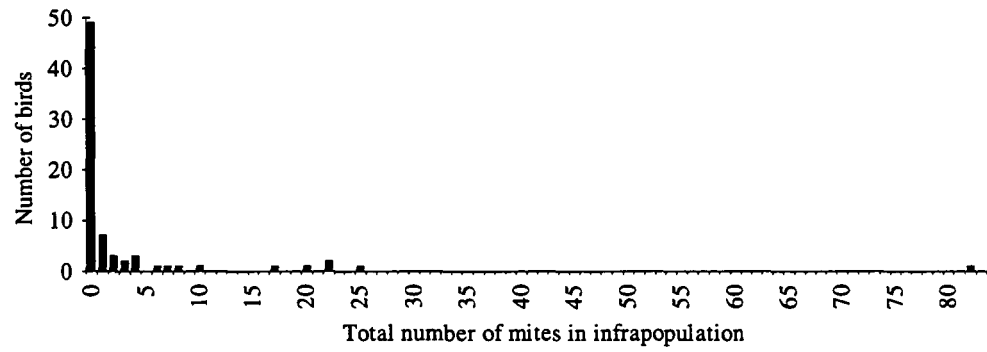
The mean parasite burden remained similar between 1992 and 1994 at Newry Station for *P. astridae* in the Long-tailed Finch (Kruskal-Wallis Test; $\chi^2 = 1.5$, df = 2, $P = 0.47$) and the Masked Finch (Kruskal-Wallis Test; $\chi^2 = 0.67$, df = 2, $P = 0.72$) and *S. tracheacolum* in the Budgerigar (Kruskal-Wallis Test; $\chi^2 = 0.31$, df = 2, $P = 0.86$) and the Masked Finch (Kruskal-Wallis Test; $\chi^2 = 1.52$, df = 2, $P = 0.47$). The mean parasite burden of *S. tracheacolum* and *P. emberizae* in the Pictorella Mannikin increased significantly between 1992 and 1994 (Kruskal-Wallis Test: *S. tracheacolum*, $\chi^2 = 6.46$, df = 2, $P = 0.04$; *P. emberizae* $\chi^2 = 23.97$, df = 2, $P = 0.0001$).

Figure 7.2 Frequency distribution of *S. tracheacolum* in the Gouldian Finch and 3 co-occurring host species in the Northern Territory.

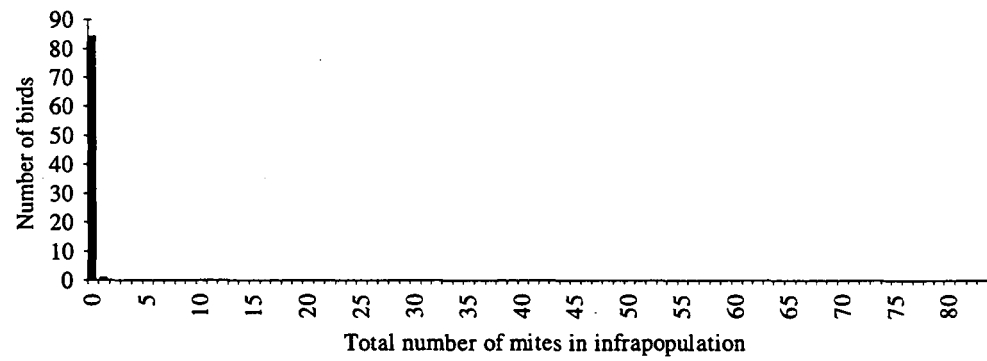
A. Gouldian Finch (n = 19)



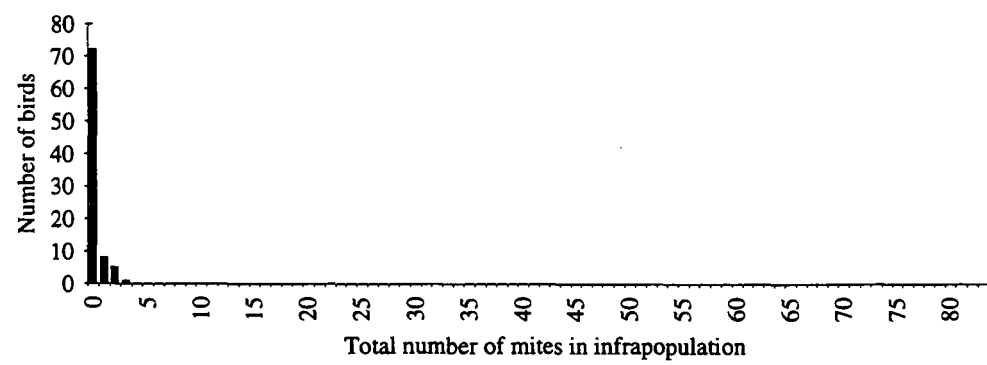
B. Pictorella Mannikin (n = 74)



C. Masked Finch (n = 85)



D. Budgerigar (n = 86)



7.3.5 The frequency distribution of *S. tracheacolum* mites in wild hosts

The frequency distribution of mites in pooled host samples is shown in Figure 7.2. The frequency distributions in the Gouldian Finch and the Pictorella Mannikin did not differ significantly (Kolmogorov-Smirnov 2-Sample Test; KSa = 0.89, $P = 0.4$), however, significant differences were detected in the frequency distributions of mites between the Gouldian Finch/ Budgerigar (KSa = 0.59, $P = 0.01$), Gouldian Finch/ Masked Finch (KSa = 2.12, $P = 0.0002$), Pictorella Mannikin/ Budgerigar (KSa = 0.78, $P = 0.$) and the Pictorella Mannikin/ Masked Finch (KSa = 1.40, $P = 0.04$).

7.4 A GLOBAL PERSPECTIVE

7.4.1 Host records for *S. tracheacolum*

Table 7.6 lists all known wild hosts for *S. tracheacolum*. The list includes 32 host species, 28 genera, 9 families and 2 orders. Including captive records (Table 7.7), the list is increased to 37 species, 32 genera and 11 families. Psittaciformes encompasses 8.1% of the host species and 6.3% of the host genera. The remainder are spread across Tyrannidae, Hirundinidae, Sturnidae, Motocillidae, Muscicapidae, Nectariniidae, Emberizidae, Fringillidae, Passeridae and Estrildidae. Emberizidae accounts for 41% of the host species records.

7.4.2 Host records for *Sternostoma*

Appendix V lists all known host family records for *Sternostoma*. Sixty one species are listed (a small number of records may have been overlooked). All species (excluding *S. tracheacolum*) are known from only a single family except for *S. boydi* Strandtmann, *S. cuculorum* Fain, *S. hirundinis* Fain, *S. laniorum* Fain, *S. nectarinia* Fain and *S. thienponti* Fain, that are known from two families within the orders Charadriiformes, Cuculiformes, Passeriformes, Passeriformes, Passeriformes and Passeriformes respectively. No species (except for *S. tracheacolum*) is known from more than one order. *Sternostoma* appears to be a parasite primarily of the Passeriformes with 61% of the species known only from this order. Of all species, 8.1% (i.e. 5 species) are found in the Charadriiformes, 3.3% in the Strigiformes, 3.3% in the Cuculiformes, 3.3% in the Galliformes, 3.3% in the Piciformes and 1.6% in the Coraciiformes, Gruiformes and Coliiformes respectively. *S. tracheacolum* is the only species known from the Psittacidae.

7.4.3 Prevalence and intensity of infection by *S. tracheacolum* in recorded hosts

Table 7.8 lists the published data for intensity and prevalence of *S. tracheacolum* infection in wild hosts. Prevalence in the Gouldian Finch is significantly higher than that reported for other species listed in the table (Overall $\chi^2 = 154.6$, df = 6, $P < 0001$; Gouldian Finch cell $\chi^2 = 123.71$, df = 6, $P < 0.0001$). This includes the Tree Swallow (2.7%, n = 75), Brown-headed Cowbird (14.3%, n = 14), Great Crested Flycatcher (20%, n = 20) and the Red-winged Blackbird (2.2%, n = 223), all

Table 7.6 Wild host records for *S. tracheacolum*.

Host species	Common name	Family	Locality	Reference	First reported
PSITTACIFORMES					
Agapornis cana Gmelin	Madagascar Lovebird	Psittacidae	Madagascar	Fain & Hyland (1962)	Gretillat *et al.* (1959)
Agapornis sp.	Lovebird	"	"	"	"
Melopsittacus undulatus (Shaw)	Budgerigar	"	Australia	Domrow (1992)	This study
PASSERIFORMES					
Tyranni					
Tyrannus melancholicus Vieillot	Tropical Kingbird	Tyrannidae	Mexico, Veracruz	Hyland & Moorhouse (1970)	Hyland & Moorhouse (1970)
Myiarchus crinitus L.	Great Crested Flycatcher	"	USA, Louisiana	Pence (1972)	Pence (1972)
Tachycineta bicolor (Vieillot)	Tree Swallow	"	"	"	"
Passeres					
Hirundo rustica L.	Barn Swallow	Hirundinidae	USSR, Volga delta	Furman (1957)	Bregetova (1950)
Riparia riparia (L.)	Bank Swallow	"	USA, Michigan	Fain & Hyland (1962)	Fain & Hyland (1962)
Macronyx croceus Vieillot		Motocillidae	Africa, Ruanda-Urundi	"	Fain (1956)
Acrocephalus arundinaceus (L.)	Great Reed Warbler	Muscicapidae	USA, Michigan	"	Fain & Hyland (1962)
Arachnothera longirostris (Latham)	Little Spiderhunter	Nectariniidae	Malaysia	McClue & Ratanaworabhan (1973)	McClue & Ratanaworabhan (1973)
Nectarinia jugularis flammaxilaris Blyth	Purple-throated Sunbird	"	Thailand	Strandtmann (1960)	Strandtmann (1960)
Passerina cyanea (L.)	Indigo Bunting	Emberizidae	USA, Michigan	Fain & Hyland (1962)	Fain & Hyland (1962)
Melopspiza melodia (Wilson)	Song Sparrow	"	"	"	"
Spizella pusilla (Wilson)	Field Sparrow	"	"	"	"
Sturnella magna (L.)	Eastern Meadow lark	"	"	"	"
Pooecetes gramineus (Gmelin)	Vesper Sparrow	"	"	"	"
Icterus bullocki (Swainson)	Bullock's Oriole	"	USA	Furman (1957)	Furman (1957)
Agelaius tricolor (Audubon)	Tricolored Blackbird	"	"	"	"
A. phoeniceus L.	Red-winged Blackbird	"	Canada	Hood & Welch (1980)	Hood & Welch (1980)
Molothrus ater (Boddaert)	Brown-headed Cowbird	"	USA, Rhode Is.	Fain & Hyland (1962)	Fain & Hyland (1962)
Passerella iliaca (Merrem)	Fox Sparrow	"	USA, Massachusetts	"	"
Seiurus aurocapillus (L.)	Ovenbird	"	"	"	"
S. noveboracensis (Gmelin)	Northern Waterthrush	"	"	"	"

Table 7.6 Continued, Wild host records for *S. tracheacolum.*

Host species	Common name	Family	Locality	Reference	First reported
Cardinalis sinuatus (L.)	Pyrrhuloxia	Emberizidae	USA, Texas	Pence & Castro (1975)	Pence & Castro (1975
Pipilo fuscus	Brown Towhee	"	"	"	"
Passer domesticus (L.)	House Sparrow	Passeridae	USA, Michigan	Fain & Hyland (1962)	Fain & Hyland (1962)
Estrilda troglodytes (Lichtenstein)	Red-eared Waxbill	Estrildidae	Hawaii*	Smith (1973)	Smith (1973)
Uraeginthus angolensis (L.)	Cordon-bleu Waxbill	"	"*	"	"
Erythrura gouldiae (Gould)	Gouldian Finch	"	Australia	Tidemann *et al* (1992)	Tidemann et al (1992)
Poephila personata (Gould)	Masked Finch	"	"	"	"
Heteromunia pectoralis (Gould)	Pictorella Mannikin	"	"	"	"

(* Introduced species)

Table 7.7 Captive host records for *S. tracheacolum.*

Host species	Common name	Family	Locality	Reference	First reported
PSITTACIFORMES					
Melopsittacus undulatus (Shaw)	Budgerigar	Psittacidae	Belgium	Fain & Hyland (1962)	Fain & Hyland (1962)
PASSERIFORMES					
Passeres					
Cinnyrinclus leucogaster verreauxi (Bocage)	Starling	Sturnidae	Belgium (coming from the Congo)	"	Fain & Hyland (1962)
Cyanerpes cyaneus (L.)	Red-legged Honeycreeper	Emberizidae	Belgium (coming from Brazil)	"	"
Serinus canarius (L.)	Canary	Fringillidae	South Africa	Fain & Hyland (1962)	Lawrence (1948)
Carduelis carduelis (L.)	European Goldfinch	"	Italy	"	Lombardini (1953)
C. spinus (L.)	Siskin	"	Italy	Vaccari & Ballarini (1963)	Vaccari & Ballarini (1963)
Pyrrhula pyrrhula (L)	Common Bullfinch	"	Germany	Kummerfeld & Hinz (1982)	Kummerfeld & Hinz (1982)
Erythrura gouldiae (Gould)	Gouldian Finch	Estrildidae	South Africa	Fain & Hyland (1962)	Cumming (1959)
Lonchura malacca (L)	Chestnut Munia	"	Germany	Kummerfeld & Hinz (1982)	Kummerfeld & Hinz (1982)
L. striata (L)	White-rumped Mannikin	"	"	"	"
Taeniapygia guttata (Vieillot)	Zebra Finch	"	"	"	"

from North America. The intensity of infection reveals for the most part low numbers of mites, however, an infrapopulation of 43 mites was recorded from a Great Crested Flycatcher and 21 mites from a Brown-headed Cowbird (Pence, 1972). The heaviest infection was reported from a Gouldian Finch with an adult only mite population of 102 mites. Considering the mean intensity of infection against available data, the Gouldian Finch with a mean intensity of 31.8 (n = 16) stands out from a background ranging from 1.6 (n = 223) for the Red-winged Blackbird to 13.5 (n = 14) for the Brown-headed Cowbird.

7.4.4 Prevalence and intensity of infection by rhinonyssids in recorded hosts

For the most part the numbers of individual rhinonyssid mites occurring in any given infection is low. Domrow (1967) found a mean of 4 mites per infected bird during the 'wet' season and 3 during the 'dry' season for all host families in North Queensland. The corresponding mean for the passeriforms was 4 and 3 for the 'wet' and 'dry' respectively. Spicer (1987) found similar levels of infection by rhinonyssids and turbinoptids in birds from a Guatemalan rain forest (i.e. 4.3 mites per infected host, 3.4 for *Sternostoma* infections only). Amerson (1967) reported a mean intensity of 7 mites per infected host for *Sternostoma* and *Larinyssus* infecting the Laridae. All studies indicate that large numbers of mites in single infections are uncommon.

Amerson (1967) reported a range in the intensity of infection of between 1 and 29 mites for *Sternostoma* and *Larinyssus* in Larids and Pence (1973) reported a range of between 1 and 162 individual mites for rhinonyssid infections in a survey of 1900 birds from 193 species. Other authors have not indicated the extremes of infection however a perusal of the literature would indicate that ranges do not exceed that of Pence (1973). Large infections in the Gouldian Finch are, however, common and during the course of this study infections up to 267 mites for wild caught birds and 371 mites for captive reared birds have been found. The largest infection in a wild bird came from an immature female bird collected from Yinberrie Hills in 1991. These figures probably represent the heaviest rhinonyssid infections ever recorded. When considered in relation to the size of the host (i.e. approximately 15 grams in weight and 14 cm in length) it becomes easier to appreciate the conspicuous nature of the infection. An infection of 371 mites laid end to end would stretch for approximately 20 cm.

The overall prevalence of infection reported from large studies, and summarised in Table 7.9, (for total numbers of individual birds of all species) range from 15.3 (n = 841) Domrow (1967); 16.2 (n = 1927) Pence (1973); 17 (n = 257) Amerson (1967); 17 (n = 502) Spicer (1987); 18.7 (n = 1526) Maa & Kuo (1965); 24 (n = 78) Spicer (1984); 32.4 (n = 590) Hyland & Moorhouse (1970) and 34.6 (n = 489) Kaneko, Matsudaira and Masahito (1978). The present study with a prevalence of 33% (n = 249) falls within the upper region of this range.

Table 7.8 Intensity and prevalence of infection by *S. tracheacolum* in wild hosts.

Host	Family	Locality	Date	Author	Prevalence of infection	Intensity of infection
PASSERIFORMES						
Tyranni						
Myiarchus crinitus	Tyrannidae	USA, Louisiana	8 April 1970	Pence (1972)	20 (n = 20)	41 F 1 M 1 N
Tyrannus melancholicus	"	Mexico, Veracruz	31 August 1963	Hyland & Moorhouse (1970)		1 F
"	"	"	10 September 1963	"		1 F
Passeres						
Tachycineta bicolor	Hirundinidae	USA, Louisiana	11 November, 1970	Pence (1972)	2.7 (n = 75)	1 F
"	"	"	"	"		2 F
Nectarinia jugularis flammaxilaris	Nectariniidae	Thailand, Chaiyaphum	24 December 1952	Strandtmann (1960)		2 F
Cardinalis sinuatus	Emberizidae	USA, Texas	30 May 1974	Pence & Castro (1975)		1 F
Pipilo fuscus	"	"	27 June 1974	"		1 F
Molothrus ater	"	Mexico, Veracruz	10 April 1969	Pence (1972)	14.3 (n = 14)	6 F 4 N
"	"	"	1 December 1970	"		21 F
Agelaius phoeniceus	"	Canada	April 1975-June 1976	Hood & Welch (1980)	2.2 (n = 223)	1.6, SD 0.9
Erythrura gouldiae	Estrildidae	Australia, Northern Territory and Western Australia	1987-1991	Tidemann *et al.* (1992)	62 (n = 26)	X 31.8, SD 12.8 (R 1-102) J 15, SD 6
Heteromunia pectoralis	"	"	"	"	13 (n = 8)	1T
Poephila personata	"	"	"	"	0.85 (n = 118)	1 1T

(M = Male; F = Female; J = Subadult; N = immatures; X = mean ; T = Total; SD = Standard deviation; R = Range)

Table 7.9 Intensity and prevalence of infection by rhinonyssid mites in wild hosts.

Author	Locality	Parasite group	Percentage of species infected	Prevalence of infection	Intensity of infection	Number of birds examined	Number of bird species examined
Amerson (1967)	Central Pacific	Rhinonyssidae	-	17	7, R 1-29	257	1 Laridae
Domrow (1967)	Australia	Rhinonyssidae	39.8	15.3	5 (3) / 4 (3)	841	108 All host species
"	"	"	46.5	16.9	4 (4) / 3 (2)	384	43 Passeriformes
Domrow (1969)	"	Rhinonyssidae, Turbinoptidae & Speleognathidae	36	-	-	-	330 All host species
"	"	"	64.4	-	-	-	160 Passeriformes
"	"	"	41.7	-	-	-	12 Estrildidae
Hyland & Moorhouse (1970)	Mexico	Rhinonyssidae	-	32.4	-	590	120 All host species
Maa & Kuo (1965)	Taiwan	Rhinonyssidae, Turbinoptidae Speleognathidae & Kytoditidae	45	18.7 (5.2 - 81.8)	-	1,526	105 All host species
Kaneko (1978)	Japan	Rhinonyssidae, Speleognathidae	100	34.6 (2.2-73.5)	-	489	6 Anatidae
Pence (1973)	USA, Louisiana	Rhinonyssidae, Turbinoptidae Speleognathidae & Kytoditidae	48.2	16.2	-	1,927	193 All host species
"	"	Rhinonyssidae	40.1	15.6	-	1075	95 Passeriformes
Spicer (1984)	Guatemala	Rhinonyssidae, Turbinoptidae	37	24	4.3, SD 3.4	78	18 All host species
Spicer (1987)	Central & North America	Rhinonyssidae, Speleognathidae	39	17		502	103 All host species

(SD = Standard deviation; R = Range) Intensity of infection presented for Domrow (1967) is seasonal; bracketed figures represent adult mites only.

7.5 DISCUSSION

7.5.1 Geographic variation in the prevalence of rhinonyssid infections

Variations in the prevalence of mites between geographic localities is suggested to be a common phenomenon in the Rhinonyssidae (Spicer, 1987). This is illustrated quite well in the present study by the presence of *P. neochmiae* and *S. paddae* at Yinberrie Hills but the complete absence of these parasites in potential hosts at Newry Station. Maa and Kuo (1965) reported that the prevalence of nasal mites in the White-eared Sibia *Heterophasia auricularis* (Swinehoe) in Puli (47.9) was much higher than in 2 other places (25%, 6.7%) though they gave no value to the significance of these variations. Spicer (1987) reported statistically significant variations in the prevalence of nasal mites among geographic locations. He considered that given many of the birds examined in his study were migratory there could be mixing of different populations and so the apparent prevalences may not reflect local parasite-host dynamics. Variations in the present study could be explained by differences in the presence and abundance of host species between localities and the population distributions within host species. For example at Yinberrie Hills there may be an additional reservoir host species that is infected by *P. neochmiae* and *P. paddae*, not present at Newry Station. The data suggest that there is probably little exchange of mites between Gouldian Finch, Long-tailed Finch and Masked Finch populations at Newry Station and Yinberrie Hills whether directly or through a third reservoir host species.

7.5.2 The prevalence of double infections by rhinonyssid mites

The prevalence of double and multiple infections (more than two species) vary greatly between studies. Spicer (1987) considers that multiple infections occur rarely in nasal mites and found only a single multiple infection from a collection of 87 infected hosts. Conversely, Pence (1973) noted two and sometimes even three species parasitising the same host, though he gave no specific details. Domrow (1969) found 22 cases of naturally occurring double infections amongst individuals of 330 bird species examined but did not find any multiple infections. In the present study double infections by rhinonyssids invariably included *S. tracheacolum* as one of the pair (i.e. *S. tracheacolum* with *S. paddae* in the Gouldian Finch and *S. tracheacolum* with *P. emberizae* in the Pictorella Mannikin).

Ten double infections were found, all in subadult birds (note also that the only double infection in a captive reared Gouldian Finch found by the author i.e. *S. tracheacolum* with *P. neochmiae*, was also from an immature bird). The prevalence of double infections in young birds was significantly higher than for adult birds. The reasons for this are not known though competition between mites species for the same internal host habitat may possibly lead to a reduction in the proportion of double infections with age.

7.5.3 The prevalence and intensity of rhinonyssid infection over time

Generally, the prevalence and intensity of infection remained stable at Newry Station between 1992 and 1994. This was the case for *S. tracheacolum* in the Budgerigar and the Masked Finch, *P. astridae* in the Long-tailed Finch, Masked Finch and the Zebra Finch and *P. emberizae* in the Double-barred Finch. In contrast, the intensity of infection by *S. tracheacolum* and *P. emberizae* increased significantly in the Pictorella Mannikin over the same period. Unfortunately data on the prevalence and intensity of infection by *S. tracheacolum* in the Gouldian Finch over time are not available. The requirement to sacrifice hosts in order to assess the prevalence and size of the infection and the ethical constraints imposed by the endangered status of wild Gouldian Finches inhibited the taking of specimens. However, it is clear, despite relatively small samples, that both the prevalence and the intensity of infection in the Gouldian Finch have remained high since the original samples were collected by Tidemann *et al.* (1992a) between 1987 and 1990.

7.5.4 Kytoditid mites in nasal mite surveys

Kytoditid mites are only occasionally encountered in nasal mite surveys. This may be due in part to their low prevalence (i.e. 6% overall for *K. amandavae* infecting the Masked Finch and 1% overall for *K. andrei* infecting the Long-tailed Finch). The Kytoditidae is a small family of endoparasitic mites of birds comprising two genera, *Kytodites* Mégnin and *Kytonyssus* Fain. *Kytodites* is most often found in the lower respiratory system and includes the ubiquitous and well known Airsac mite *K. nudus* (Vizioli), a parasite of the Domestic Fowl *Gallus domesticus* (L.). Kytodites is known from galliform, coraciiform, passeriform, psittaciform and columbiform hosts (Fain, 1960; Fain & Bafort, 1964; Hyland, 1969; Fain & Lukoschus, 1979). *Kytonyssus* on the other hand tends to parasitise the nasal cavity and is only known from gruiform and passeriform hosts, particularly estrildids (Fain & Bafort, 1964; Pence, 1975). Although Airsac mite is known to be pathogenic in heavy infections in its domestic hosts, no species has been shown to cause respiratory disease in their natural hosts in the wild.

7.5.5 Are the measures of *S. tracheacolum* infection in wild Gouldian Finches anomalous?

The prevalence of *S. tracheacolum* infection is significantly higher in the Gouldian Finch than the Masked Finch and the Budgerigar at Newry Station, the Tree Swallow, the Brown-headed Cowbird and the Great Crested Flycatcher in North America (Pence, 1972), the Red-winged Blackbird in Canada (Hood and Welch, 1980), and the Masked Finch in Australia (Tidemann *et al.*, 1992). However, it is not significantly higher than the prevalence recorded in the Pictorella Mannikin at Newry Station in 1993 and 1994. When all rhinonyssids are considered, the difference in the prevalence between the Gouldian Finch and the Pictorella Mannikin is further reduced (in fact the prevalence of rhinonyssids in the Pictorella Mannikin is higher than that found in the Gouldian Finch).

Similarly, the intensity of infection and the mean parasite burden were significantly higher in the Gouldian Finch than in the Budgerigar and the Masked Finch but not significantly higher than those in the Pictorella Mannikin. Mean intensity of infection is published for only two host species outside of Australia (i.e. Brown-headed Blackbird, Pence (1972) and the Red-winged Blackbird, Welch and Hood (1987)). In comparison to both these studies, the mean intensity in the Gouldian Finch is substantially larger. Overall, the parameters of *S. tracheacolum* infection in the Gouldian Finch (i.e. prevalence, intensity of infection and mean parasite burden) cannot be statistically separated from those found in the Pictorella Mannikin and therefore cannot be considered aberrant or at least, exclusively aberrant.

Assuming that intensity of infection or the number of mites within an infrapopulation is related to the level of associated pathology (Chapter 4: Section 4.4, Gross lesions and the intensity of *S. tracheacolum* infection), then *S. tracheacolum* is likely to be as influential in the population dynamics of the Pictorella Mannikin as in populations of the Gouldian Finch. Both the Pictorella Mannikin and the Gouldian Finch are similar in size, they overlap in distribution and habitat, and are ecologically similar species. The way each species is affected by *S. tracheacolum* infection is therefore likely to be similar.

Given the hypothesis that *S. tracheacolum* may be an introduced species (Tidemann *et al.*, 1992a) it is notable that the Pictorella Mannikin is the only host species examined during the present study that showed significant changes in the measures of infection over time. The prevalence showed an apparent increase from 12.5% in 1987 (Tidemann *et al.*, 1992a) to 20% in 1992 and to 47% in 1993 and 41% in 1994 though the difference overall was not significant. The increase in the mean intensity of infection (i.e. 1, 1.8, 11.4 and 13.9) and the mean parasite burden (i.e. 0.13, 0.37, 5.3 and 5.76) was highly significant and echoed the apparent change in prevalence.

7.5.6 Implications of the nasal mite survey for an 'introduction hypothesis'

On the evidence gathered in the present study it is possible to muse further on *S. tracheacolum* scenarios that may be implicated in the recent demise of wild Gouldian Finches. If Fain and Hyland (1962) are correct, and the Canary is not a natural host for *S. tracheacolum* (Chapter 1: Morphology), then captive birds have probably been hosts to this parasite for only a few centuries. The natural range of the Canary is the Canary Islands, the Madeiras and Azores. The species was imported to Europe early in the 16th Century (Newton, 1896) and today is one of the most common caged birds in the world.

For many rhinonyssids, accidental occurrences in unusual hosts is a common phenomenon, and the cosmopolitan occurrence of *S. tracheacolum* in captive reared birds may to some extent illustrate this point. *S. tracheacolum* in captive Canaries alone has been found in Europe (Lombardini, 1953;

Fain & Carpentier, 1958; Geyer, 1959; Zwart, 1962; Blasco-Sabio & Portús-Vinyeta, 1974; Guewara-Benítez & Ubeda-Ontiveros, 1974; Bygrave, 1980; Szeleszczuk & Kruszewicz, 1987), Africa (Stephan *et al.*, 1950), South America (Torres *et al.*, 1951; Cassamagnaghi, 1952, Amaral, 1968), North America (Baker *et al.*, 1956; Mathey, 1967), Asia (Iwasaki, *et al.*, 1983) and Australasia (Domrow, 1965; Riffkin & McCausland, 1972) and they are often implicated in the infection of other captive host species (e.g. Cumming, 1959; Riffkin & McCausland, 1972; Szeleszczuk & Kruszewicz, 1987). If natural host specificity does not account for previously unexposed but potentially susceptible host species (and this is particularly pertinent to a rapidly radiating parasitic species) then the extensive movement of infected captive birds across the world may have created a 'fuzzy picture' of natural host specificity in *S. tracheacolum.*

It is interesting that *S. tracheacolum* (such an obvious mite in terms of visibility and associated pathological changes at postmortem and its impact on host morbidity and mortality) could have remained unknown to biology until 1948. This is in spite of over three hundred years of Canary captivity. Similarly, *S. tracheacolum* infection in the Gouldian Finch was first reported overseas in 1959 in captive birds that were associated with infected Canaries. Not till five years later was infection identified in captive Gouldian Finches in Australia.

Tidemann *et al.* (1992a) considered that the *S. tracheacolum/* Gouldian Finch association is of recent origin and further, suggested that *S. tracheacolum* was introduced to Australia since European settlement. For the most part, this suggestion is consistent with the results of the present study. The wild Budgerigar appears to be infected by a distinct form *S. tracheacolum* (Chapter 1: Morphology; Chapter 8: Host Susceptibility) which has not been found infecting Gouldian Finches. The 'Psittacine form' may have speciated in psittacid hosts and may not be infective to passerines. The 'Passerine form' found in the wild Gouldian Finch, Pictorella Mannikin and Masked Finch and highly infective to the captive reared Gouldian Finch and Canary may have speciated elsewhere and has only recently spread to Australia with the importation of susceptible avicultural species and other the House Sparrow.

However, measures of infection found in wild birds would suggest that the 'Psittacine form' of *S. tracheacolum* is not a recent introduction to Australia. The 'Psittacine form' is the only rhinonyssid species found to infect wild Budgerigars, it was commonly present (i.e. prevalence of 16% for pooled data from Newry Station between 1992 and 1994) and the intensity of infection is low (i.e. intensity of 1.6 mites per infected host for pooled data from Newry Station between 1992 and 1994). There was also no significant variation in the measures of prevalence, intensity and mean parasitic burden over the 3 year survey period.

Tidemann and her associates (1992a) have suggested that infected Canaries, imported to Australia prior to the implementation of appropriate quarantine laws and procedures, may have inadvertently introduced *S. tracheacolum* to captive Canary populations in Australia. Gouldian Finches are also an extremely popular captive bird in Australia and both Canaries and Gouldian Finches are often housed together or in neighbouring enclosures. *S. tracheacolum* can be transmitted between species under both these conditions (Chapter 2: Life History, Transmission). By avicultural association with the Canary the Gouldian Finch (a possible naive and susceptible host species) may have first come in contact with the 'Passerine form' of *S. tracheacolum*. Gouldian Finch escapees (and undoubtedly this must have occurred frequently since Gouldian Finches were first held in captivity) could have completed the scenario by introducing the parasite to wild populations.

Pictorella Mannikins are susceptible to infection (note also that Pictorella Mannikins are popular aviary kept birds and may also have served to transfer the 'Passerine form' of *S. tracheacolum* from the aviary situation to the wild) and we may be currently observing the movement and establishment of the 'Passerine form' of *S. tracheacolum* in native host species. The 'Passerine form' of *S. tracheacolum* could have been introduced to the wild firstly in Queensland where Pictorella Mannikins and Gouldian Finches both appear to have declined dramatically to very small numbers.

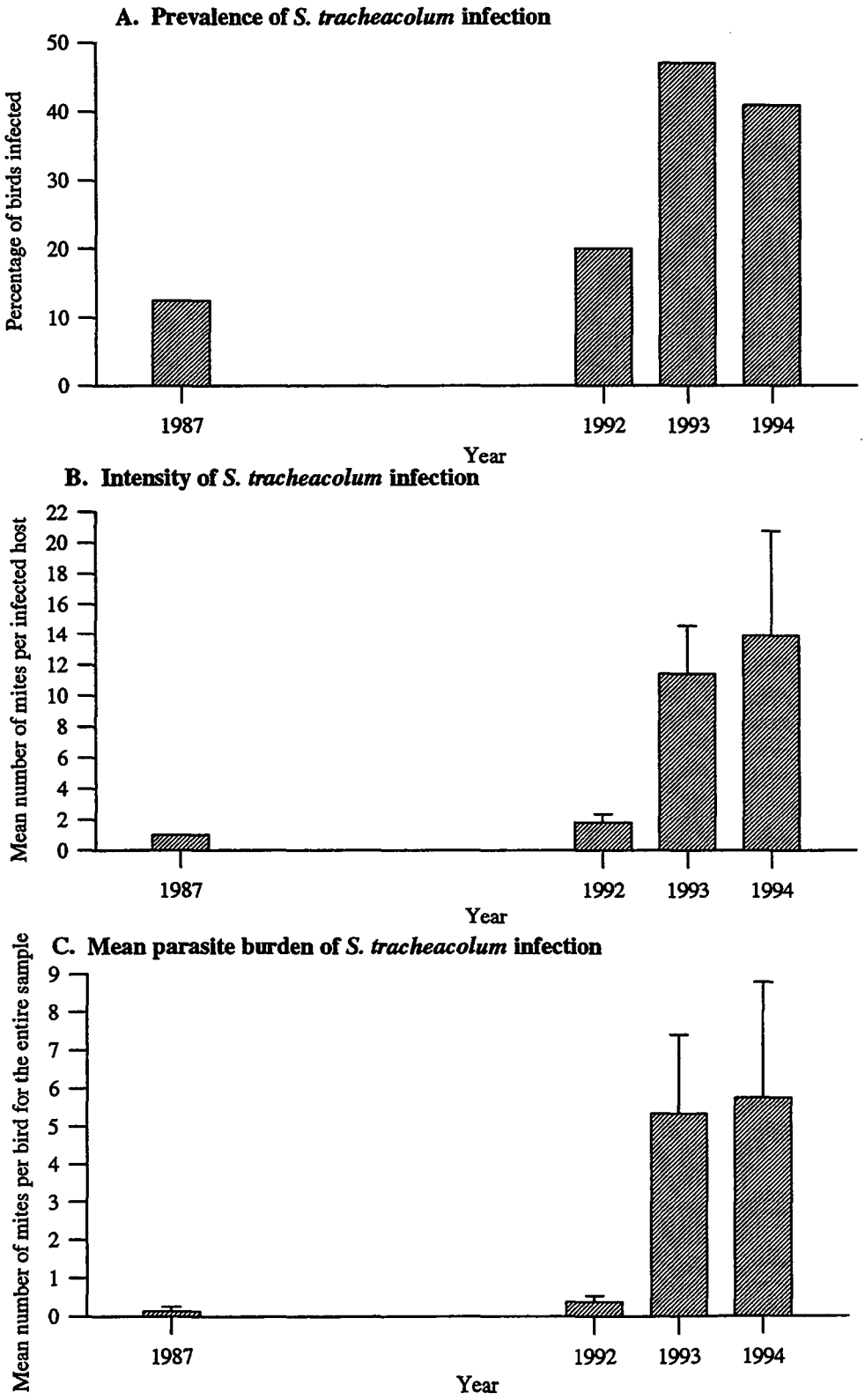
Masked Finches appear to show resistance to infection by *S. tracheacolum* (see Chapter 8: Host Susceptibility) and prevalence remains consistently low (i.e. 1 of 117 birds collected by Tidemann *et al.* (1992a) and 1 of 85 birds collected during the present study). Consequently, Masked Finch populations have remained virtually unaffected by the presence of the 'Passerine form' of *S. tracheacolum*. The Masked Finch is also infected by a another mite species that inhabits the lower respiratory system, *K. amandavae*. This association may confer some pre-adaptive resistance to the 'Passerine form' of *S. tracheacolum* infection.

With spread of the parasite we may only now be detecting the impact of the 'Passerine form' of *S. tracheacolum* on the dynamics of the Gouldian Finch and Pictorella Mannikin populations in the Northern Territory and Western Australia. Numbers and distribution of Gouldian Finches have dramatically declined and we may soon see a detectable impact on western populations of the Pictorella Mannikin. Concern regarding the Pictorella Mannikin may involve elements of speculation but given the concern for the potential involvement of *S. tracheacolum* in the decline of the Gouldian Finch, then it would be irresponsible to ignore the prospect that this mite may be adversely impacting wild populations of the Pictorella Mannikin.

7.5.7 Conclusion

Although sample sizes in the present study were small and the duration of the survey spanned a relatively short period (3 years), some robust conclusions can be drawn regarding the relationship

Figure 7.3 Measures of the level of infection by *S.tracheacolum* in the Pictorella Mannikin: 1987 (n = 8), from Tidemann *et al.* (1992); 1992 (n = 30), 1993 (n = 15), 1994 (n = 29) from Newry Station, NT.



between rhinonyssids and their wild host populations. Within sites there are recognisable and apparently stable patterns in relative levels of intensity and prevalence in different host populations. However, significant differences in the prevalence of infection occur between geographic regions (i.e. between Newry Station and Yinberrie Hills, approximately 500 km apart). These differences may be related to factors influencing the local rates of transmission such as the number of susceptible host species (and reservoir host species likewise), the local densities of host species, and the availability and forms of water sources.

The notion of stability and hence the presence of the rhinonyssid mites as a 'normal' element of the biology of the Region's birds is supported by the study of nasal mite infections in birds at Mitchell River Mission, Queensland during the wet and dry seasons by Domrow (1967). But it is contradicted by differences in the prevalence and intensity of infection and the trend for increase in these values over time in the Pictorella Mannikin (Figure 7.3). While environmental influences cannot be entirely discarded as a potential source of this variation, the apparent absence of change in other species with similar biology suggest that the parasite-host relationship of *S. tracheacolum* and the Pictorella Mannikin may be unstable. These differences were not limited to *S. tracheacolum* but also included *P. emberizae*. There are a number of potential explanations for these changes such as the recent introduction and spread of *S. tracheacolum* in Pictorella Mannikins, hyper-parasitism resulting from a weakened immune facility brought about by some other environmental stress or stresses on host populations or normal variations in the levels of infection in response to variations in the host population density.

Ethical constraints and the inability to detect *S. tracheacolum* infection without sacrifice of the host severely limits study of this parasite in wild Gouldian Finches. However, continuation of the study of infection in the Pictorella Mannikin (a species currently considered to be numerous in the Kimberley region of north western Australia (Garnett, 1992) at Newry station and other sites would provide the data for an investigation of the relationship between changes in the levels of infection over time and corresponding trends in the size and the density of host populations. Ultimately, this study could provide insight into the role, if any, of *S. tracheacolum* in the demise of the wild Gouldian Finch.

Chapter 8. Host Susceptibility

8.1 INTRODUCTION

Significant differences have been detected in the morphology of *S. tracheacolum* between specimens coming from estrildid and psittacid host species in northern Australia (Chapter 1: Section 1.4.2, Comparative morphology of female *S. tracheacolum* from Australian hosts). This is in contrast to the morphological similarity of mite specimens coming from different estrildid host species (i.e. Gouldian Finch, Pictorella Mannikin and Masked Finch). Indeed, the morphology of specimens from Gouldian Finches is similar even though hosts were collected from over 1000 km apart (see Figure 8.1). Subspecies names have proposed for the two distinct forms of mites found, the 'Passerine form' of *S. tracheacolum* for mites from the Gouldian Finch, Pictorella Mannikin and the Masked Finch and the 'Psittacine form' of *S. tracheacolum* for mites from the Budgerigar (Chapter 1: Section 1.5.5, Implications of the study of *S. tracheacolum* morphology on an 'introduction hypothesis').

Assuming that the host is not responsible for inducement of phenotypic variation, the observed morphological differences suggest that there is probably little or no genetic flow between mite populations infecting psittacid and estrildid hosts. Using the same argument, the data suggest that for the estrildid host species there is considerable genetic flow between mite populations.

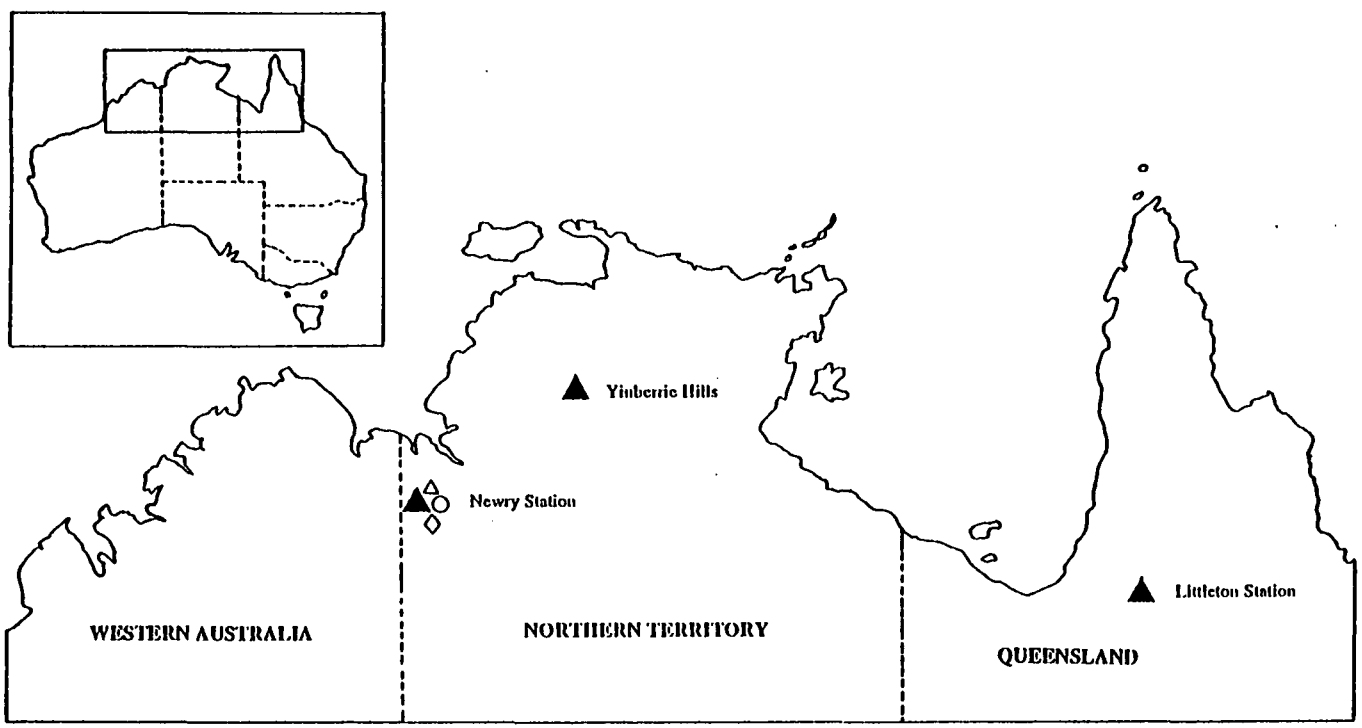
In the discussion of morphological variation of *S. tracheacolum*, Fain and Hyland (1962) suggested that 'geographical or biological isolation of the host probably plays a more important role than the host itself in the production of variation'. The present study further examines this hypothesis through an investigation of the role of short term host-induced phenotypic variation to explain the significant morphological differences observed between mite populations sharing the same host habitat in Northern Australia. A simple experiment is undertaken whereby the 'Passerine form' of *S. tracheacolum* mites from estrildid finch hosts (collected from wild Gouldian Finches) are used to experimentally infect other bird species known either in captivity or in the wild to be susceptible to *S. tracheacolum*. Consistent changes in the morphology of mites over short periods of time in a new host species would suggest a host role in the production of these variations. No detectable changes in morphology would not support the suggestion.

8. 2 METHODS

8.2.1 Captive reared hosts

Following treatment with an acaricide to eliminate any existing *S. tracheacolum* infection, 10 captive reared Gouldian Finches, 14 Canaries and 14 Budgerigars were experimentally infected with the 'Passerine form' of *S. tracheacolum*. The procedures used for drug administration and

Figure 8.1 Localities in northern Australia where hosts for *Sternostoma tracheacolum* were collected: ▲ = Gouldian Finch; △ = Masked Finch; ○ = Pictorella Mannikin; ◇ = Budgerigar.



experimental infection of birds is described in the Experimental Design: 6. Experimental infection procedure, P 66 and 7. Ivermectin pre-treatment procedure, P 67.

Each bird received two adult female mites (1 gravid; 1 non-gravid) coming originally from wild Gouldian Finches collected from Yinberrie Hills, Northern Territory. An additional 10 Gouldian Finches, 6 Budgerigars and 6 Canaries were used as controls. The controls received an acaricide treatment prior to the experiment but were not experimentally infected with the 'Passerine form' of *S. tracheacolum* mites.

Experimentally infected birds were then maintained in aviary enclosures (one species per enclosure). Gouldian Finch controls were also maintained in an aviary enclosure. However, due to housing limitations, Canary and Budgerigar controls were housed in small cages. All birds were regularly observed and symptoms of infection were monitored over a period of twelve months.

After six months, a sample of experimentally infected birds and control birds were euthanased and dissected. Blood samples were also taken prior to euthanasia for haematological analysis (Chapter 5: Haematology).

Remaining Gouldian Finches were retained in a large enclosure and remaining Canaries and Budgerigars were housed together in small cages (i.e. 2 Canaries per cage and 2 Budgerigars per cage). After 12 months, all surviving birds were euthanased and dissected.

8.2.2 Wild caught hosts

Wild caught Masked Finches *P. personata* (collected from Yinberrie Hills, NT in 1991) were experimentally infected with the 'Passerine form' of *S. tracheacolum* mites coming from a wild Gouldian Finch collected from the same locality. After intervals of up to 23 days following experimental infection, birds were euthanased and dissected.

8.2.3 Analysis

Morphological measurements, following Fain and Hyland (1962), were taken of adult female mites from captive reared Gouldian Finches and Canaries (experimentally infected with mites coming originally from wild Gouldian Finches). Comparisons were made between mite groups from each host species using ANOVA (SAS: PROC GLM) (SAS Institute INC., 1988).

Two sample t-tests, were used to compare the mean size of the 'Passerine form' of *S. tracheacolum* infections between Gouldian Finches and Canaries. Data describing the proportion of live mites and adult mites in infrapopulations were compared by t-tests following arcsine transformation using SYSTAT (SYSTAT Inc., 1992).

Measurements (n = 17) of female mites (n = 29) from wild Gouldian Finches and captive reared Gouldian Finches and Canaries were ordinated using PCA (principal components analysis) (PROC FACTOR, SAS).

8.3 RESULTS

8.3.1 Susceptibility of captive hosts

8.3.1.1 Passerine hosts

All captive reared Canaries and Gouldian Finches, experimentally infected with the 'Passerine form' of *S. tracheacolum* and examined after 6 months, retained infections of *S. tracheacolum.* Mean measurements of the levels of infection in each species are shown in Table 8.1. After 6 months the mean intensity of infection was significantly higher in the Gouldian Finch than the Canary (mean intensity overall: $t = -6.82$, df = 8, $P = 0.0001$; total number of mites found live: $t = -7.03$, df = 9, $P = 0.0003$).

Table 8.1 Measurements of the prevalence, size and demography of the 'Passerine form' of *S. tracheacolum* infections in captive reared Canaries and Gouldian Finches at 6 months and 12 months following initial infection (for mites coming originally from wild Gouldian Finches).

Duration of infection/ Host species	Number of hosts examined	Prevalence	Mean intensity of infection (Range)	Mean percentage of mites found live (Range)	Mean percentage of adult mites in infrapopulation (Range)
6 months					
Canary	5 adults (3M, 2F)	100%	**54.2** (26-112)	**82.6** (68.8-91.9)	**71.8** (67.6-80.8)
Gouldian Finch	5 adults (3M, 2F)	100%	**221.8** (178-273)	**86.7** (77-94.9)	**79.3** (69.7-87.6)
12 months					
Canary	4 adults (2M, 2F)	100%	**14.5** (10-21)	**77.2** (70.6-80)	**84.2** (76.2-100)
Gouldian Finch	4 adults (2M, 2F)	100%	**81.8** (22-192)	**72** (45.5-96.3)	**76.5** (54.5-93.9)

Prevalence = Percentage of hosts infected; Intensity of infection = number of mites in infrapopulation, including live and dead mites of all stages; Mites found live = mites of all stages in an infrapopulation that were found to be alive at the time of host dissection; Adult mites in the infrapopulation = all adult mites, live and dead, in the infrapopulation.

The proportion of live mites and the proportion of adult mites within infrapopulations did not significantly differ between the two host species (i.e. proportion of adult mites: $t = 1.89$, df = 8, $P = 0.1$; proportion of mites found live: $t = 0.65$, df = 8, $P = 0.54$).

After 12 months, all Gouldian Finches and Canaries examined were found to be infected. However, there was a large drop in the mean intensity of infection in both host species between 6 and 12 months. The decrease was highly significant for the Gouldian Finch (i.e mean intensity overall: $t = 3.46$, df = 7, $P = 0.0005$; number of mites live: $t = 2.75$, df = 7, $P = 0.01$), significant for the decrease in the number of mites found live in the Canary ($t = 2.65$, df = 7, $P = 0.03$) but not significant for the decrease in mean intensity overall in the Canary ($t = 2.22$, df = 7, $P = 0.062$). At 12 months the intensity of infection in the Gouldian Finch was no longer significantly higher than that in the Canary ($t = 1.72$, df = 7, $P = 0.14$).

After 12 months there were no significant changes in the proportion of mites found live ($t = 0.75$, df = 6, $P = 0.48$) or the proportion of adults present in the infrapopulations ($t = 0.48$, df = 6, $P = 0.65$) between host species.

8.3.1.2 Psittacid hosts

No evidence of infection by the 'Passerine form' of *S. tracheacolum* was found in Budgerigars examined 6 months following initial infection. Nine birds that had been experimentally infected, together with 6 newly fledged birds from experimentally infected parents, were also examined but no evidence of infection was found.

Four Budgerigars that had been maintained with 4 experimentally infected Canaries between 6 and 12 months (all later found to have retained infections) were examined but no birds were found to be infected.

8.3.2 Wild caught hosts

Table 8.2 presents details of the experimental infection of wild caught Masked Finches. Of 6 birds examined (i.e. at 7, 21 and 23 days following experimental infection) none were found to have retained an infection.

8.3.3 The morphology of progeny of mites transferred to a new host species

Table 8.3 shows morphological measurements of the 'Passerine form' of *S. tracheacolum* from the Canary and the Gouldian Finch at 6 months following initial infection. No significant differences were found in the morphology of specimens coming from the two host species.

An ordination of morphological measurements of mites from captive reared Gouldian Finches and Canaries at 6 months following initial infection is presented in Figure 8.2. Included in the ordination are the measurements of mites from wild caught Gouldian Finches from Newry Station, Yinberrie Hills and Littleton Station (Figure 8.1). Individual mites from wild Gouldian Finches,

Table 8.2 Details of attempts to experimentally infect wild caught Masked Finches *Poephila personata* with mites *S. tracheacolum passeriformes* (coming originally from wild caught Gouldian Finches).

Identity	Sex	Age	Moult	Date	Experimental infection	Date	Experimental infection	Number of days following experimental infection	Number of mites recovered
MF62	Male	Adult	No	10/7/91	3FE, 1F	-	-	7	nil
MF63	"	"	"	"	2FE, 2F	-	-	"	"
MF64	"	"	Yes	"	"	-	-	"	"
MF65	"	Immature	"	23/7/91	1FE	31/7/91	2FE	23	"
MF66	Female	Adult	"	"	2FE	"	2E	23	"
MF67	"	"	"	"	1FE	"	1FE, 1F	21	"

Mites originally collected from Yinberrie Hills, NT on 8/7/91; F = female mite; E = gravid mite.

Figure 8.2 Ordination of morphological measurements (n = 17) of mites *S. tracheacolum* (n = 29) from wild Gouldian Finches and captive reared Gouldian Finches and Canaries:

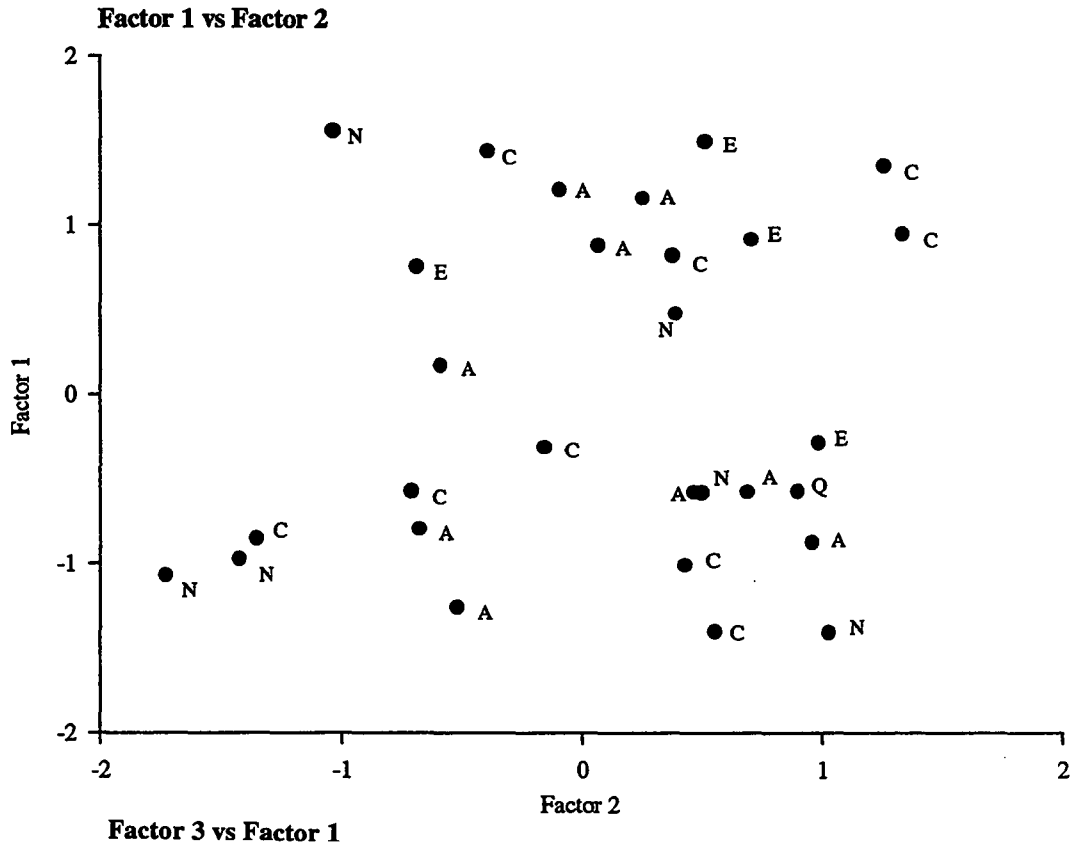
A mites from captive reared Gouldian Finches, 6 months following initial infection. All mites used in experimental infection came originally from wild caught Gouldian Finches from Yinberrie Hills, Northern Territory

C mites from captive reared Canaries, 6 months following initial infection. All mites used in the initial infection came originally from wild caught Gouldian Finches from Yinberrie Hills, Northern Territory

E mites from wild caught Gouldian Finches from Yinberrie Hills, Northern Territory

N mites from wild caught Gouldian Finches from Newry Station, Northern Territory

Q mites from wild caught Gouldian Finches from Littleton Station, Queensland


Factor 1 vs Factor 2
Factor 1
Factor 2
2
1
0
-1
-2
-2
-1
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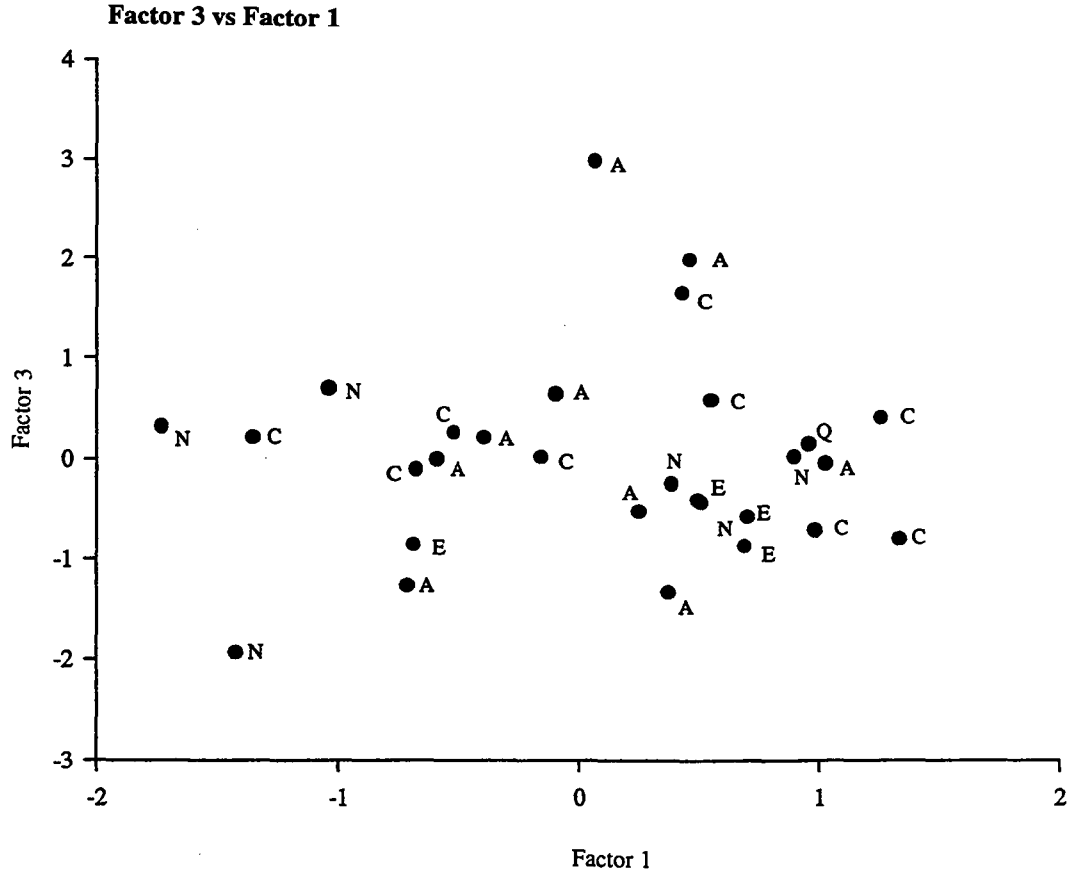
1
2


Factor 3 vs Factor 1
Factor 3
Factor 1
4
3
2
1
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-1
-2
-3
-2
-1
0
1
2

captive Gouldian Finches and captive Canaries are scattered throughout the ordination space, reflecting a lack of consistent variation in morphology among host groups.

No mites were available from the Budgerigar for analysis.

Table 8.3 Mean morphological measurements of adult female mites the 'Passerine form' of *S. tracheacolum* (coming originally from wild Gouldian Finches) reared for 6 months in captive reared Gouldian Finches (n= 5) and Canaries (n = 5).

	Gouldian Finch		Canary		ANOVA	
	Mean	Range	Mean	Range	F value	*P*
Length of idiosoma	443	(396-467)	498	(406-609)	-	
Width of idiosoma	238	(213-274)	247	(183-284)	-	
Length of podosomal plate	249	(243-253)	247	(228-264)	0.21	0.65
Width of podosomal plate	195	(188-203)	200	(183-213)	1.59	0.23
Length of opisthosomal plate	128	(123-140)	130	(120-145)	0.36	0.56
Width of opisthosomal plate	62	(58-68)	64	(55-75)	0.66	0.43
Length of gnathosoma	109	(100-118)	107	(98-113)	0.4	0.53
Width of gnathosoma	82	(75-95)	79	(77-80)	2.69	0.12
Length of palps	39	(38-40)	39	(38-40)	0.21	0.65
Total length of chelicera including fixed digit	131	(125-135)	133	(125-138)	1.34	0.26
Length of movable digit of chelicera	13	(13-15)	13	(13-15)	0.04	0.84
Length of leg I	283	(274-305)	274	(253-294)	0.0	0.98
Length of leg IV	265	(253-284)	267	(253-284)	0.04	0.85
Width of leg I	55	(50-58)	55	(53-58)	2.58	0.13
Width of leg IV	45	(43-50)	43	(40-45)	2.77	0.12
Length of sternal plate	114	(110-125)	116	(107-122)	0.55	0.47
Width of sternal plate	97	(88-105)	105	(98-112)	3.16	0.11
Length of genital plate	81	(75-85)	81	(78-86)	1.73	0.21
Width of genital plate	112	(103-117)	115	(108-122)	0.00	0.95

8.4 DISCUSSION

8.4.1 Susceptibility of wild Masked Finches to the 'Passerine form' of *S. tracheacolum*

Experimental infection failed to produce reproductive infrapopulations in the wild Masked Finch. This finding is consistent with the extremely low prevalence and intensity of infection found in wild birds (i.e. 0.85%, n = 117, Tidemann (1992a); 1.2%, n = 87, the present study (1992-1994)). The results of this study suggest that Masked Finches are probably not limited in their exposure to infection in the wild, but rather, are generally not susceptible to infection by the 'Passerine form' of *S. tracheacolum.*

The presence of a single dead mite in the respiratory system of a bird from a sample of 29 birds at Newry station in 1992 would indicate that Masked Finches are exposed to infection from reservoir species such as Gouldian Finches and Pictorella Mannikins but most infective mites probably fail to establish or to reproduce in this host.

8.4.2 Susceptibility of captive reared Budgerigars to the 'Passerine form' of *S. tracheacolum*

No success was achieved in the establishment of viable the 'Passerine form' of *S. tracheacolum* infections in captive reared Budgerigars. This is a stark contrast to the absolute success achieved in establishment of infections in both captive reared Gouldian Finches and Canaries. Given the simplicity of the experimental infection technique (i.e. direct placement of mites in the nares or mouth of recipient birds and ensuring that those mites were active following placement), it is unlikely that chance could explain a complete failure of the procedure.

A more acceptable explanation for the failure of infection establishment is that the Budgerigar is not susceptible to the 'Passerine form' of *S. tracheacolum* coming from the wild Gouldian Finch. In this light one could imagine that the 'Passerine form' of *S. tracheacolum* mites survived for a short period in the Budgerigar host but were killed by the host's immune system or were unable to reproduce and establish viable infections. This explanation is supported by morphological and ecological data. The morphology of the 'Psittacine form' of *S. tracheacolum* infecting the wild Budgerigar is significantly and consistently different from the 'Passerine form' of *S. tracheacolum* infecting the wild Gouldian Finch, Pictorella Mannikin and Masked Finch. However, all four species share habitat and most importantly share drinking sites providing what could be considered an ample opportunity of interspecific transmission. It is unlikely that two distinct morphological forms of *S. tracheacolum* would share macro habitat but not share host species unless there existed a behavioural or physiological barrier to genetic flow.

If Budgerigars are resistant to infection by the 'Passerine form' of *S. tracheacolum* then additional support is given to the hypothesis that the two forms of *S. tracheacolum* represent two distinct but closely related species of *Sternostoma*. However, the overall prevalence of infection by *S. tracheacolum* in wild Budgerigars is only 16% and the intensity of infection is a mere 1.6 mites per infected host (Chapter 7: Section 7.3.2.1, Prevalence of infection by *S. tracheacolum*). In the captive reared Budgerigar, some strains may exhibit an even higher level of resistance to *S. tracheacolum* and under the experimental conditions of the present study a generally resistant group of Budgerigars may have been used.

Live mites from wild caught or captive reared Budgerigars were not available to undertake the reciprocal experiment (i.e. the experimental infection of captive reared Gouldian Finches with the 'Psittacine form' of *S. tracheacolum* obtained from Budgerigars). Given the demonstrated susceptibility of Gouldian Finches to the 'Passerine form' of *S. tracheacolum*, failure to successfully infect these birds would have provided a more convincing illustration of the variation in susceptibility and resistance of these host species to the two forms of *S. tracheacolum*.

8.4.3 Susceptibility of captive reared Canaries to the 'Passerine form' of *S. tracheacolum*

Experimental results indicate that the Canary is highly susceptible to infection by the 'Passerine form' of *S. tracheacolum*. Although both the Gouldian Finch and the Canary are susceptible to infection, the Gouldian Finch is susceptible to heavier infections (i.e. the size of the mite infrapopulation in the Gouldian Finch is significantly higher than the Canary at 6 months following initial infection). It is not known whether Canaries are naturally infected in the wild though Fain and Hyland (1962) considered they were secondarily infected and that the House Sparrow *P. domesticus* may have served to transfer mites between natural native hosts and captive birds. Fain and Hyland based this suggestion on the poor tolerance to infection observed in Canaries but not in native hosts. In the light of the results from the present study Fain and Hyland's hypothesis remains appealing. An ideal study for clarification of this point would be to examine wild Canaries in their native habitat. Such a study could determine whether Canaries are naturally infected with *S. tracheacolum*, identify the morphological form or forms of specimens present and establish whether wild birds suffer similar pathology to that described for captive reared hosts.

8.4.4 The morphology of progeny of *S. tracheacolum* transferred to a new host species

After six months, mite progeny in the Canary remained morphologically indistinguishable from specimens from captive reared Gouldian Finches. They also remained indistinguishable from specimens taken from wild Gouldian Finches. The implications of this study are clear. Movement to a new host species, and in this case also a movement to a new host family (Estrildidae to Fringillidae) does not, at least in the short term, lead to morphological change in *S. tracheacolum* phenotypes. The morphology of characters that are typically measured by rhinonyssid taxonomists remain stable.

8.4.5 Conclusion

The morphological forms of *S. tracheacolum*, as they are currently placed taxonomically, have to date been found in four host species of the Australian avifauna. Although all these host species share habitat a distinctly different morphological form of *S. tracheacolum* is present in the Budgerigar. As there is no reason to suggest that the mechanism for transmission between species cannot operate between Budgerigars and estrildid finches, the reason for the existence of the two forms is considered to relate to variations between host species in their susceptibility to the different morphological forms.

Results from the present study indicate that changes in morphology of *S. tracheacolum* cannot be found (in the short term) in the progeny of mites transferred between host species (Gouldian Finch to Canary) and that Budgerigars cannot be experimentally infected with the morphological form of *S. tracheacolum* found in wild Gouldian Finches. These results support the proposition that the

'Passerine form' and the 'Psittacine form' of *S. tracheacolum* are probably distinct-species and their relegation to specific host families is the result of physiological barriers to cross infection.

Chapter 9. DRUG TREATMENT

9.1 INTRODUCTION

The first successful attempts at control of *S. tracheacolum* in captive birds used an inhalation of DDT and Benzine Hexachloride (Stephan *et al.*, 1950). The treatment was conducted on Canaries and involved repeated exposures to a powder over a few weeks. An improvement in symptoms was noted and on examination of several sacrificed birds both live and dead mites were found. A 5% Malathion powder was used effectively on Gouldian Finches and Canaries by Cumming (1959) as an inhalation repeated over several weeks. Other malathion solutions have also been used as inhalations and aerosols (e.g. Zwart, 1962; Lafeber, 1967; Morrow, 1986).

Following the reported success of the systemic activity of carbaryl (1-naphthyl-N-methyl-carbamate) on ectoparasitic mites of poultry (e.g. Kraemer & Furman, 1959), Murray (1966) tested the efficacy of a wettable powder containing 80% carbaryl (Sevin®, Union Carbide Australia), on *S. tracheacolum* in Gouldian Finches. Birds were fed treated grain (i.e. 0.04g 80W Sevin® per 50g millet) and following 3 repeat doses over 3 weeks a reduction in the number of living mites was found. Other authors have reported success with carbaryl fed to birds on grain (e.g. Flammer, 1985) and also added to the host's drinking water (e.g. Schultz, 1981). Blasco-Sabio & Portús-Vinyeta (1974) trialed carbaryl on Canaries and although they were unable to eliminate infections completely, they considered that the drug would be an effective control if used periodically. Lafeber (1977) reported success with a systemic treatment of a 0.05% solution of sulfaquinoxaline mixed in the bird's drinking water over a period of six weeks. However, Brownell (1984) found sulfaquinoxaline at equivalent concentrations to be ineffective in 10% of treated Canaries.

Jolivet (1975) found aerosols containing pyrethrins were quite successful in the treatment of infection by *S. tracheacolum* in Gouldian Finches. Bygrave (1980) found that a single exposure of infected Canaries to an aerosol spray containing pyrethrum extract and piperonyl butoxide (Johnson's Anti Mite Spray®) within a confined space produced rapid remission of acute clinical signs. However, some symptoms returned after 2 to 4 weeks. Control without toxic effects has also been reported with the use of other pyrethrin/piperonyl butoxide aerosol products such as Pea-Beu® (Adams National Industries) and Mortein® (Harrigan, 1981; Anon, 1979).

Pest strips with an insecticidal base of dichlorvos, such as 'No Pest Strips' and Shelltox Pest Strips® (Shell Chemical) (e.g. Morelli, 1973; Murray, 1977; Schultz, 1981; Harrigan, 1981; Greyling, 1982) have been used for the control of *S. tracheacolum* in aviary and cage environments though Flammer (1985) considers that their use may have little long term effect on the mite.

Kummerfeld and Hinz (1982) and Kummerfeld (1989) showed that the use of a spot-on-application of Trichlorphon (Neguvon®, Fd. Bayer, Leverkusen) diluted to 2% in propylene glycol, was an effective treatment for infection by S. tracheacolum in both Canaries and Gouldian Finches. Trichlorphon (TCPG) was applied to the shoulder region three times a day in a three day to weekly cycle. A reduction in the clinical symptoms was detected within 24 to 48 hours and no live mites were detected in birds killed after 60 days. Within the dosage range 40-70 mg/kg (i.e. 0.03-0.05 ml/bird), TCPG had negligible affects on Gouldian Finch breeding. Kummerfeld and Hinz found that at three times the dosage some birds died and that death from toxicity usually occurred within 48 hours of the high dosage. A dramatic weight loss of 2 grams per day occurred but pathological symptoms could not be detected histologically. Other symptoms of intoxication included salivation, dyspnoea, 'rattling breathing' muscle spasm and increased defecation. Szeleszczuk and Kruszewicz (1987) also found TCPG, used as a spot-on-application, was a successful treatment in Gouldian Finches. Doses between 0.03 and 0.06 ml per bird (dependant on the bird's age) were administered on day 1, 5 and 9. However, the authors expressed some concern for potential toxicity, particularly in birds exhausted by longer disease.

Most recently, ivermectin has been used effectively against a variety of adult and larval nematodes, microfilariae and mites of birds (e.g. Thomas-Baker, 1986; Ryan, 1986). The avermectins are a group of drugs produced by the actinomycete *Streptomyces avermitilis.*

Kummerfeld and Schäfer-Nolte (1987) used ivermectin as a spot-on-application at doses between 0.1 ml and 5 ml of a 0.02% solution of ivermectin (i.e. 0.4-20.0 mg/kg Ivomec® MSD) for the treatment of *S. tracheacolum* infection and Scaly-leg disease *Knemidokoptes jamaicensis* (Turk), in Canaries, Goldfinches, *Carduelis carduelis*, and Bullfinches, *Pyrrhula pyrrhula* (L.), and also for Knemidocoptic disease (*Knemidokoptes* pilae) of Budgerigars. No toxic effects were observed in Budgerigars within this range and Canaries at 0.4 mg/kg, but Bullfinches and Goldfinches died within 24 hours following a spot-on-application of 0.3 and 0.4 mg/kg respectively. Spot-on-application of ivermectin was considered a suitable treatment for infection by *S. tracheacolum* in Canaries and fading of clinical symptoms occurred within four days.

In tests at various doses of ivermectin (Ivermectin®) injected subcutaneously in Golden Pheasants *Chrysolophus pictus* (L.), Airsac mites *Kytodites nudus* were found to be killed only by very high doses i.e. 50 mg/kg body weight (Grimm & Centurier, 1985). Ivermectin also produced noticeable systemic effects on in the Fowl *Gallus gallus domesticus* when injected intra-abdominally in infested chickens at rates greater than 0.6 mg/kg. Toxicity was found to occur at levels exceeding 5.4 mg/kg and at this dose ivermectin was found to be active for 70 hours following injection (Zeman, 1987). Hogan *et al.* (1984) found a single intra-muscular injection of ivermectin

(Ivomec®) at a dose of 200 mcg/kg eliminated *Knemidokoptes mutans* (Robin & Lanquetin) in Parakeets and no evidence of toxicity could be found from histopathological examinations. However, Harrison (1986) claims that the use of ivermectin at normal suggested dose rates (i.e. 200 mcg/kg body weight) has been associated with deaths in Budgerigars. Deaths have also been reported with the use of ivermectin oral paste (Eqvalan®) but it would appear that the deaths were associated with the stabiliser in the paste rather than the active ingredient.

Brownell (1984) administered ivermectin (Eqvalan®) by intramuscular injection to both infected and non-infected Canaries and Finches. He found a degree of immobility in both host species but more pronounced in birds given 0.04 ml of a 1:10 dilution. These symptoms disappeared within 20 hours following injection and respiratory symptoms ceased altogether within 10 days. Brownell found dead mites and mite fragments in birds sacrificed for post-mortem examinations 24 and 48 hours following treatment at the 1:10 dilution. As spastic movement was observed in the legs of mites in birds given a 1:100 dilution he suggested that the proper dilution is important in eliminating *S. tracheacolum* mites.

Tidemann *et al.* (1991) began trialing ivermectin (Ivomec®, 0.8 g/L ivermectin), given orally to captive wild Gouldian Finches in 1991. They found that successive doses between 6, 10, 15 and 20 µl of ivermectin per bird at two weekly intervals killed *S. tracheacolum* and did not appear to be toxic to the birds. Accidental overdosing of 22 captive reared Gouldian Finches at the Territory Wildlife Park in the Northern Territory, Australia in 1991 using 0.01 ml ivermectin (i.e. 100 µl per bird) resulted in the death of 7 birds within two days (Oosterweghel, pers. comm.). Considered together, these results suggest that ivermectin tolerance in Gouldian Finches is quite high and that lethal toxicity is likely to occur somewhere between 20 and 100 µl Ivomec® for oral administration.

The results of treatment regimes are usually assessed either in terms of the subsequent health of the birds (e.g. assessment of the presence of symptoms) or by some estimation of the number or proportion of mites killed from examination of host tissues at autopsy. For example, Murray (1966) assessed the success of carbaryl treatment by comparing the numbers of live and dead mites (counted in the lung, airsacs and trachea during a five minute observation period) between treated and non-treated birds. Currently there are few data for any host species on which to assess the proportion of *S. tracheacolum* mites killed by ivermectin, either for entire infrapopulations, for individual mite stages or for individual localities within the host. The proportion of mites killed by single dose oral application has never been investigated. The present study further examines the efficacy of ivermectin as a single dose treatment for the elimination of *S. tracheacolum* in captive

bred Gouldian Finches. Efficacy is assessed through exhaustive examination of host tissues for mites following treatment of the host.

9.2 METHODS

9.2.1 Dosage and administration

Captive reared Gouldian Finches of unknown infection history were experimentally infected with *S. tracheacolum* and subsequently maintained in small cages or aviary enclosures until they showed clinical signs characteristic of infection. From this point onwards, birds were deemed eligible for inclusion in treatment trials.

Due to limitations on the availability of birds and holding facilities, as well as ethical considerations regarding the involvement of vertebrate animals in sacrificial experiments, treatment trials were not balanced for sex, age or size of infection. For the same reason, controls were also limited once it had been established that the act of dosing (capture, handling and forced ingestion of fluid) did not have a significant effect on birds. The details of trials are shown in Table 9.1.

In controlled experiments, birds were randomly allocated to treatment or control groups. Birds in treatment groups received a measured oral dose of ivermectin administered with the aid of a 1-25 gradiculed microlitre syringe. Control birds received identical doses of distilled water in the same manner. Birds in each group were weighed prior to drug administration and again prior to euthanasia The general behaviour of birds was monitored during the first day following drug administration. After a period of at least 3 days all birds were killed by lethal anaesthetic injection and examined.

All captive reared Gouldian Finches, Budgerigars and Canaries used in monitoring experiments were pre-treated with oral dose Ivomec® (Experimental Design: 6. Ivermectin pre-treatment procedure, P 67). Details of the dose rates given to these birds is shown in Table 9.2.

Following the results of drug treatment studies (as at April 1993) a pilot study was undertaken to assess the short term effect of a 3.2 µl/g b.w. oral dose of ivermectin on wild captured Gouldian Finches. Juvenile birds were targeted for treatment at both Yinberrie Hills and Newry Station, NT (Table 9.3).

Table 9.1 Details of the treatment of captive reared Gouldian Finches with ivermectin (Ivomec®).

Dose rate (microlitres of ivermectin per gram body weight)	Quantity of ivermectin administered (microlitres)	Number, age and sex of birds	Month of drug administration	Ambient Temperature
Experiment 1				
1.27 (1.12-1.4)	20	4 adult females, 4 adult males	July	26 C (constant)
Controls received equivalent doses of distilled water		3 adult females, 3 adult males		
Experiment 2				
1.69	25	1 juvenile male	July	26 C (constant)
2.17	30	"	"	"
2.46	35	1 adult female	September	"
3.15	40	1 juvenile female	"	"
2.71	45	1 juvenile male	October	"
Experiment 3				
2.0	28-36.5	1 adult female, 4 adult males	April	23 C (constant)
Experiment 4				
2.85	43.7-49.9	2 adult females, 2 adult males	May	26 C (constant)
Controls received equivalent doses of distilled water		2 adult females and 1 adult male		
Experiment 5				
3.5	50.6-60	5 adult females, 2 adult males	September	23 C (constant)
Experiment 6				
4.0	64.4-74.8	1 adult female, 3 adult males	February	23 C (constant)

Table 9.2 Captive reared Gouldian Finches, Budgerigars and Canaries treated with an oral dose of ivermectin.

Dose rate (microlitres of ivermectin per gram body weight)	Quantity of ivermectin administered (microlitres)	Number, age and sex of birds	Month of administration	Ambient temperature on day of administration
Gouldian Finches				
1.36-1.88	25	36 adult females and 36 adult males (first years birds)	January	15 - 28 C (range)
"	"	"	February	15 - 34 C (range)
2.0	28-40	24 adult females, 24 adult males (36 first year birds; 6 females and 6 male had bred previously)	February	18 - 36 C (range)
Budgerigars				
2.0	72-120	15 adult females, 5 adult males	February	18 - 28 C (range)
Canaries				
2.0	34-44	10 adult females, 10 adult males	February	18 - 32 C (range)

Birds were mist netted at natural or artificial drinking sites between 800 and 1100 hrs and subsequently returned to the field station. Each bird was randomly allocated to a treatment or control group. After weighing, treatment birds were then administered a 3.2 µl/g b.w. oral dose of ivermectin. Control birds were handled in a similar manner but received an equivalent dose of distilled water instead of ivermectin. Both treated and non-treated birds were then housed in small cages and observed regularly over the following 6 hours. On the following morning birds were reweighed, returned to their site of capture, and then released.

9.2.2 Post-mortem examination of birds

The nasal and buccal cavities, trachea, syrinx, bronchi, lungs, airsacs, humerus airsac extensions and the general body cavity of each bird were thoroughly examined for *S. tracheacolum* mites. All mites and mite fragments found were removed from host tissues and stored in 70% alcohol. They were then cleared in Nesbitt's solution and mounted in Hoyer's medium on microscope slides. The sex, stage and reproductive condition of all mites found, both live and dead, (whole and fragmented) was then determined.

Table 9.3 Treatment of wild caught Gouldian Finches with an oral dose of ivermectin.

Dose rate (microlitres of ivermectin per gram body weight)	Quantity of ivermectin administered (microlitres)	Number and maturity of birds	Month
Gouldian Finches (Newry Station, NT)			
3.2	42-49	6 juveniles and 7 immatures	July 1993
Controls received equivalent doses of distilled water		12 juveniles	"
Gouldian Finches (Yinberrie Hills, NT)			
3.2	38-51	22 juveniles	July 1993
Controls received equivalent doses of distilled water		23 juveniles	"

The determination of whether a mite was live or dead was made at the time of dissection. The exoskeleton of live *S. tracheacolum* adults and immatures (following the protonymph blood meal) is light in colour and translucent in appearance. Dead mites are brown-yellow to very dark brown-black in colour (usually depending on the time since death) and this colour change appears to occur quite rapidly following death. All discoloured mites were therefore considered to be dead. Mites that were not discoloured but immobile and unresponsive to frequent prodding with a micro probe were also considered to be dead. Unfed immatures that were not obviously dead (i.e. yellow brown in appearance) were also put to 'the response to prodding test' and determined to be live if any movement could be detected, and dead if no movement could be detected.

9.3 RESULTS

9.3.1 The percentage of mites killed following treatment of host with ivermectin

The results of ivermectin treatment trials for individual birds are shown in Table 9.4 and summarised in Figures 9.1 and 9.2.

9.3.1.1 Experiment 1: single oral doses of 20 µl of ivermectin without regard to host weight

The resultant dosage rate was 1.12-1.4 µl/g b.w. Treated birds were examined between 6 and 13 days and non-treated birds between 8 and 14 days following treatment. No significant difference was found in the mean weight variation following treatment between treated and non-treated birds ($t = 1.56$, df = 11, $P = 0.15$). The mean infrapopulation size following treatment (i.e. all mites, dead and live of both sexes and all stages) was 25.9 mites (R = 1-147, SD = 18.1) for treated birds and

Table 9.4 Results from the experimental treatment of captive reared Gouldian Finches *E. gouldiae* using oral doses of ivermectin (Ivomec®).

Host identity number	Sex of host	Maturity of host	Quantity of ivermectin administered (microlitres)	Dose rate of ivermectin (microlitres per gram body weight)	Number of days following treatment that bird was euthanased and examined	Weight variation of host between date of treatment and date of euthanasia	Total number of mites found in the host's respiratory system	Number of mites found live	Number of mites found dead	Percentage of mites found dead
6	Male	Adult	20.0	1.12	7	+1.0	20	2	18	90
8	Female	"	"	1.16	9	-0.6	36	9	27	75
3	"	"	"	1.24	13	-1.9	48	29	19	40
7	"	"	"	1.26	7	-0.6	1	0	1	100
9	Male	"	"	1.32	9	-0.3	5	0	5	100
4	Female	"	"	1.39	11	+0.3	28	22	6	21
5	Male	"	"	1.4	6	-0.3	40	30	10	25
10	Male	Adult	nil	nil	8	-0.1	6	5	1	17
11	Female	"	"	"	"	0.0	36	35	"	2.7
2	Male	"	"	"	10	+0.1	90	82	8	8.8
14	Female	"	"	"	14	+0.2	25	22	3	12
13	Male	"	"	"	"	+0.2	55	54	1	1.8
12	Female	"	"	"	10	+1.7	147	144	3	2
109	Male	Juvenile	25.0	1.69	8	-0.2	76	9	67	88.2
108	"	"	30.0	2.17	7	+0.6	24	5	19	79.2
104	Female	Adult	35.0	2.46	6	-0.3	142	10	132	93
114	Male	Juvenile	45.0	2.71	11	-1.5	115	3	112	97.4
107	Female	"	40.0	3.15	10	+1.3	60	14	46	76.7

Table 9.4 Continued, Results from the experimental treatment of captive reared Gouldian Finches *E. gouldiae* using oral doses of ivermectin (Ivomec®).

Bird identity number	Sex of host	Maturity of host	Quantity of ivermectin administered (microlitres)	Dose rate of ivermectin (microlitres per gram body weight)	Number of days following treatment that bird was euthanased and examined	Weight variation of host between date of treatment and date of euthanasia	Total number of mites found in the host's respiratory system	Number of mites found live	Number of mites found dead	Percentage of mites found dead
185	Male	Adult	32.4	2.0	9	+0.5	263	23	240	93.3
183	Female	"	28.0	"	7	-0.8	13	4	9	76.9
184	Male	"	35.0	"	8	-0.4	65	15	50	78.6
186	"	"	36.5	"	10	+0.5	29	1	28	96.7
187	"	"	28.2	"	10	0.0	42	23	19	44.2
136	Female	"	49.9	2.85	8	-0.7	24	2	22	91.6
126	Male	"	43.7	"	14	-0.5	39	0	39	100
124	"	"	49.6	"	11	-0.6	8	0	8	"
122	Female	"	47.0	"	14	-1.0	3	0	3	"
120	Male	"	nil	nil	15	-1.4	63	51	12	19.4
123	Female	"	"	"	16	+0.6	2	1	1	50
129	"	"	"	"	12	0.0	5	1	4	80
203	Male	"	54.6	3.5	12	-0.3	23	0	23	100
202	Female	"	51.5	"	"	+0.1	14	3	11	78.6
201	"	"	50.6	"	14	+0.5	119	4	115	96.6
701	"	"	70.0	"	4	-0.3	-	-	-	-
702	"	"	64.0	"	"	+0.7	-	-	-	-
451	"	"	60.0	"	5	-0.1	4	0	4	100
450	Male	"	55.0	"	4	+0.1	38	1	37	97.4
458	Female	"	68.4	4.0	4	-0.6	71	0	71	100
460	Male	"	67.5	"	3	+0.3	132	"	132	"
459	"	"	74.8	"	"	-0.9	24	"	24	"
461	"	"	64.4	"	5	-0.7	116	"	116	"

Figure 9.1 The mean percentage of mites *S. tracheacolum* of all stages found dead in captive reared Gouldian Finches *E. gouldiae* following oral treatment with ivermectin.

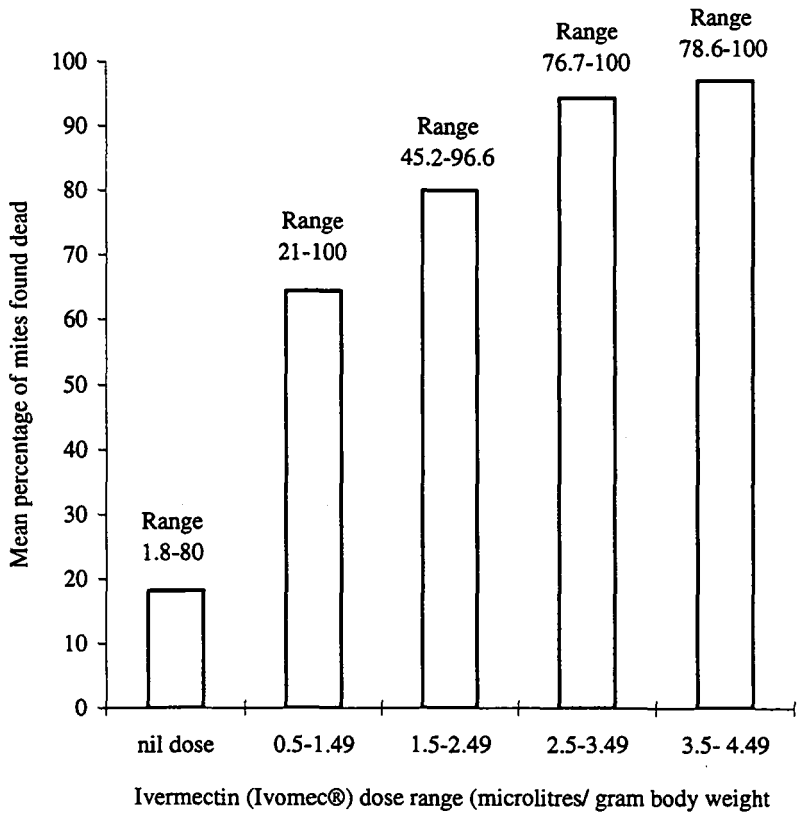
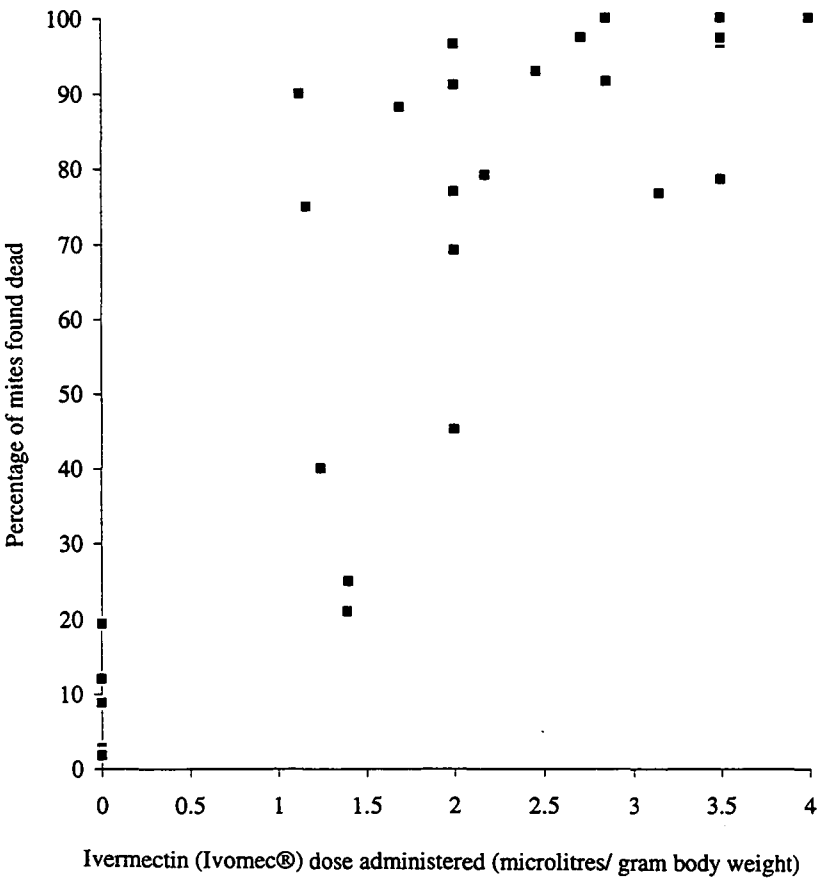


Figure 9.2 The percentage of mites *S. tracheacolum* of all stages found dead in captive Gouldian Finches *E. gouldiae* following oral treatment with ivermectin (for infestations > 10 mites).



59.8 mites (R = 6-147, SD = 51.4) for non-treated birds and was not significantly different between the two groups (Wilcoxon 2-Sample Test; $P = 0.12$). The mean percentage of mites found dead was significantly higher in the treated group than the non-treated group ($t = -3.04$, df = 11, $P = 0.016$). Overall the percentage of mites killed was 63.6% (R = 21-100, SD = 34.7) for treated birds and 7.4% (R = 2-17, SD = 6.3) for non-treated birds.

9.3.1.2 Experiment 2: 5 µl incremental doses of ivermectin above 20 µl per bird

Oral doses of 25, 30, 35, 40 and 45 µl were administered to determine the most appropriate dose range for further trialing with the aim of complete elimination of *S. tracheacolum* infection. Birds were dosed on different dates and the experiment was not controlled. High proportions of mites were found dead following treatment in all birds. However, very high percentages of mites were killed (i.e. 93% and 97.4%) at 35 µl (2.46 µl/g b.w.) and 45 µl (2.71 µl/g b.w.) for infections containing 132 and 112 mites respectively.

9.3.1.3 Experiment 3: dose rate dependent on bird weight

Five birds were treated with an oral dose of 2.0 µl/g b.w. representing an overall dose range of 28-36.5 µl per bird. The birds were killed between 7 and 10 days following treatment. Weight variations, all within 1g, were considered to be normal. The mean infrapopulation size was 82.4 mites per host (R = 13-263, SD = 102.7) and the mean percentage of mites killed was 77.9% (R = 44.2-96.7, SD = 20.8).

9.3.1.4 Experiment 4: oral dose of 2.85 µl/g b.w.

An overall dose range of 43.7-49.9 µl per bird was given to 4 birds. A further 3 birds were used as controls. The mean weight variation for treated birds was -0.7 (R = -1.0--0.5, SD = 0.17) and control birds 0.3 (R = -1.4-0.6, SD = 1.03). The mean infrapopulation size for treated birds was 18.5 mites per host (R = 3-39, SD = 16.3) with a mean percentage of dead mites of 97.9% (R = 91.6-100, SD = 4.2). For non-treated birds the mean infrapopulation size was 23.3 mites (R = 2-63, SD = 34.4) with a mean percentage of dead mites of 49.8 (R = 19.4 - 80, SD = 30.3).

9.3.1.5 Experiment 5: single dose of 3.5 µl of ivermectin/g b.w.

Seven birds were treated with an overall dose range of 50.6-54.6 µl per bird. The experiment was not controlled. Two birds, both female (mean weight = 19.1g; R = 18.2-20), were found to be uninfected when killed and examined. As all airsac membranes were found to be clear it was considered unlikely that either bird was previously infected. The mean weight of the 5 remaining birds was 15.7g (R = 15.0-16.74) with a mean weight variation following treatment of 0.01g (R = -0.3-0.5). The mean infection size was 39.6 mites (R = 4-119; SD = 46.1) with a mean percentage of mites killed of 94.5 (78.6-100).

9.3.1.6 Experiment 6: a single dose of 4.0 µl of ivermectin/g b.w.

Four adult birds with a mean weight of 17.2g (R = 16.1-18.7) were dosed. The mean weight variation was -0.34g (R = -0.9-0.3). The mean infection size was 85.8 (R = 24-132; SD = 48.6) and all mites were found to be dead at post-mortem.

9.3.2 An abnormal development site for *S. tracheacolum* following ivermectin treatment of the host

The normal life cycle of *S. tracheacolum* involves the laying of an egg (containing a developed larva) within the lung of the host. All available evidence suggests that the larva hatches shortly afterwards (Chapter 2: Section 2.6, Duration of the life cycle). Following oral treatment of the host with ivermectin, and this occurred at all doses trialed, the egg of ivermectin killed gravid female mites did not necessarily die but continued development inside the carcass of the dead mother. In most cases a hatched larva was found, however, in a number of cases development had continued to protonymph, deutonymph and in two cases, to adult male. This phenomenon was never recorded for *S. tracheacolum* outside ivermectin treatment experiments. The orientation of developing mites within the mother's carcass is illustrated in Chapter 2: Figure 2.5 (The presence of immature and adult mites within the carcass of ivermectin killed gravid females *S. tracheacolum*).

9.3.3 Impact of ivermectin on *S. tracheacolum* infrapopulation structure and site

Site data on the proportion of mites killed suggest that mites in the nasal cavity, trachea and syrinx of the host have the highest chance of surviving oral dose treatment of the host with ivermectin (Figure 9.3).

Figure 9.4 shows the mean distribution of mites from 21 birds treated with ivermectin against a foreground comprising the mean distribution data for mites of 84 infected non-treated birds that were examined over a 2 year period (Chapter 2: Section 2.3 Life history). The mean infection size was not significantly different between the treated and non treated groups (Wilcoxon 2-Sample Test; $P = 0.32$) and the infection size data from both groups was similarly distributed (Kolmogorov-Smirnov 2-Sample Test, $P = 0.84$). However, the distribution of mites throughout the respiratory system of treated birds was significantly different from that of non-treated birds (Overall $\chi^2 = 550.4$, df = 11, $P < 0.00001$). Significantly less than expected frequencies of mites were found in the nasal cavity ($\chi^2 = 40.08$, df = 11, $P < 0.00003$), upper trachea ($\chi^2 = 78.79$, df = 11, $P < 0.00001$) and lower trachea ($\chi^2 = 68.54$, df = 11, $P < 0.00001$) and significantly more than expected frequencies of mites were found in the thoracic ($\chi^2 = 179.88$, df = 11, $P < 0.00001$) and posterior airsacs ($\chi^2 = 49.22$, df = 11, $P < 0.00001$). The majority of mites in treated birds (whether live or dead) were found deeper within the respiratory system (i.e. lungs and airsacs versus trachea, mouth and nasal cavity) than mites of untreated birds ($\chi^2 = 340.96$, df = 1, $P < 0.00001$).

Figure 9.3 Survival of mites *S. tracheacolum* in each locality of the respiratory system following ivermectin treatment of the hosts *E. gouldiae*: A, 0.5-1.49 µl Ivomec®/g b.w. (n = 6); B, 1.5-2.49 µl Ivomec®/g b.w. (n = 8); C, 2.5-3.49 µl Ivomec®/g b.w. (n = 6); D, 3.5-4.49 µl Ivomec®/g b.w. (n = 9).

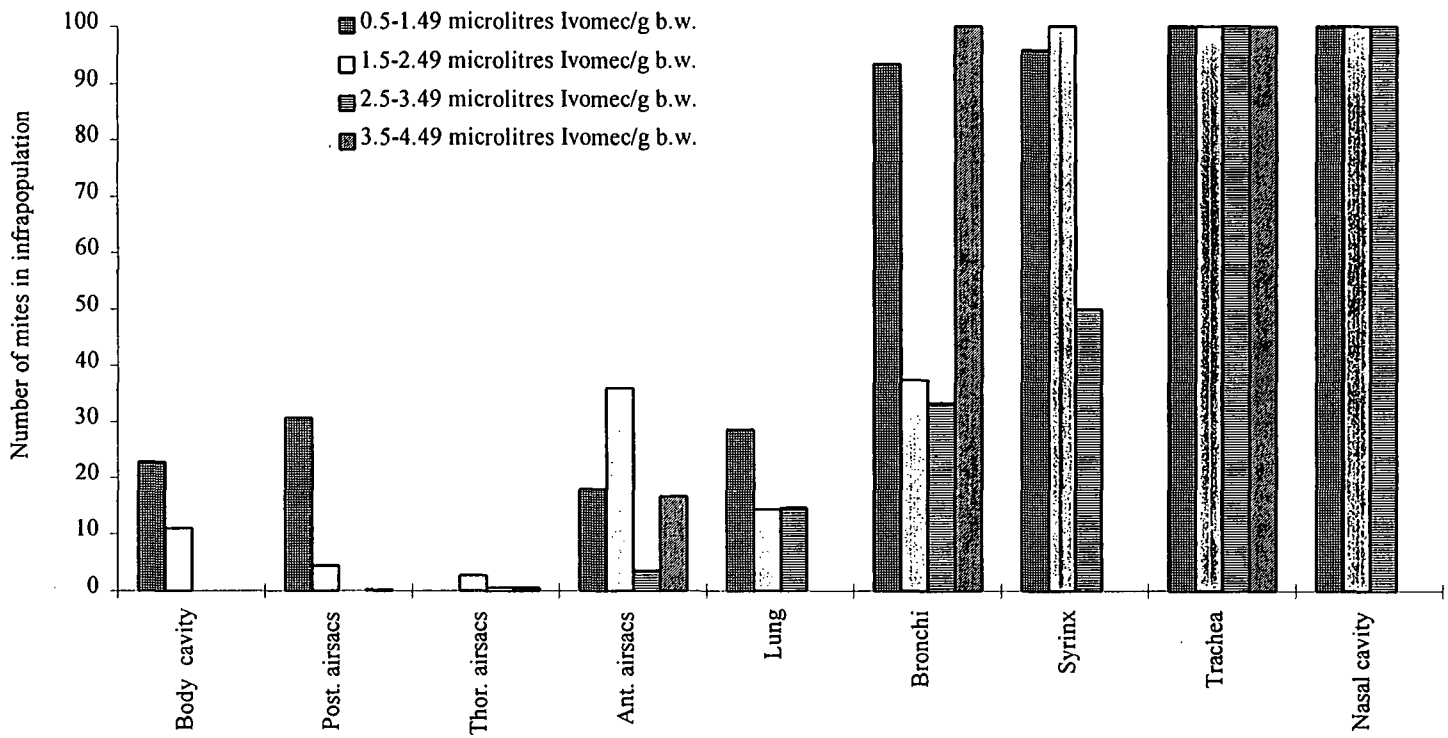
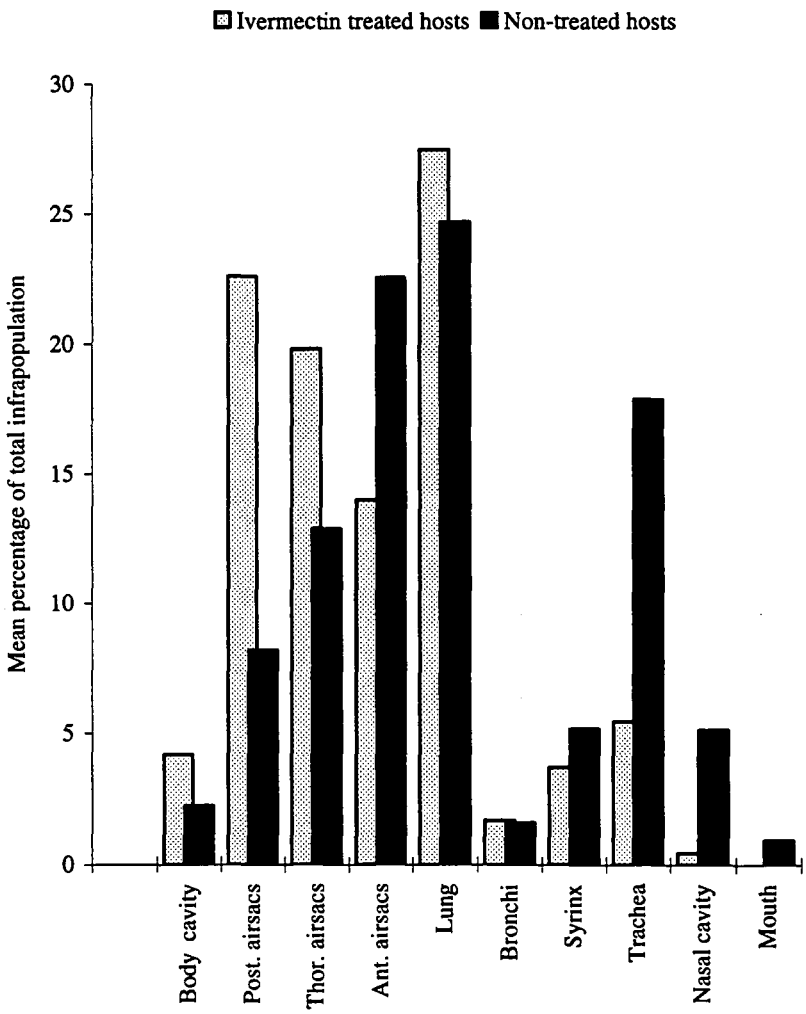


Figure 9.4 The influence of ivermectin treatment of Gouldian Finches *E. gouldiae* on the distribution of mites *S. tracheacolum* within the host's respiratory system: Ivermectin treated hosts (n = 24; mean infrapopulation size = 51.7; SD = 83.2); non-treated hosts (n = 84; mean infrapopulation size = 73.1; SD = 58.7).



Of the general demographic composition (both live and dead mites), significantly higher than expected frequencies of adult male mites were found in the respiratory system of treated than non-treated birds. Conversely, significantly less than expected frequencies of larvae were found in treated birds. The proportions of other stages (i.e. egg, protonymph, deutonymph and adult female) were similar between the treated and non-treated groups.

9.3.4 Ivermectin pre treatment of captive reared Gouldian Finches, Budgerigars and Canaries

Of 72 adult first year Gouldian Finches treated with a 25 µl oral dose of ivermectin and a similar dose 14 days later, and a further 48 adult birds that received a 2.0 µl/g b.w. oral dose of ivermectin (overall dose range 28-40 µl) and a second dose 14 days later, no obvious signs of toxicity were detected. All birds were closely observed over 4 days following each dose treatment during which time no deaths occurred. In the longer term, birds proceeded to breed and did not appear to be adversely affected by ivermectin treatment.

Twenty Budgerigars and 20 Canaries were given a 2.0 µl/g b.w. oral dose of ivermectin. The overall dose range for Canaries was 34-44 µl for a mean bird weight of 19.2g (R = 16.5-21.7, SD = 1.46). Budgerigars received doses ranging from 72 to 120 µl for a mean bird weight of 49.6 (R = 37.4-60.1, SD = 6.44). Both species were observed for 4 days following treatment during which time no deaths were observed. In the longer term birds appeared little affected by ivermectin treatment and successful breeding occurred in both species following treatment.

9.3.5 Ivermectin treatment of wild Gouldian Finches

At Newry Station, 13 birds were treated with a 3.2 µl/g b.w. dose of ivermectin (overall dosage range 42-49
µl per bird) with a further 12 birds used as controls. At Yinberrie Hills 16 birds were treated at the same dose rate (overall dosage range 38-51 µl per bird) with a further 17 birds used as controls.

At Newry Station the initial mean weight was 14.3g (R = 13.5-15.5, SD = 0.75) for treated birds and 13.6g (R = 10.5-15, SD = 1.2) for non-treated birds (an initial weight was not recorded for 1 non-treated bird; the release weight was not recorded for 3 treated birds, and one treated bird and 2 non-treated birds died within the period of captivity). The mean variation between weight at capture and weight at release, for remaining birds, was 0.56g (n = 9, R = -0.5-3.5, SD = 1.18) for treated and -0.43g (n = 7, R = -1.5-0.5, SD = 0.73) for non-treated birds. The difference in weight variation between the two groups was not significant (t = 1.65 df = 14, P = 0.12). The initial mean weight for the 3 birds that died (12.3g; n = 3, R = 10.5-13.5) was notably less than the initial mean weight for all surviving birds from both treated and non-treated groups (n = 21, mean = 14.2, R = 13.0-15.5).

A low initial weight may have related to bird deaths. Deaths during captivity did not appear to be related to ivermectin treatment. Mean weights were similar between treated and non-treated birds and the behaviour of birds from both groups appeared to be similar at the time of release.

At Yinberrie Hills, the mean initial weight for treated birds was 14g (R = 12.5-16, SD = 0.98) and for non-treated birds was 14.5g (R = 12-16, SD = 1.01). The mean weights were not significantly different (t = 1.17 df = 31, P = 0.25). One treated bird died during captivity. The cause of death was attributed to holding rather than the treatment. It became very wet and cold after falling in water provided for drinking. The mean weight variation between capture and release weights was -0.7g (R = -0.5-1.0, SD = 0.25) for treated birds and -0.66g (R = -0.5-1.0, SD = 0.26) for non-treated birds. The difference between the two groups was not significant (t = 0.71 df = 30, P = 0.48).

9.4 DISCUSSION

The difference in distribution of mites between treated and non-treated birds may reflect the speed of the host's response to the presence of dead mites in the upper respiratory system (i.e. trachea and nasal cavity). This is also supported by the rapidity of clinical sign remission observed by other authors investigating the treatment of infection by *S. tracheacolum* (e.g. Kummerfeld & Hinz, 1982; Kummerfeld & Schäfer-Nolte, 1987). Conversely, the higher relative frequency of mites found within the lower respiratory system of treated birds may reflect the inability of hosts to clear the airsacs, and to some extent the small air passages of the lungs, of the same material. In the absence of excessive mucus and large agglomerations of mites in the trachea, wheezing, 'clicking' and other respiratory symptoms soon cease. As mites die, or even if mites merely become paralysed through the actions of ivermectin, they are presumably unable to maintain themselves within the trachea and are swept out with the flow of mucus and by the action of coughing. For this reason it is likely that both the total size of the infection prior to treatment and the percentage of mites killed in the upper respiratory system are underestimated by observations made at post-mortem examination. Earlier examination of birds following treatment may to some extent reduce this problem. However, early examination may also result in an underestimation of the efficacy of the drug by reducing the percentage of mites found dead (i.e. it does not allow for the potential ongoing action of the drug if the host were sacrificed at a later date following treatment).

Significant differences in the demographic structure of *S. tracheacolum* following ivermectin treatment of the host may be related to factors of the life history of the parasite. The larval stage is extremely short lived and without continual recruitment its presence within the lung would be soon exhausted. As adult females are killed following ivermectin treatment no further eggs are laid. Instead, the eggs hatch and the larvae continue development incarcerated in their mother's carcases. The greater than expected frequency of male mites in ivermectin treated hosts is discussed in

Chapter 2: Life History. One hypothesis to explain the phenomenon relates to the mechanism of sex determination employed by *S. tracheacolum*. Demographic evidence supports a parthenogenetic form of reproduction with a haploid-diploid arrangement for sex determination. Within this system virgin females produce haploid males and mated females produce diploid females. If males are rapidly killed following ivermectin treatment then surviving unmated females will only produce males.

By comparison with co-occurring finch species such as the Masked Finch and the Long-tailed Finch, the wild Gouldian Finch is not prone to recapture (Woinarski & Tidemann, 1992). This is considered to be due to a learned aversion to recapture, a high emigration rate from breeding sites, a high mortality rate or some combination of these factors. Low recapture rates are found within the breeding season and extremely small recapture rates are found between breeding seasons. It is therefore important, whether for experimental manipulation of infection for the purposes of field based experiments or for a management program aimed at the control of *S. tracheacolum* in wild host populations, that the impact of single dose treatment on individual birds is clearly understood. Opportunities for additional dosing can be taken in the event of recapture and indeed, if *S. tracheacolum* is responsible for existing poor recapture rates through a direct or indirect impact on Gouldian Finch mortality rates, a feedback effect on recapture may take place. However, unless recapture rates could be substantially increased and assured in the short term, any proposed program of control in the wild should be based on the outcome of a single dose treatment regime.

For the purposes of the current study, complete elimination of *S. tracheacolum* in individual Gouldian Finches may be the only satisfactory means of controlling infection in host populations at large. This is the case both from the need to significantly increase the probability of survivorship of individual birds and from the practical viewpoint of developing a succinct probability model for the potential impact of any given treatment regime. Incomplete elimination through a single dose would leave individual hosts infected at largely unknown levels (i.e. due to the high variability in the proportion of mites killed at dose levels less than 3.0 µl/g b.w.). If *S. tracheacolum* infection of a bird is in a rapid growth phase (see Chapter 3: Section 3.3.2, Infrapopulation growth of *S. tracheacolum*), and this would probably be the case for the majority of infected wild juvenile Gouldian Finches, a reduction in the size of the infection through ivermectin treatment would be short lived, perhaps lasting only a few weeks. On the other hand complete elimination, while presumably not influencing the probability of reinfection, will increase the probability of survivorship over the long term by eliminating mortality directly or indirectly attributable to the presence of *S. tracheacolum*.

In view of the forgoing requirements it is recommended that any program of treatment in the wild, whether for experimental or management purposes, use single oral doses of ivermectin in excess of 3.5 µl/g b.w. Ivomec® though less than or equal to 4.0 µl/g b.w. Doses as high as 3.2 µl/g b.w. appear to be well tolerated by wild caught Gouldian Finches and doses as high as 4.0 µl/g b.w. appear to be tolerated by aviary bred Gouldian Finches, without obvious toxic affects. Lower dose rates can result in highly variable rates of mites killed. It should be noted that because weights of captive birds tend to be higher than those of wild birds, and fat is likely to account for the differential, the overall dose given to captive bred birds is generally larger than those given to leaner wild birds.

Oral doses of ivermectin appear to be a relatively safe treatment for Budgerigars and Canaries. If the efficacy of its action reflects that in the Gouldian Finch it may also be an effective treatment for infection by *S. tracheacolum* in these species. Although high doses provide the opportunity for the elimination of infrapopulations in a single dose, management for eradication of this parasite from captive host populations would be advantaged by repeated dosing of individual birds.

In conclusion, oral dosing with ivermectin is considered appropriate (from an efficacy perspective) for the control of *S. tracheacolum* in wild host populations. It should be noted however, that only ivermectin and only oral dosing have been investigated in this study and no previous studies on alternative drugs for the treatment of infection by *S. tracheacolum* are sufficiently detailed to allow meaningful comparisons. Furthermore, other drugs with a known acaricide action are available but are untested on *S. tracheacolum* (e.g. Levamisole®). Some drugs already known to have an action on *S. tracheacolum* may be potentially more suitable than ivermectin but remain inadequately tested for confident use (e.g. Trichlorphon). Alternative forms of drug administration result in variations in rate and quantity of absorption. Loss of drug solution from the mouth can occur, both during and following oral administration, and the quantity of food in the crop may influence the rate of drug absorption. Better results may be achieved with the use of a crop needle for administration, at least as a means for ensuring complete ingestion of intended dose. Intra-muscular or intra-abdominal injection of drugs may have some advantage over oral administration though significant bruising may occur in small birds; the use of micro-needles may alleviate this problem.

Chapter 10. POPULATION DYNAMICS OF THE HOST

10.1 INTRODUCTION

The impact a macroparasite has on the size of its host population is largely dependent on the level of pathogenicity and the distribution of the parasite within the host population (Anderson, 1979; McCallum, 1994). If a parasite is highly pathogenetic, a low intensity of infection will kill the host leading to a low transmission rate and consequently an inability for the parasite to influence the size of the host population. Hence, an extremely virulent parasite will tend to have a greater impact on its own survival than that of the host population. However, for a parasite of moderate pathogenicity the intensity of the infection will tend to be higher, the rate of transmission will also tend to be higher and as a consequence the parasite will have the potential for significant influence on the size of the host population (Anderson & May, 1992).

It is now generally accepted that parasites play an important role in the persistence and adaptation of host species (Anderson & May, 1982; O'Brien & Evermann, 1988). If a parasite is introduced to a naive host population it can cause extinction of the host population, debilitate or reduce the equilibrium level of the host population or have no detectable impact at all. Which of the alternative paths a parasite takes is largely dependent on a group of ecological parameters that control the spread of the parasite through the host population, the pathogenicity of the parasite, and the course of the parasitic disease in host individuals (O'Brien & Evermann, 1988). Mathematical models have been developed which provide insights into the dynamics of real parasite-host relationships and determine which trajectories the parasite and the host populations are likely to follow under different parameter levels (e.g. Crofton, 1971b; May, 1977, 1983, 1991; Anderson & May, 1978, 1979, 1982, 1992; May & Anderson, 1978, 1979; Bremermann & Pickering, 1983; McCallum, 1994).

The most impressive documented examples of the impact of parasites on the dynamics of their host populations come from the introduction of hosts or parasites to areas outside their natural range. One commonly quoted example is the impact of avian malaria on Hawaiian drepaniids following the inadvertent introduction of one of its vectors, the night flying mosquito *Culex pipiens fatigans* (O'Brien & Evermann, 1988; Toft & Karter, 1990; McCallum, 1994). The introduction of *Culex* provided a vector, previously absent, for the spread of avian malaria and bird pox from migrating shorebirds and waterbirds (as well as domestic avian stock) to the native avifauna. As a consequence, the more vulnerable drepaniid species were forced to extinction by a combination of epizootics and other changes in their habitats. Remnant populations of surviving drepaniids were subsequently limited to areas where the mosquito was unable to survive (Warner, 1968; van Riper

et al., 1986). In this case it is thought that the pre-malaria drepaniids completely lacked any resistance to avian malaria (Toft & Karter, 1990).

Woinarski and Tidemann (1992) found that the survival rate of Gouldian Finches was lower than that of co-occurring species (Masked Finch and Long-tailed Finch). One hypothesis they suggested may explain the higher mortality rate observed for Gouldian Finches (both within and between breeding seasons) is the presence of *S. tracheacolum*. Whereas Gouldian Finches are heavily infected by *S. tracheacolum*, the parasitological data suggest that Masked Finches and Long-tailed Finches are not susceptible to infection by the same parasite. The Long-tailed Finch has never been found to be infected by *S. tracheacolum* and only 1% of Masked Finches have so far been found to be infected (Tidemann *et al.* 1992A; This study: Chapter 7). The present study investigates the influence of *S. tracheacolum* infection on captive Gouldian Finches in an attempt to explain apparently high mortality rates in wild populations. Direct comparisons are made of the survival and fecundity rates between infected and uninfected birds in captive populations.

10.2 METHODS

10.2.1 Host mortality

The experimental procedure for the establishment of infected and uninfected Gouldian Finches is set out in the Experimental Design: 3 Experimental procedure, P 62. Essentially, groups of experimentally infected birds and groups of birds maintained free of infection were housed under identical conditions but in separate aviary enclosures for periods of up to 12 months (each enclosure was initially stocked with 12 birds (6M; 6F)). The first experiment was conducted in 1992 and following considerable mortality among both infected and uninfected bird groups the experiment was repeated in 1993.

During the 1992 experiment the mortality of birds was monitored in 4 enclosures (2 infected; 2 uninfected) over the first 3 months, and 2 enclosures (1 infected; 1 uninfected) over the first 6 months of infection. During the 1993 experiment the mortality of birds was monitored in 4 enclosures (2 infected and 2 uninfected) over the first 9 months, and 2 enclosures (1 infected and 1 uninfected) over the first 12 months of infection.

10.2.2 Host Fecundity

Each enclosure was provided with six nest boxes and ample supplies of nesting material (fine dry grasses). During the 1993 experiment nest boxes were examined every second day and a record was made of the number of eggs and/ or nestlings present. After 200 days nest boxes were removed.

10.3 RESULTS

10.3.1 Host mortality

The mean percentage of birds surviving per enclosure (for both male and female birds) is shown in Figure 10.1. The data are pooled from the 1992 and 1993 aviary experiments. Mortality rates were high among both infected and uninfected groups. The mean survival rate of birds was 69 and 63% over the first 3 months of infection, 64 and 58% over the first 6 months of infection and 42 and 29% over the first 9 months of infection for uninfected and infected birds respectively. Raw values for the survival rate of birds was 50% for uninfected birds and 25% for infected birds over 12 months of infection. Although the mean percentage of infected surviving birds was consistently less than that of uninfected birds throughout the 12 month period the differences in survival rates were not significant (Table 10.1).

The survival rate of male and female birds for each 3 month interval is shown in Figure 10.2. Survival rates were similar for both infected and uninfected groups over 0 - 3 months and 3 - 6 months following initial infection. The greatest differences in survival rate occurred over the period 6 - 9 months and 9 - 12 months following initial infection. In each quarter the survival rate of infected birds was less than that of uninfected birds.

10.3.2 Host fecundity

Figure 10.3 shows the cumulative number of eggs laid per enclosure (10.3A, number of enclosures = 2) and the cumulative number of eggs laid per surviving female per enclosure (10.3B, number of enclosures = 2) for infected and uninfected birds groups. Whereas the number of eggs laid by females in uninfected enclosures steadily increased over 200 days, after two months there was very little addition to the egg total by females in infected enclosures.

Figure 10.4 shows the cumulative number of eggs hatched per enclosure (10.4A, number of enclosures = 2) and the cumulative number of eggs hatched per surviving female per enclosure (10.4B, number of enclosures = 2) for infected and uninfected birds groups. Over the 200 days there was a steady increase in cumulative number of eggs laid per surviving female in uninfected bird groups. A similar pattern was evident for infected birds groups for the first three months of infection. However, the overall rate of increase for infected birds groups was less than that for uninfected birds groups.

10.4 DISCUSSION

10.4.1 Experimental mortality rates and the decline of the wild Gouldian Finch

In the present study birds were experimentally infected at the beginning of the breeding season, or for some hosts, as they were about to lay their first eggs. In the wild, however, birds entering their first breeding season would probably carry infections acquired as nestlings or fledglings. Hence, the

Table 10.1 Number of infected and uninfected birds surviving for 3, 6, 9 and 12 months following initial infection: pooled data for the 1992 and 1993 aviary experiments.

Duration of Infection	Infected birds				Uninfected birds			
	Total number of birds at start of period	Number of birds surviving	Number of males surviving	Number of females surviving	Total number of birds at start of period	Number of birds surviving	Number of males surviving	Number of females surviving
3 months	48	30	15	15	48	33	18	15
6 months	36	21	10	11	36	23	11	12
9 months	24	7	5	2	24	10	5	5
12 months	12	3	2	1	12	6	3	2

Tests of association	All birds	Males	Females
3 months	$\chi^2 = 0.42$, $P = 0.52$	$\chi^2 = 0.87$, $P = 0.35$	$\chi^2 = 0.00$, $P = 1.00$
6 months	$\chi^2 = 0.23$, $P = 0.63$	$\chi^2 = 0.11$, $P = 0.74$	$\chi^2 = 0.12$, $P = 0.73$
9 months	$\chi^2 = 0.82$, $P = 0.37$	Fisher Exact Test, $P = 1.00$	Fisher Exact Test, $P = 0.37$
12 months	Fisher Exact Test, $P = 0.40$	Fisher Exact Test, $P = 1.00$	Fisher Exact Test, $P = 1.00$

Figure 10.1 Mean percentage survival of birds (male and female), experimentally infected by *S. tracheacolum*, over a period of 12 months following initial infection.

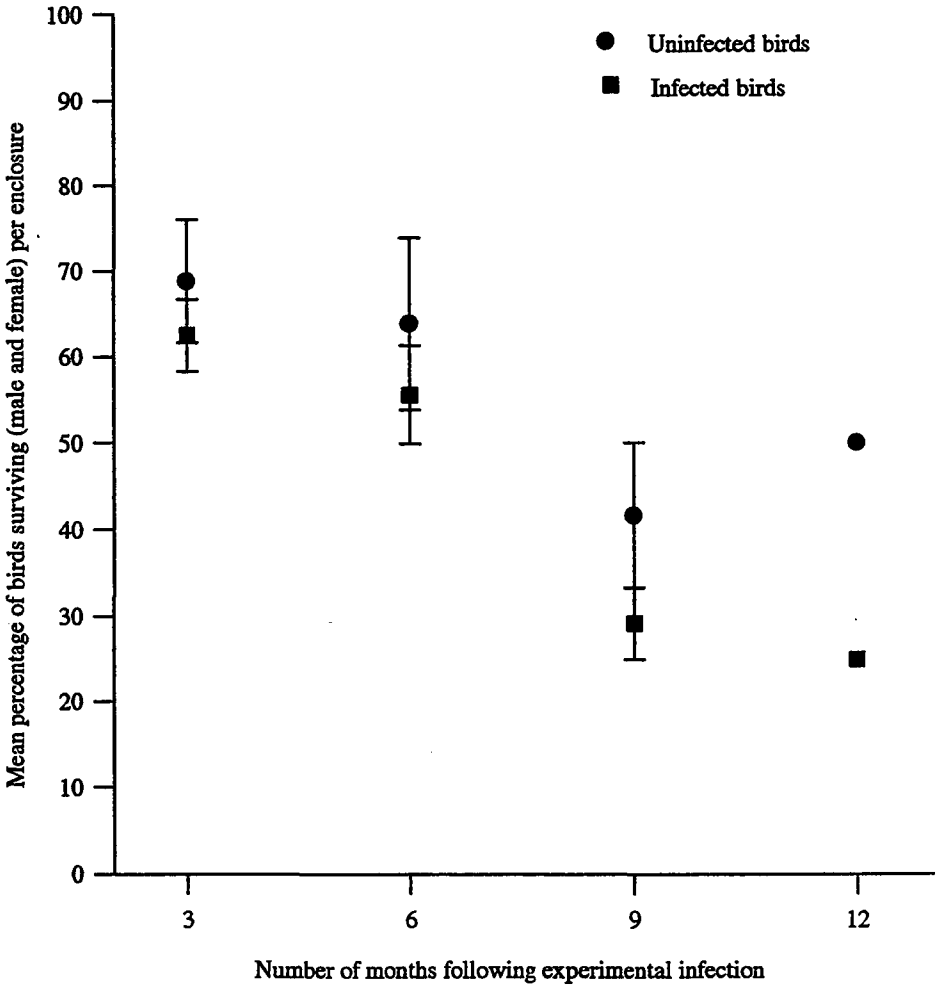


Figure 10.2 Mean percentage survival of birds (male and female) experimentally infected by *S. tracheacolum* from 0 - 3 months, 3 - 6 months, 6 - 9 months and 9 - 12 months following initial infection.

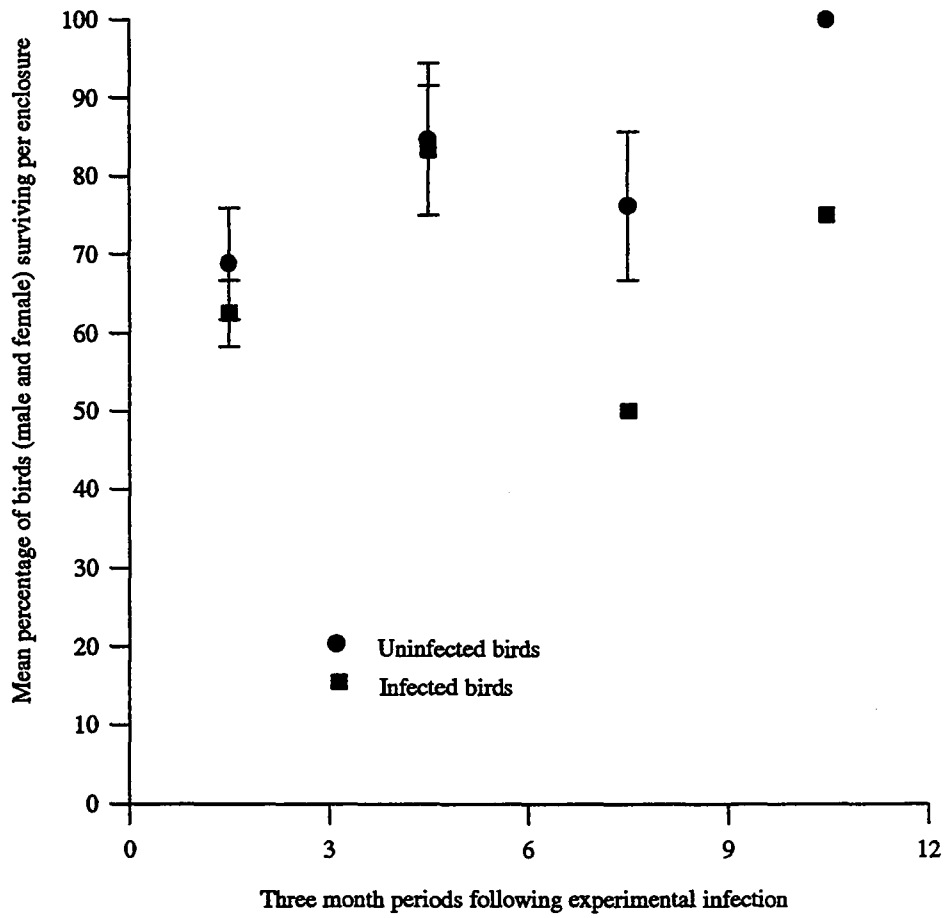
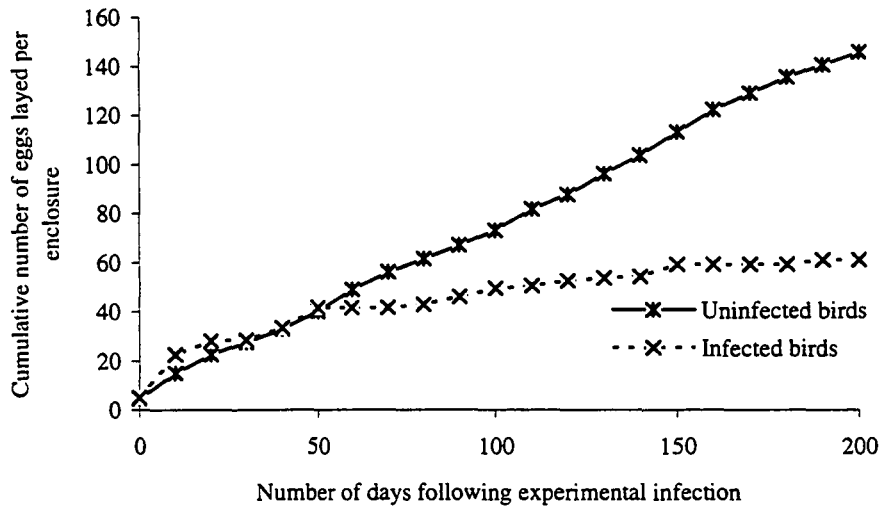


Figure 10.3 Cumulative number of eggs layed by birds experimentally infected with *S. tracheacolum*, over a period of 200 days following initial infection: A, number of eggs layed per enclosure (n =2); B, number of eggs layed per surviving female (infected, n = 12 at time 0; uninfected, n = 12 at time 0).

A.



B.

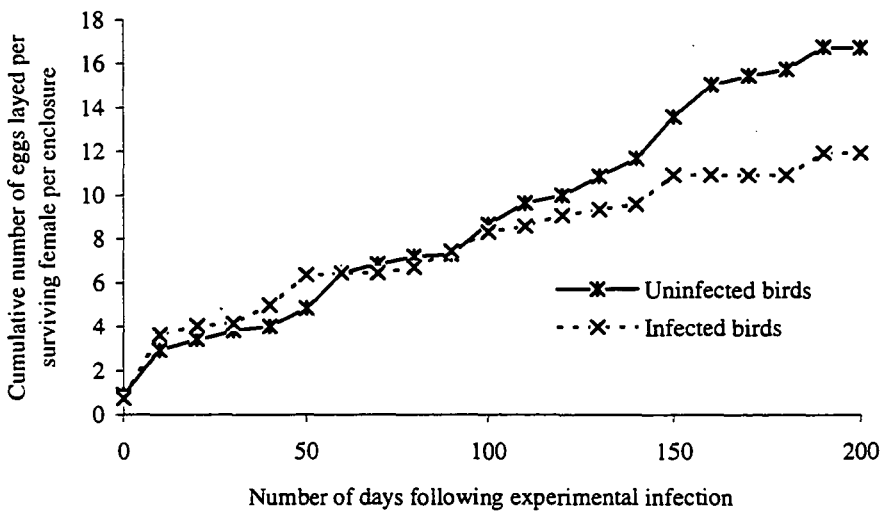
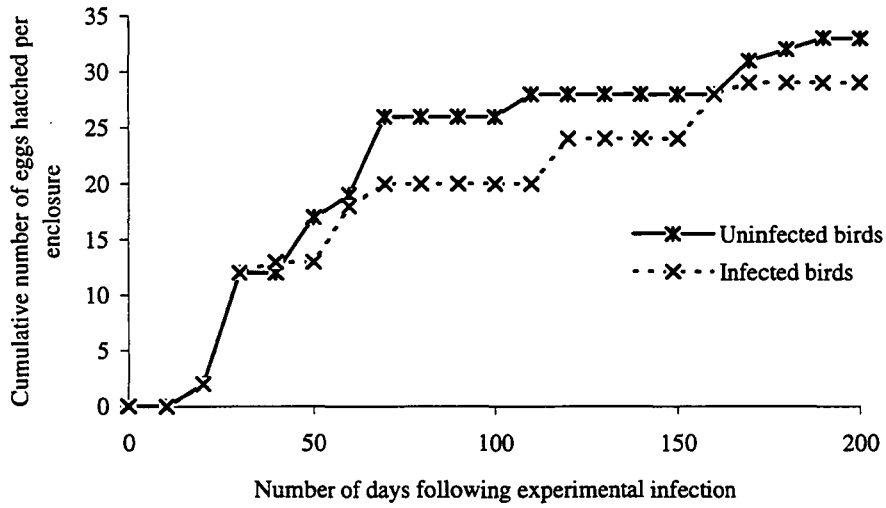
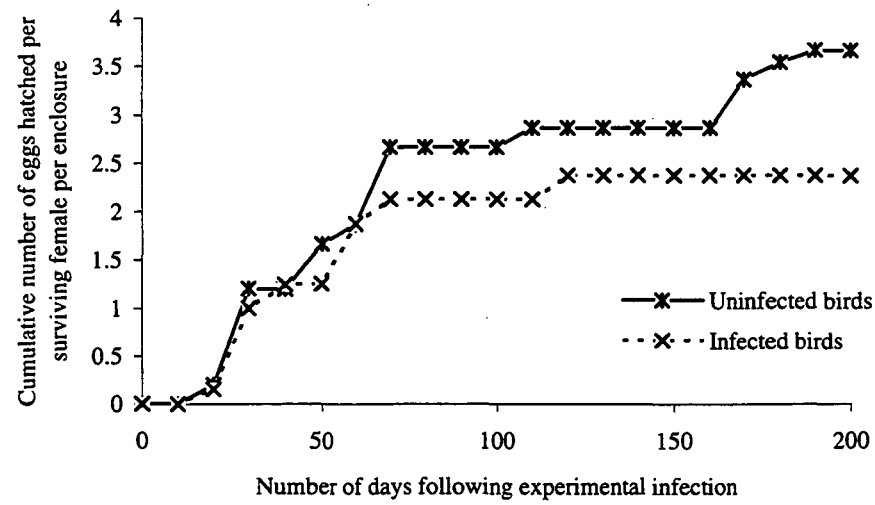


Figure 10.4 Cumulative number of eggs hatched from parent birds experimentally infected with *S. tracheacolum*, over a period of 200 days following initial infection: A, number of eggs hatched per enclosure (n = 2); B, number of eggs hatched per surviving female (infected, n = 12 at time 0; uninfected, n = 12 at time 0).

A.



B.



size of infections in wild birds would be considerably larger at the beginning of the breeding season than those of birds in the present study. Experimental infection just prior to breeding lead to a delay in development of heavy infections until late in the breeding season. If birds had been infected some months in advance of the breeding season a different pattern of fecundity and mortality may have emerged in the experimental situation. Infected birds may have weakened earlier and substantial differences may have been evident in breeding performance. Furthermore, the period of greatest differential mortality may have occurred earlier in the breeding season.

Although no significant differences were found in the mortality rates between groups of infected and uninfected birds, the morbidity associated with *S. tracheacolum* infection (described in detail in Chapter 6) could still translate to mortality in wild host populations. Factors contributing to mortality are likely to be interactive rather than additive, and thus, the majority of captive birds infected by *S. tracheacolum* in the aviary experiments may have been mortality rather than morbidity statistics in the wild. It is certainly difficult to extrapolate the wild situation from observations made on the captive populations though it is not difficult to appreciate the increased likelihood of mortality from sources other than those directly attributable to *S. tracheacolum* infection such as predation or starvation because of a reduced ability to forage (brought about by a compromised respiratory fitness). It is without doubt that the respiratory ability of individual birds is significantly hampered by *S. tracheacolum* infection (Chapter 6: Section 6.33, Activity level and respiratory ability).

Brown Falcons *Falco berigora*, Brown Goshawks *Accipiter fasciatus* (during field studies this species commonly attacked finches caught in mist nets) and the Australian Hobby *Falco hypoleucos* regularly predate finches. Other known predators include Olive Pythons *Liaisis oliveceous* and Ghost Bats *Macroderma gigas* (Tidemann, pers. comm.) Subtle changes in the speed or agility of Gouldian Finches may translate to significant changes in the predation rate by these species in wild populations. Furthermore, a bottleneck in the seed availability for granivorous birds purported to occur in the early wet season may have a significantly heavier impact on the mortality rate of Gouldian Finches than on non-*S. tracheacolum* infected granivorous species.

10.4.2 Population parameters required to model the dynamics of the *S. tracheacolum*/ Gouldian Finch relationship.

A number of population parameters have been estimated for use in mathematical models that describe the dynamical association of parasite and host populations (Anderson & May, 1978, Toft, 1991). The most important parameters include: the host death rate due to the influence of the parasite α, the birth rate of parasite transmission stages where birth results in the production of infective stages λ, the death rate of parasites within the host due to natural or host induced factors μ , the death rate of transmission stages c, the transmission rate or the probability that a transmission

stage will successfully establish itself in a new host, β, the rate at which infected hosts recover and become immune to new infections ν, the rate at which immunity to the parasite is lost γ, the birth rate of parasites where the birth results in the production of parasite stages that remain within the host of origin r and measures of the degree of parasite overdispersion in the host population k. Only some of these parameters could be estimated in any meaningful sense for the *S. tracheacolum*/ Gouldian Finch relationship from the present study.

A typical phenomenological assumption in parasite-host dynamical models is that the parasite distribution is described by a negative binomial (Anderson & May, 1979). Indeed, the negative binomial adequately describes a range of real parasite distributions (Crofton, 1971a; Anderson & May, 1979). The graphical presentation of the frequency distribution of mites in Gouldian Finches (Figure 7.2; though the data set is limited, n = 19) would suggest that the distribution of *S. tracheacolum* is potentially under-dispersed rather than clumped among hosts, at least in comparison to the distribution within co-occurring host species. Under-dispersion of the *S. tracheacolum* distribution throughout the Gouldian Finch sample may be an expected outcome in view of the limited immunity to infection, direct transmission, and direct reproduction of the parasite within the host. Furthermore, the factors that determine exposure to infection are not random but are governed by the association of birds at nest sites, as well as other gregarious behaviour such as communal roosting. A small random element is present, however, in the exposure of birds to mites at small drinking sites frequented by large gregarious groups of estrildid finches. Drinking sites provide the vehicle for the movement of *S. tracheacolum* between host individuals and species that would otherwise not come in close contact with each other (e.g. between Pictorella Mannikins and Gouldian Finches).

Neither the rate at which infected hosts recover and become immune to new infections ν, or the rate at which immunity to the parasite is lost γ, were investigated in the present study. However, Anderson and May (1991) noted that vertebrates are not generally able to develop a complete immunity to reinfection and this leads to the persistent nature of macroparasites in wild host populations. Observations on infrapopulation growth in Gouldian Finches (Chapter 3) would suggest that if individual birds survive an initial period of heavy infection the size of the infection is thereafter under the control of intensity-dependent infrapopulation processes and/ or host immune responses. Whatever this control mechanism it would presumably extend to some level of immunity to ongoing challenge by *S. tracheacolum*. Under this assumption, parameter ν could be adequately estimated as the difference between the proportion of mortalities directly attributable to *S. tracheacolum* and the overall proportion of the population infected, at least in an experimental setting. No data are available on which to attempt to quantify parameter γ, though given that the duration of infection was found to be at least two years in captive Gouldian Finches (Chapter 3), for the purposes of a model, this parameter could be virtually ignored

The rate of host mortality due to the influence of the parasite cannot be adequately assessed from laboratory experiments particularly if major mortality is the result of the interaction of several factors such as those outlined above. However, for the purposes of exploring the potential of a model to provide insights into the dynamics of the *S. tracheacolum*/ Gouldian Finch relationship the annual survival rate could be initially considered to be 25% greater than that of uninfected hosts (i.e. the difference between the 0.5 and the 0.25 probability of survival for uninfected and infected birds respectively over the 12 months period of the experiment). These mortality rates were not significantly different (due in part to small host sample sizes) though such values may provide a starting point from which to explore the influence of changes in *S. tracheacolum* caused mortality in hosts and the resulting implications to the size of host and parasite populations.

The birth rate of parasites where the birth results in the production of parasite stages that either remain within the host of origin r, or where the birth results in the production of infective stages λ, are parameters that could be estimated from the experimental study of infrapopulation biology. Given the potential role of intensity-dependant processes and or host immune responses in the production of female mites that either remain within the host of origin or become an infective stage, both r and λ are likely to change during the course of the infection. Reliable data for estimates of these parameters would necessitate isolation experiments such as those suggested in Chapter 3: Infrapopulation Biology. Experimentally infected birds (infected by a single infective mite) could be maintained in isolation from other birds for various periods following initial exposure. Both the size and composition of an infrapopulation could then be determined with a reliable knowledge of the size of the founding infection (i.e. one mite) and the timing of that initial infection. An assessment of the overall production of infective mite would require regular examination of infected birds and their caged environments for the presence of female mites. The number of infective mites produced per unit time could be determined by this technique. The overall values could be subsequently related to the size of the infrapopulation at the time of host death or euthanasia.

The rate at which susceptible hosts become infected upon contact with infectious hosts or the probability that an infective stage will successfully establish itself in a host cannot be estimated from the current study. However, the aforementioned isolation experiments would provide a reasonably accurate picture of the susceptibility of hosts to infection by single challenge events. The results of experimental infections undertaken throughout the course of the present study would suggest a high susceptibility of Gouldian Finches to challenge and a high probability that susceptible hosts become infected upon contact with infectious hosts.

The death rate of parasites within the host due to natural or host-induced (immunological) causes

μ, would be extremely difficult to estimate directly. However, there may be some scope for an indirect estimate of the parasite death rate following further studies of the life history of the parasite and the role of both intensity-dependent infrapopulation processes and host immune responses to infection. Here again, the relationship between the presence of dead mites within the hosts respiratory system and the parasite mortality rate is discussed in Chapter 3: Infrapopulation Biology. Similar to the alternative life strategies for female mites, the parasite mortality rate is likely to be dependent on the size of the parasitic infection and therefore it may change during the course of the infection.

10.4.3 Destabilising effects on the population dynamics of the *S. tracheacolum*/ Gouldian Finch relationship.

Anderson and May (1978) identified three important biological processes that tend to have a destabilising effect on the dynamics of the parasite-host relationship. These include a reduced reproductive capacity caused by the parasite, direct reproduction of the parasite within the host (in addition to the production of reproductive stages) and delays in parasite reproduction and transmission within the host. Two of these processes may be of particular relevance in the *S. tracheacolum*/ Gouldian Finch relationship.

Parasites do not only have the potential to increase the mortality rate of their hosts but they also have the potential to retard host reproduction through either a direct impact on the host's reproductive system or indirectly through deprivation of host nutrients (through parasite feeding or as trade-offs between host reproduction and immunological defences). In Anderson and May's models, equilibrium host and parasite populations are possible only under situations of overdispersed parasite distributions (distributions characterised by large k values). For random or underdispersed parasite distributions with small k values stable equilibriums are less likely to occur. For underdispersed parasite distributions both the underdispersion and the parasite induced decrease in host reproduction are destabilising. However, a density-dependent parasite death rate can produce net stability but only under restricted parameter conditions.

Anderson and May (1978) have also explored the dynamics of parasite and host populations under scenarios whereby parasites reproduce within their host of origin. The dynamical behaviour of these relationships is more complex than for parasites that only produce transmission stages. If $r > d$ (i.e. the instantaneous birth rate in which the births result in the production of parasitic stages which stay within the host in which they were produced is larger than the combination of parasitic death rates due to intrinsic mortality, and host population growth rates) both the host and the parasite populations can move steadily to extinction. On the other hand small values of r can lead to unregulated population growth. Extinction of host and parasite populations is avoided under conditions of large values of k. Under natural conditions parasite-host associations persist in the

face of high direct parasite reproduction (though this relates primarily to microparasites) which suggests that other interactions have evolved to ensure the persistence of the respective host and parasite populations.

10.4.4 Conclusion

In the present study mortality rates of captive bred Gouldian Finches infected by *S. tracheacolum* were found to be apparently higher than those of uninfected birds. A significant difference could not be found between the respective mortality rates. However, in the wild, *S. tracheacolum* infection together with other interactive factors is likely to result in a disproportionately larger increase in the mortality rate of *S. tracheacolum*-infected birds than in uninfected birds.

Although our understanding of the biology of *S. tracheacolum* and its relationship with the Gouldian Finch has been greatly expanded by the present study (Chapter 1 - 10) the data and observations remain inadequate for the development of a meaningful mathematical model of the relationship. However, they do provide a basis for the determination of important *S. tracheacolum* population parameters and provide a possible framework for estimation of those parameters through further studies.

GENERAL DISCUSSION

1. The life history of *S. tracheacolum* and its ecological consequences

The mode of transmission and potential for parthenogenesis in *S. tracheacolum* enables a single female mite to found an entire infrapopulation in a new host (Chapter 3). However, under natural conditions nestlings may be exposed to several mites from one or both parents prior to leaving the nest, and if fledglings are fed by parent birds, further exposure to infective mites is likely. For birds infected at a drinking site, the founding infrapopulation is far more likely to comprise a single mite (given the low probability of transmission at this locality). The maximum infrapopulation size will tend to be a function of the resistance or immunity of the host individual or species rather than the size of the founding infrapopulation. However, differences in the size of the initial infection will result in variations in the period required to attain maximum infrapopulation levels, and the rate at which an infrapopulation can grow will be governed by *S. tracheacolum* mortality rates, generation time and the time between the laying of successive eggs.

Following establishment, the founding infrapopulation of non-gravid, non-gorged female mites will presumably gorge on host blood and subsequently become gravid. If as proposed in Chapter 2, arrhenotoky does take place, then male mites will be produced from the haploid eggs of founding females. Males will comprise the first generation and males will continue to be produced until the founding females are mated. Thereafter, females will be produced from fertilised eggs, assuming only a single copulation is required for the ongoing fertilisation of eggs.

Adult female *S. tracheacolum* produce only a single egg at a time. Consequently, their reproductive output is governed by the time taken to produce each successive egg. *In vitro* culturing of mites on the chorio-allantoic membrane of the domestic chick egg suggests that the interval between successive egg laying may exceed 10 days (Chapter 2). Calculations of the interval required for simple doubling of infrapopulation size to reach the levels observed in the present study (in the absence of parasite mortality and ignoring the production of male mites) indicate that the maximum interval between successive egg laying for an individual female is less than 20 days.

S. tracheacolum is ovoviviparous rather than larviparous and oviposition takes place in the lungs of the host. Superficially, this seems disadvantageous, given the high likelihood that an egg would be expelled from the lungs through the production of mucus and the action of coughing. Nonetheless, the larva (a quiescent, non-feeding stage) hatches from the egg within hours of oviposition and undergoes a moult to the protonymph within its first day of hatching. The choice of the lung as the site for oviposition ensures that the newly moulted protonymph has a ready access to host blood.

Following a blood meal in the host's lung, the locality of further development is determined by the sex of the mite. The male protonymph moults to the deutonymph (a quiescent, non-feeding stage) in the respiratory passages of the lungs or on airsac membrane adjacent to the lungs of the host. It is here that the final moult to adult male is completed. Although adult males can be found throughout the respiratory system, excepting the nasal cavity, they occur primarily in the lungs.

Following a blood meal, female protonymphs move out of the host's lungs to the most dorsally positioned posterior airsacs to complete their final moults. From the posterior airsacs, young female mites radiate throughout the respiratory system (including the airsac extensions of the humerus, and in some infections, also the general body cavity) where they most commonly occur in the trachea and the anterior airsacs.

Why different localities of the host's respiratory system should be favoured by male and female mites is not known. However, the significant sexual dimorphism observed in this species would favour the use of the lungs by the smaller male. The large and often lumbering females (gravid and non-gravid blood gorged females) are more likely to stimulate non-specific host responses, such as the production of mucus, in the confined spaces of the host's lungs than the small and less robust males. Furthermore, male mites may enhance their potential for encountering females for copulation (assuming that adult female mites must enter the lungs for blood feeding) by remaining in the lungs or on airsac membrane immediately adjacent to lung ostia (Chapter 2).

Young adult females mature and subsequently reproduce within the respiratory system of the host. Thus, they further contribute to infrapopulation growth. However, some young female mites forego reproduction (assuming that infective mites are virgins and have not previously produced eggs) and migrate to the host's nasal cavity as part of a process by which they seek a new host. The mechanism that determines these alternative life strategies, to either reproduce in the host of origin or to actively seek a new host prior to reproduction, is not known. However, a genetic or an intensity-dependent mechanism may be involved (Chapter 3). The number of mites present in the nasal cavity of the host, and presumably this gives some indication of the infectivity or numbers of mites available for the initiation of new infections, is strongly correlated with the total size of the infrapopulation. Therefore, when birds are heavily infected, they are correspondingly, highly infective to other susceptible hosts.

The process that controls transmission has implications to the interpretation of the susceptibility of hosts when indirectly measured as the size of the infrapopulation. The production of infective mites, rather than the production of females that reproduce within the host of origin, will tend to have a governing influence on the size of the infrapopulation. If this process is controlled by

intensity-dependent factors, then, in the absence of appropriate host immune responses, Gouldian Finches would suffer heavy infections as a matter of course following their initial exposure to infection, both in the wild and under experimental circumstances. There may be an absence or delayed onset of host immune responses. Consequently, infrapopulation levels overshoot what would otherwise be threshold levels in natural hosts.

Although mites in the lower respiratory system of the host are usually greatly engorged, feeding observations indicate that following the initial engorgement adult female mites take only small blood meals. The observation of fresh blood and old blood in the caeca indicates that the infective stage does feed on the original host's blood but does not gorge. However, little or no change is detectable in the size of the idiosoma of the infective stage in comparison to newly moulted females. A reduced period of feeding for secondary and subsequent blood meals may provide an advantage to mites in the avoidance of host immune responses at the blood feeding site. Alternatively, it may be a result of host immune responses that limit the feeding success of mites, as has been demonstrated in tick-host associations (e.g. Wikel & Whelen, 1986; Brown, 1988; Kaufman, 1989). Unfortunately, too little is known of the blood feeding strategies of *S. tracheacolum*, or any other rhinonyssids, and the host's immune responses to develop this idea.

S. tracheacolum mortality rates cannot be determined directly. However, the presence of dead mites within the respiratory system may provide at least some indication of the relative levels of mortality. The proportion of immature stages found dead within the respiratory system are not necessarily indicative of the relative mortality between adults and immatures, particularly in view of the rapidity of development from larva to adult (i.e. probably less than 6 days) and the continuous production of eggs. However, given the obvious brevity of all immature stages, the data do have the potential to provide pertinent details on the relative stage specific mortality rates among the immatures. Indeed, of particular note is the high proportion of mites found dead during the process of moult (i.e. larval-protonymph, protonymph-deutonymph and deutonymph-adult moult, both male and female) when compared to the non-moulting larva, protonymph and deutonymph stages. It comes as little surprise that the highest mortality rates should occur during moult. Unfortunately there is little evidence on which to determine the relative roles of natural and host induced mortality. Without a knowledge of the relative life spans of adult male and female mites, though general observations would suggest a much shorter life span for males than females, direct comparisons may not be indicative of real parameters. Nonetheless, the proportion of adult males found dead was significantly larger than that found for adult females (30% of all males found were dead; 8.7% of adult females and less than 2% of gravid females were dead). Further experimentation *in vitro* on the chorioallantoic membrane of the domestic chick egg and with the

use of the acaricide, ivermectin, may provide critical data for the assessment of life spans and life expectancies of all stages and both sexes.

The mode of transmission by *S. tracheacolum* will tend to ensure the persistence of a high prevalence of infection irrespective of fluctuations in the size or density of the host population. Mites are directly transmitted and the ability for the infective stage to return to the nasal cavity following a foray onto the external surface of the host further enhances the potential for any one infective mite to survive and successfully infect a new host. Other studies on rhinonyssids suggest that transmission is inefficient (e.g. Brooks & Strandtmann, 1960; Amerson, 1967). For *S. tracheacolum* the opposite is clearly the case.

The present study provides no evidence to suggest that *S. tracheacolum* infections respond to the behaviour or biological condition of their host for the enhancement of transmission. Juvenile, immature and adult Gouldian Finches of both sexes were prone to heavy infection with the associated production of infective mites. Nonetheless, the biology of the host will determine the most likely timing and localities for transmission via proximate behaviour such as allopreening (a behaviour not observed in Gouldian Finches), communal roosting and other gregarious behaviours, as well as the association between parent birds and their offspring at the nest site.

Natural infection of Gouldian Finches at the nest site (provided nestlings survive) would render young birds highly infective during the early part of their first breeding season. The short period between hatching and maturity observed for this host species (though there is evidence to suggest that maturation of infected Gouldian Finch fledglings is retarded by the presence of *S. tracheacolum* infection (Chapter 6)), would ensure that at least some infected birds survive to maturity to infect partner birds and offspring. Birds remain infective for over a year following initial infection (Chapter 3). Thus, for birds surviving an initial period of heavy infection, the level of infectivity, although reduced over time, could span at least two breeding seasons.

The first phase of infrapopulation growth rate of *S. tracheacolum* in the captive Gouldian Finch is exponential. From a founding infection of two mites (one gravid female and one non-gravid non-gorged female), an infrapopulation can grow to as many as 371 mites in 148 days. In the present study a typical peak in the size of the infrapopulation was reached following 6 months of infection. For birds surviving these heavy parasite burdens there was a subsequent decline in the size of the infection. Significantly smaller infections were observed in birds infected for greater than 12 months. Comparative studies of the size of infrapopulations between Gouldian Finches and Canaries examined after 6 and 12 months of infection indicate that the pattern of rapid

infrapopulation increase followed by a gradual decline in the size of the infrapopulation may be typical, at least for species that are known to be susceptible to heavy infection.

The mortality rate of *S. tracheacolum* measured as the proportion of dead mites found within the respiratory system of the host, increases with the size of the infection and continues to increase throughout the course of infection in spite of a subsequent negative infrapopulation growth rate. If changes in the proportion of dead mites correlate with changes in the parasite mortality rate, then changes in the mortality rate over time suggests the existence of a parasite infrapopulation regulatory process. This process may be a host immune response that is elicited at heavy infection levels or after a certain period of infection. Once elicited, the response appears to be operative for the remainder of the period of infection. Interpretation of composite infrapopulation data in the present study assumes that all birds were equally susceptible to infection and all surviving birds passed through a similar period of heavy infection. The notion that birds examined later that six months following initial infection had survived an earlier period of heavy infection is supported by similarities in the presence of clinical signs between surviving birds and birds that died during the period of heavy infection (e.g. severe respiratory clinical signs and presence of infective mites on external surface of hosts).

2. Variability in the morphology of *S. tracheacolum*

Variability in the morphology of *S. tracheacolum* was clearly demonstrated by Fain and Hyland (1962). They noted that the size of the idiosoma, plates, legs, chelicerae and the gnathosoma of adult female specimens coming from many host species and geographic localities (Africa, America, Europe and Asia), were the features that were most subject to variation. Although extremes were found in the length of the cheliceral digit (i.e. 6-14 microns), intermediate forms were found in specimens from among the large group of host species examined. They concluded that the plates, the base of the chelicerae and the basic chaetotaxy of all specimens examined were sufficiently similar to those of the original description to be included in the same species.

In Fain and Hyland's study two forms were found in the same host species, the Song Sparrow *Melopspiza melodia* and the Indigo Bunting *Passerina cyanea.* These forms were found in different host individuals and given that the hosts were collected from widely separated localities they may have been exposed to different reservoir host species. As yet, no phenotypic differences have been detected in specimens coming from the same host individual, either for this study or previous studies.

However, the most interesting discovery of Fain & Hyland's study and probably the most pertinent to a determination of the longevity of the *S. tracheacolum*/ Gouldian Finch relationship is the

presence of considerable phenotypic variation in mites from captive Canaries *Serinus canarius*. A wide morphological variation rivalling that found among specimens from all other known wild host species was present in specimens from Canaries coming from different geographic localities (i.e. Belgium, Italy, South Africa, U.S.A. and Brazil). It is not known whether wild Canaries in their natural habitat are infected or, if they are, whether large variations in the morphology of specimens exists among hosts. However, the most acceptable explanation for the variation is that Canaries have become infected secondarily during association with other host species in the countries where they have been introduced as captive birds.

It was proposed in the present study that Canaries may not be natural hosts for *S. tracheacolum* and have only come in contact with this parasite since their introduction as captive birds to the European mainland in the early 16th century. It is possible that Canaries, as non-migratory island populations, but nonetheless carrying a genetic susceptibility to infection, were not exposed to *S. tracheacolum* during its speciation in passeriform and psittaciform hosts. Since their introduction to mainland Europe and subsequently to almost every country in the world they may have been exposed, through aviculture, to a wide range of host species (particularly among the Fringillidae, Estrildidae and the Ploceidae) and consequently a wide range of *S. tracheacolum* phenotypes. However, clarification of the foregoing proposition lies in the examination of wild Canaries from their natural habitat.

Two distinct morphological forms of *S. tracheacolum* are found in wild birds in northern Australia (Chapter 1). In conjunction with experimental evidence (Chapter 8) these forms (known, for the convenience of the present study as the 'Passerine form' and the 'Psittacine form') would fit neatly into species categories. The 'Psittacine form' of *S. tracheacolum* has been reported only from psittacid hosts i.e. the Budgerigar from the East Kimberley, Northern Australia (Chapter 7) and the Antwerp Zoo, Belgium in 1958, and Lovebirds *Agapornis* spp., wild caught in Madagascar. It has never been reported from Canaries or Gouldian Finches in captivity, even though these birds have often been kept in association with Budgerigars. In Australia, the 'Passerine form' *S. tracheacolum* is only recorded from estrildid finches (Gouldian Finch, Pictorella Mannikin and Masked Finch). Further, there is consistency in the morphology among specimens from these host species despite generic host differences and despite the separation of more than 1000 km between host populations. The morphological differences suggest genetic isolation of the 'Psittacine form' within Psittacidae (represented by the Budgerigar) and the 'Passerine form' within Estrildidae (represented by the Gouldian Finch, Pictorella Mannikin and Masked Finch). The morphological similarities suggest considerable genetic flow of the 'Passerine form' among estrildid host species. Isolation, of the two types, whether produced by biological or physiological barriers would suggest that the dynamics of the 'Psittacine form' is unlikely to influence that of the 'Passerine form' and that the Budgerigar is

unlikely to act as a reservoir host species for the 'Passerine form'. Consequently, management for the amelioration of *S. tracheacolum* infection in the wild Gouldian Finch is unlikely to be affected by levels of *S. tracheacolum* infection in the Budgerigar.

The presence of two distinct forms of *S. tracheacolum* in the Australian avifauna tends not to support the hypothesis espoused by Tidemann *et al.* (1992a) (i.e. that *S. tracheacolum* was recently introduced to Australia), unless two forms have been introduced and found their way into two different wild host groups. The presence of *S. tracheacolum* in wild Budgerigars has been known for at least 36 years, assuming birds held at the Antwerp Zoo, Belgium were infected prior to their exportation from Australia. Further, the prevalence and intensity of infection in the Budgerigar are relatively low in comparison to the Gouldian Finch and the Pictorella Mannikin, and consistent over time. Using a traditional parasitological axiom, these low levels of infection suggest a parasite-host species association of relatively long standing. In contrast, the parameters of infection in the Gouldian Finch and more recently the Pictorella Mannikin (Chapter 7), are significantly higher than those in the Budgerigar and suggestive of a more recent parasite-host species association.

The morphological data of *S. tracheacolum* (as its various forms are currently placed taxonomically) from wild Australian birds tends not to support the hypothesis of introduction. However, in combination with other evidence such as the levels of infection in wild birds (Chapter 7) and the experimental examination of susceptibility (Chapter 8), there is considerable support for an introduction hypothesis and hence, for some acceptable modification of the original hypothesis; that *S. tracheacolum* has been present in Australian psittacids for some time. A distinct but closely related species to *S. tracheacolum*, to which some of Australia's estrildids are particularly susceptible has been recently introduced.

The present study demonstrates that important variations occur between immatures of *S. tracheacolum* coming from different host species. The morphological differences found between immature specimens described from wild caught Gouldian Finches (this study) and those described by Guevara-Benitez and Ubeda-Ontiveros (1974) from the Canary in Spain are considerable. Indeed, these differences are reflected by significant morphological differences between adult female specimens (in the size of the cheliceral digit) and adult male specimens (in the size of the ambulacral apparatus) described from the two host species.

Based on the observed stability in the size of the cheliceral digit within hosts, Fain and Hyland (1962) contemplated the separation of *S. tracheacolum* specimens with short cheliceral digits (approximately 6 microns in length) and those with long cheliceral digits (approximately 12 microns in length) into two distinct species. The finding of cheliceral digits of an intermediate

length in specimens from Canaries from Brazil quelled that proposition. However, significant differences found between immature specimens from wild Gouldian Finches in Australia and Canaries in Spain provides additional support for resurrection of the division of *S. tracheacolum* into separate taxa.

Morphological variation in adult female, adult male and immature *S. tracheacolum* mites among and within host species and localities requires further investigation. *S. tracheacolum* is currently considered to be the least host specific of the Rhinonyssidae. Reinvestigation of the variability and an assessment of the role of secondary infection in the production of within host species variation is warranted. Such a study may radically change the impression currently held of the evolution and the 'natural' host specificity of this species.

Current rhinonyssid taxonomy is primarily based on the morphology of adult female specimens. Furthermore, few adult males and immatures of any species have been adequately described. Existing knowledge of the morphology of immature rhinonyssids (e.g Mitchell, 1963) and the morphological and observational data from the present study (i.e. that transmission of *S. tracheacolum* is effected by the adult female (Chapter 2); and life cycle stage data from *S. paddae* infection of estrildid finches suggests that transmission of *S. paddae* is effected by one of the immature stages (Chapter 7)), suggests that the stage responsible for transmission may vary among genera and, at least for *Sternostoma*, among species. Given the above, evolutionary selective pressures are likely to be acting differently on adult and immature stages among rhinonyssid species. Therefore, any natural system of classification would benefit from a consideration of the morphology and biology of all stages of the mite's development.

Based on the morphological variation of specimens among and within host species there may be grounds for the erection of two separate but closely related species of *S. tracheacolum.*

3. Unravelling *S. tracheacolum* host specificity and zoogeography

Of particular interest to the present study and the proposition that *S. tracheacolum* has been introduced to Australia is the evolution and radiation of the finches (i.e. Fringillidae, Estrildidae, Ploceidae, Passeridae and the Emberizidae). Studies on the biology of the finches suggest that the true finches (Fringillidae) and the buntings and allies (Emberizidae) evolved independently from each other and also independently from the estrildids (Estrildidae), the weavers and allies (Ploceidae) and the old world sparrows (Passeridae) (Goodwin, 1982).

The weavers and allies (Ploceidae) have a distribution spanning the Ethiopian and Oriental faunal regions of the world. Australia has two species which are introduced, the White-winged Whydah *Euplectes albonotatus* (established only on the Hawkesbury River, New South Wales) and the Red

Bishop *E. orix* (established on the Murray River, south Australia). Both originate from the grasslands of Africa, south of the Sahara. These species have never been examined for *S. tracheacolum* infection though in view of their restricted distribution in Australia it is unlikely that either could be considered as a contender for introduction of this parasite.

The old world sparrows (Passeridae) occur in the Ethiopian, Palaearctic and Oriental regions. Australia has only two species and both were introduced during the mid 1800's (Clemments, 1981). The House Sparrow *Passer domesticus*, which has been successfully introduced worldwide was released in Hobart, Melbourne, Sydney and Brisbane (Simpson & Day, 1986). It is now common wherever humans live in southern and eastern Australia (from central Queensland to the Western Australia border). The Tree Sparrow *P. montanus,* is only common in Victoria and New South Wales between Melbourne and Sydney. The morphology of *S. tracheacolum* from the House Sparrow introduced to Michigan, U.S.A (Fain & Hyland, 1962), is very similar to that found in Australian estrildids. Further, the successful introduction of the House Sparrow to Australia, its distributional overlap with that of the Gouldian Finch and other probable host species such as the Yellow-rumped Mannikin, *Lonchura flaviprymna* and the introduced Nutmeg Mannikin, *L. punctulata*, make this species a serious contender for the introduction of *S. tracheacolum.*

The true finches (Fringillidae) are a very large family with a worldwide distribution excepting Australasia. Two species were successfully introduced to Australia during the mid 1800's, the European Goldfinch *Carduelis carduelis* and the European Greenfinch *C. chloris*. Both are fairly sedentary and urban living (Simpson & Day, 1986). The Goldfinch is now common throughout settled urban and rural areas of south-eastern Australia. The Greenfinch is found in parks and gardens of settled areas in south-eastern Australia. The European Goldfinch is a known host for *S. tracheacolum*, at least in captive situations. However, the restricted distribution of both these species in Australia make them unlikely contenders for introduction of this parasite.

The buntings and allies (Emberizidae) are primarily a New World group spanning the Nearctic and Neotropical regions though a few occur in the Palaearctic and Oriental regions. No species are known from Australia (Clemments, 1981).

The estrildids (including the waxbills, firefinches, twinspots, mannikins, avadavats and the parrot-finches) occur in the Ethiopian, Oriental, Australasian and the Oceanic regions. Two species were successfully introduced to Australia, the Black-headed Mannikin *Lonchura malacca* and the Nutmeg Mannikin, *L. punctulata*. The Black-headed Mannikin is restricted to the southeast coast between New South Wales and Victoria and the Nutmeg Mannikin is distributed along the eastern seaboard of Australia from New South Wales to Cape York Peninsula. Both species are widespread in the Oriental region.

The estrildid finches which include all known Australia finches are most diverse in Africa with 79 species in 18 genera. Throughout the Oriental region there are 19 species in 3 genera. The Australasian region has 36 species in 9 genera. The Pacific includes 5 species in one genus and one species is found in Madagascar. Species diversity provides strong evidence for the origin of estrildid finches in Africa. Further, the African estrildids also show the greatest diversity in size and shape (Goodwin, 1982). This is supported by evidence from biochemical systematics (Christidis, 1986a; 1986b). It is generally held that the estrildids spread from Africa to Asia and Australia in a series of invasions, however, the number of dispersal events and their direction remains controversial (Christidis, 1986b). Chromosomal and electrophoretic data support the division of the Estrildidae into three monophyletic tribes: Estrildini, Poephilini and Lonchurini. The first lineage to evolve in Africa was the Estrildini which subsequently spread into Asia. A single early wave of estrildines to Australasia established the Poephilini. The Lonchurini are a later specialisation which may have arisen from an estrildine invasion of Southern Asia which spread back to Africa and on to Australia (Christidis, 1986a).

Introduced aviary birds from within the aforementioned finch groups abound in Australia. Some commonly kept species include the emberizids: Cuban Grassquit *Tiaris canora,* Blue-black Grassquit *Volatina jacarina*, Saffron Finch *Sicalis flaveola* and the Red-crested Cardinal *Paroaria coronata*; fringillids: Siskins *Carduelis cucullata, C. magellanica, C. sinica, C. chloris* (also successfully introduced to the wild), *C. carduelis* (also successfully introduced to the wild), Canaries, *S. canaria, S. mozambicus, S. flaviventris, S. leucopygius*, and Purple Finches *Carpodacus purpureus*; estrildids: Mannikins *Lonchura malabarica, L. molacca* (also successfully introduced to the wild), *L. maja, L. bicolor, L. punctulata* (also successfully introduced to the wild), *L. leucogaster*, Pytilias *Pytilia phoenicoptera, P. melba*; Waxbills, *Estrilda troglodytes, E. astrild, Lagonosticta senegala*, Cordon-bleus, *Uraeginthus bengalus, U. angolensis, U. cyanocephala*, Amandinas, *Amandina fasciata, A. erythrocephala*, Avadavats, *Amandava amandava, A. formosa*, Java Sparrow, *Padda oryzivora* and Parrot-finches *Erythrura psittacea* and the ploceids, Red Bishop *Euplectes orix* (also successfully introduced to the wild), Madagascar Fody *Foudia madagascariensis* and the Pin-tailed Whydahs *Vidua macroura* and Passeridae: Sparrows, *Passer luteus*. Many of these species may be hosts for *S. tracheacolum* though such records have not been confirmed or widely published. For example, Kingston (1994) suggests that no 'finch', assuming that the author is referring to the aforementioned families, is immune to these mites. He considered that two species were particularly susceptible to infection, the Red-cheeked Cordon-bleu *U. bengalus* (a native of the Ethiopian region) and the Red-billed Waxbill *L. senegala* (widespread in Africa, south of the Sahara). Both these species are estrildids.

Given the lack of knowledge of the existence of the 'Passerine form' of *S. tracheacolum* in Australia prior to the first record in Gouldian Finches in 1987, the only means of determining the antiquity of

the parasite-host association was by finding evidence of infection in historically preserved specimens. Tidemann *et al.* (1992a) sought to examine Gouldian Finch spirit specimens held in Australian and overseas collections. Although the 'World Inventory of Avian Spirit Specimens' lists 127 specimens (Wood, Zusi & Jenkinson, 1982), further inquiries revealed all specimens to be either from captive bred stock or, for one or two specimens, of unknown history. Although there were many early collecting expeditions to Northern Australia, and Gouldian Finches were collected on several occasions, the carcases of these specimens were not preserved. An early specimen of unknown origin from the British Museum was examined by the author and found to be free of infection.

Fifteen Pictorella Mannikin spirit specimens are held in various collections throughout the world. Ten are known to be wild caught. The British Museum (Natural History) Tring, Hertfordshire holds 8 wild caught specimens collected at Mount Anderson, Kimberley, Western Australia in 1969. The remaining two birds are held by the Commonwealth Scientific and Industrial Research Organisation (C.S.I.R.O) in Canberra, Australia. One was collected in 1974 from the Barkly Tableland, Northern Territory and the other was collected in the same year from the 'Gulf district' of Queensland. Both specimens have been examined by the author and found to be free of infection.

Although aviculture may have lead to the occurrence of *S. tracheacolum* in some rather odd and unexpected hosts during the last century, some aviary host species may not have yet been exposed to infection in their wild habitat. In 1995, a study will be undertaken by the author that examines the occurrence and morphology of *S. tracheacolum* in other host species related to the Pictorella Mannikin and the Gouldian Finch, both in Australia (to include other native estrildids and the introduced House Sparrow, Black-headed Finch and Nutmeg Mannikin) and neighbouring southeast Asia (to include *Lonchura* and *Erythrura* species). Such a study may provide sufficient evidence on which to decisively support or reject the 'introduction hypothesis'.

It is worthy of note that both the first record of *S. tracheacolum* infection in the captive Gouldian Finch and the majority of the subsequent published records of *S. tracheacolum* implicate infection with the association of Canaries. For example Medda (1957) was first to describe infection by *S. tracheacolum* in European Goldfinches, *C. carduelis*. These birds had been kept for over a year in an aviary with Canaries that were also found to be infected. Further, the existence of *S. tracheacolum* infection was first recorded in 1948 in South Africa and by 1959 it was considered to be widespread in Canaries in that country. The first diagnosis of *S. tracheacolum* in Gouldian Finches in South Africa came in 1959 (Cummings, 1959). These birds, which were dying from infection, had been obtained from a successful breeder of german roller Canaries. Vacarri and Ballarini (1963), from the examination of 2,645 passerines, 2,102 of which were Canaries, recognised infection in only three species, the Gouldian Finch, Canary and the Siskin, *Carduelis*

spinus. Furthermore, they found that infection was only present in Gouldian Finches and Siskins when they were kept in association with Canaries that were also infected.

4. Susceptibility to infection and the longevity of *S. tracheacolum*/ host species relationships

Susceptibility and resistance are difficult parameters to approach from an ecological perspective. The present study has used both the size of the infrapopulation and other demographic characteristics of the infrapopulation as indirect indicators of the levels of these parameters. However, with little available knowledge of the precise immunological defence mechanisms of the host species and the mechanisms by which *S. tracheacolum* may evade those responses, it is difficult to discuss these parameters with any confidence. Suffice it to say that *S. tracheacolum* infrapopulations are significantly larger in captive Gouldian Finches than Canaries (Chapter 8) and that these experimental data corroborate observations stated in the literature. Previous authors suggest that although both host species are particularly susceptible to infection in captivity the infection is far more rapidly fatal in Gouldian Finches (e.g. Cumming, 1959; Szeleszczuk & Kruszewicz, 1987). Furthermore, the literature suggests that at least for the Canary there is considerable variation in resistance to infection among breeds (e.g. Vacarri & Ballarini, 1963; Szeleszczuk & Kruszewicz, 1987). Experimental evidence from the present study suggests that Gouldian Finches are highly susceptibility to infection by *S. tracheacolum*, both in captivity and in the wild.

In tick-host species associations of long standing there is an expectation that a long period of coevolution of the host's immune system and the parasite's immune evasion system leads to levels of coadaption and virulence that settles at a moderate level. This is evidenced by presence of mild parasitosis in natural tick-host associations (Brossard *et al.*, 1991). On the other hand, disastrous associations have been observed in new tick-host associations such as that observed following the introduction of European cattle to Australia and subsequent exposure to the ixodid tick *Boophilus microplus*. Animals that are repeatedly infected with ticks generally acquire immunity and this immunity usually acts through disturbance of tick fixation and blood feeding and or by inhibitory influences on tick egg laying or embryogenesis (Brossard *et al.*, 1982). Ticks may respond with anti-inflammatory and immunosuppressive factors injected with the ticks saliva (Brossard *et al.*, 1991). To borrow this analogy, the high intensities of infection currently observed in Gouldian Finches and closely related Pictorella Mannikins may be the result of an exposure of naive host species to a new parasite, with only a limited immune mechanism available to the hosts to control the size of the infection and the subsequent pathological effects.

5. The dynamics of nasal mites in the Australian native avifauna

The present study of rhinonyssid infections in wild birds extends our view of the prevalence of mite infections as a consistent feature of Australian native avifauna (Chapter 7). The large number of

new records from such a limited host species sample indicates that there is yet considerable ground to cover until a satisfactory catalogue of Australian parasites and their hosts is achieved. Given the constant threat of introduced micro and macroparasites to Australia, particularly to endemic birds, completion of an inventory of natural parasite-host associations would appear to be an important target. Indeed, if the parasitic fauna of the Gouldian Finch had attracted just 'a moment's attention' during a century of trapping and aviculture, we might not now be guessing the history and involvement of *S. tracheacolum* in the decline of the Gouldian Finch. If we were able to conclusively determine that *S. tracheacolum* is recently introduced to Australia then research and management of the Gouldian Finch could be focused on techniques for controlling the parasite burden in wild birds. On the other hand, if *S. tracheacolum* is a native parasite with a long association with the Australian avifauna, then research may be better focused on determining the factors that have lead to changes in the susceptibility of Gouldian Finches to infection, whether these factors be exogenous such as nutritional inadequacies in the early wet season (a recognised bottle neck in seed availability for many of northern Australia's granivorous birds), or endogenous such as rapid changes in the evolution of parasite virulence.

In 1994, the conservation status of the Gouldian Finch remained endangered. Research and monitoring over the past eight years has not succeeded in providing a coherent picture of population trends. This is in spite of a considerable research effort by government conservation agencies, particularly the Conservation Commission of the Northern Territory. In essence, it is not known whether wild Gouldian Finch populations infected with *S. tracheacolum* are continuing to decline, have stabilised or are increasing in number. Proposed changes to the techniques employed for monitoring Gouldian Finch populations such as the use of traps rather than mist nets may improve capture and recapture rates and thus provide a more accurate assessment of current population trends. If recapture rates can be improved, both within and between seasons, field based parasitic manipulation experiments may be used to assess the impact of *S. tracheacolum* on host populations. If reliable assessments of host population trends and age specific recapture rates can be achieved then theoretical epidemiological models based on the known biology and ecological parameters of *S. tracheacolum* parasitism could be explored. Indeed, if host populations are increasing, an assessment of the ongoing involvement of *S. tracheacolum* parasitism in the survival of Gouldian Finches becomes redundant.

Information on the prevalence and intensity of infection in wild Gouldian Finches cannot be obtained without sacrifice of the host. Given the ethical constraints and practical considerations of this practise, available data on parasitism in wild Gouldian Finches remain extremely limited. Three random surveys of *S. tracheacolum* in Gouldian Finches have been undertaken, one in 1987 of 9 birds from 3 different localities in Western Australia and the Northern Territory (Tidemann *et al.* 1992a), one in 1991 of 7 birds in Queensland (Tidemann *et al.* 1993) and one in 1992 of 10

juvenile and immature birds from Yinberrie Hills, Northern Territory (this study). A field study of the role of parasitism would therefore be greatly enhanced by a non-destructive technique that could determine the prevalence of infection and provide at least a quantitative index of parasitic burden. For any macroparasitic survey, the parasitic burden is probably the most important parameter to assess. However, given current technologies and available funding, the development of such a technique may be some distance away.

A study, to be undertaken over the next few years, may elucidate the relationship between changes in the levels of *S. tracheacolum* infection and corresponding host population parameters. Results from such a study may provide the 'king pin' argument for what is already a strong circumstantial case for the involvement of *S. tracheacolum* in the decline of the Gouldian Finch.

The intensity of infection by *S. tracheacolum* in the wild Gouldian Finch represents the heaviest parasitism by a species of respiratory mite of any wild or captive host species recorded. Furthermore, the highest individual parasitic loads recorded come from juvenile and immature birds. The intensity of infection in the Pictorella Mannikin is increasing over time and currently rivals that found in Gouldian Finches. Individual parasite burdens in wild Pictorella Mannikins have been found to be as high as 90 mites in a single host. Furthermore, audible respiratory clinical signs were detected in at least one of the birds examined. The Pictorella Mannikin, however, is not 'endangered' and although it has declined substantially in the eastern part of its range it is still considered to be abundant in areas of the east Kimberley, Western Australia.

The proposed study will investigate the relationship between parameters of *S. tracheacolum* infection in the Pictorella Mannikin and indices of host abundance over the next three years. Data on the prevalence and parasitic burden in the Pictorella Mannikin were collected in 1987 (Tidemann, *et al.*, 1992a) and during the three years between 1992 and 1994 at Newry Station (Chapter 7). A continuation of this study may involve increases in host sample sizes and add new sampling sites for collection of birds, particularly in areas where they appear to be abundant. Counts of Pictorella Mannikins have been conducted at waterholes in the east Kimberley since 1983 (in 1983 and 1985 by Evans & Bougher (1987) and continued in 1987, 1989 and 1991 by Tidemann (pers. comm.) using the same protocol). The proposed study would continue these counts over the next three years. Larger host sample sizes will enable comparisons to be made of the levels of infection among geographic localities and sample years and between the sex and age of hosts. Assessment of the relationship between the parameters of *S. tracheacolum* infection and the parameters of abundance of Pictorella Mannikin populations will be viewed as an analogue for assessment of the relationship between *S. tracheacolum* and the Gouldian Finch.

6. Conclusion

S. tracheacolum does not slot easily into the ecological pigeon holes of other well known parasitic species groups. It is a macroparasite of considerable pathological potential in Gouldian Finches (Chapter 4) directly causing mortality (Chapter 10) and morbidity (Chapters 6 & 10) in individual hosts. Given the nature of *S. tracheacolum* both in the laboratory (Chapter 3) and in the wild (Chapter 7), there can be no doubt that wild Gouldian Finches suffer morbidity and mortality that is equal to or greater than that suffered by their captive counterparts. Gouldian Finches are susceptible to heavy infection in the laboratory (Chapter 8) and wild Gouldian Finches are the most heavily infected host species known (Chapter 7). The fundamental question that cannot be satisfactorily answered from laboratory based studies is whether the levels of morbidity and mortality are of sufficient importance in wild host populations to cause both substantial and dramatic decline. More data are required on the dynamics of *S. tracheacolum* and Gouldian Finch populations in the wild.

Consider the worst case scenario where the 'Passerine form' of *S. tracheacolum* is an introduced parasite to Australian avifauna and is largely responsible for the observed decline of Gouldian Finches in recent decades. The characteristics of the life cycle (direct reproduction within the host and the potential for parthenogenesis), transmission (directly at the nest site and during proximate behaviour, and indirectly at drinking sites) and virulence (a high mean parasitic burden with a long latent period between infection and subsequent host morbidity and mortality) of *S. tracheacolum* combine to ensure a persistence of infection in the host population that is largely unresponsive to host density. In other words, even at very small host population levels a high percentage of birds are still likely to be infected. Consequently, a decline in the number of surviving birds will not necessarily lead to the eventual extinction of *S. tracheacolum*, the parasite will only cease to exist with extinction of the host. If by chance critically low numbers of Gouldian Finches saw the local extinction of this parasite, a subsequent resurgence in the host population would remain under the constant threat of reinfection via *S. tracheacolum* reservoir species such as the Pictorella Mannikin, at least in areas where the distribution of these species overlap.

If *S. tracheacolum* is the principal cause of the decline of Gouldian Finches natural resistance is unlikely to develop before host extinction. The local extinction of Gouldian Finches in parts of Queensland would tend to support this argument. If the 'Passerine form' of *S. tracheacolum* has been introduced to Australia it may have had hundreds or even thousands of years of co-evolution with its natural passerine hosts. The rate at which Gouldian Finches could develop levels of resistance similar to those of hosts of long association could not therefore be expected to occur naturally over a short period of time. For the purposes of conservation management of Gouldian Finches, artificial selection may be the fastest and most inexpensive means of developing genetic resistance. Such programs may necessitate the removal of some birds from the wild and, through avicultural breeding programs select for *S. tracheacolum* resistance (there is already a considerable

avicultural expertise in Australia in the breeding of Gouldian Finches). Alternatively, given a century of Gouldian Finch aviculture and exposure to *S. tracheacolum*, resistance may have already arisen in captive stock. If these stock could be identified, cross breeding programs between resistant captive stock and captive wild caught birds could be implemented to expedite the genetic process. Reintroduction programs would necessarily follow.

In many ways the future direction of *S. tracheacolum* research, as it pertains to the conservation management of Australian avifauna, lies in a determination of whether this species, or a closely related but pathogenic species, has been recently introduced. If it has not, then any attempt at artificial modification of the parasitic burden in Australian wild birds would be foolhardy.

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APPENDIX I.

Survey of Gouldian Finches and some other co-occurring species in northern Australia for nasal mites - reference collection.

Table 1. Nasal mite reference collection from the nasal mite surveys (1992-1994) of the Gouldian Finch and some other co-occurring species in northern Australia (held by the author at the Zoology Department, University of Tasmania).

Slide Reference No.	Host	Parasite	No. Specimens	Locality
GF112a	*Erythrura gouldiae*	*Sternostoma tracheacolum*	2F, 1P	Lung
GF112b	"	"	18F	Trachea
GF112c	"	"	10F	"
GF112d	"	"	8F, 2N	Posterior airsac
GF112e	"	"	3F	Anterior airsac
GF112f	"	"	2F	Thoracic airsac
GF112g	"	"	3F	Bronchus
GF146a	"	"	1F	Thoracic airsac
GF146b	"	"	1P, 1L	Lung
GF146c	"	"	4F	"
GF48a	"	"	1F	Body cavity
GF2a	"	"	2D	Posterior airsac
GF46	"	"	12F	Anterior airsac
GF45	"	"	4F	"
GF48b	"	"	2D, 1P	Lung
GF2b	"	"	3F	Anterior airsac
GF146d	"	"	4F, 1M, 4D	Posterior airsac
GF146e	"	"	1F	Lung
GF146d	"	"	3F	Nasal cavity
GF146e	"	"	14F	Anterior airsac
GF2c	"	"	1P	Lung
GF146f	"	"	4F	Bronchus
GF146g	"	"	15F	Anterior airsac
GF111a	"	"	6F	Thoracic airsac
GF111b	"	"	3F, 1P	Lung
GF111c	"	"	3F, 2P	Posterior airsac
GF111d	"	"	1F	Upper trachea
GF111e	"	"	3F	Anterior airsac
GF111f	"	"	13F	"
GF111g	"	"	11F	"
GF111h	"	"	3F	Nasal cavity
GF110a	"	"	1F	Syrinx
GF110b	"	"	1D	Posterior airsac
GF48c	"	"	1F	Trachea
GF46d	"	"	1F, 1D	Posterior airsac
GF48e	"	"	23F	Anterior airsac
GF48f	"	"	21F	"
GF48g	"	"	1F, 6P	Posterior airsac
GF112	"	"	2F	Syrinx
GF50	"	"	1F	Anterior airsac
GF50	"	"	"	Trachea
GF111h	"	*Sternostoma paddae*	1D	Nasal cavity
NT2	*Heteromunia pectoralis*	*Ptilonyssus emberizae*	2F	"
NT7	"	"	6F	"
NT10	"	"	1F, 1M	"
NT11	"	"	2F, 1D	"
NT15	"	"	8F	"
NT16	"	"	3F, 2M, 2P, 1D	"
NT17	"	"	1F	"
NT31	"	"	3F	"
PM37	"	"	6F	"
PM22	"	"	6F, 1M	"
94-70	"	"	3F	"

Table 1. Continued, Nasal mite reference collection from the nasal mite surveys (1992-1994) of the Gouldian Finch and some other co-occurring species in northern Australia.

Slide Reference No.	Host	Parasite	No. Specimens	Locality
94-72	*Heteromunia pectoralis*	*Ptilonyssus emberizae*	1F	"
94-73A	"	"	1F	"
94-73C	"	"	21F, 2M	"
94-74	"	"	12F, 1D	"
94-75	"	"	13F, 4M, 2P	"
94-76	"	"	1F	"
94-77A	"	"	30F, 7M, 3P	"
94-77B	"	"	27F, 6M, 4P, 2L	"
94-77C	"	"	31F, 6M, 5P	"
94-77D	"	"	12F, 6M, 4P	"
94-90	"	"	5F	"
94-92B	"	"	18F, 1M, 2P	"
94-92A	"	"	7F, 7M, 1P, 1L	"
94-95	"	"	1F	"
94-98	"	"	15F, 2M	"
94-96	"	"	10F, 1D, 1P, 1L	"
94-99	"	"	19F, 1M, 3P, 1L	"
94-100	"	"	1F	"
94-101A	"	"	31F, 2M, 1P, 1L	"
94-101B	"	"	10F, 1M	"
94-102	"	"	8F, 1P	"
94-103D	"	"	9F	"
94-104A	"	"	28F, 7P	"
94-104B	"	"	32F, 2M, 6P	"
94-104C	"	"	22F, 5M, 1P, 3L	"
94-104D	"	"	17F, 4M	"
94-104E	"	"	2F	"
94-105B	"	"	6F, 1M, 1P	"
94-106A	"	"	16F, 4M, 3P	"
94-106B	"	"	16F, 2M, 3P	"
94-107A	"	"	10F	"
NT18	"	*Sternostoma tracheacolum*	3F	Anterior airsac
NT19	"	"	1F	Lower trachea
NT20	"	"	4F	Anterior airsac
NT24	"	"	1F	Anterior airsac
PM140a	"	"	2P	Lung
PM84a	"	"	1P, 1L	"
PM84b	"	"	1F	"
PM84c	"	"	3F	"
PM84d	"	"	6F, 2D	Posterior airsac
PM84e	"	"	3F	Thoracic airsac
PM84f	"	"	4F	Anterior airsac
PM140b	"	"	1P	Posterior airsac
PM140c	"	"	2F	"
PM140d	"	"	5F	Anterior airsac
PM30a	"	"	1P	Lung
PM20a	"	"	3F, 1M, 1P	Posterior airsac
PM20b	"	"	5F, 2M	Anterior airsac
PM28a	"	"	1F	Trachea
PM28b	"	"	"	Syrinx
PM28c	"	"	"	Posterior airsac
PM28d	"	"	"	Anterior airsac
PM20c	"	"	"	Body cavity
PM30b	"	"	2F	Nasal cavity
PM30c	"	"	4F	Syrinx
PM37	"	"	2F	Anterior airsac
PM20d	"	"	6F	"
PM28e	"	"	7F	"
PM28f	"	"	3F	Posterior airsac
PM20e	"	"	1F	Lung
PM68	"	"	2F	Posterior airsac

Table 1. Continued, Nasal mite reference collection from the nasal mite surveys (1992-1994) of the Gouldian Finch and some other co-occurring species in northern Australia.

Slide Reference No.	Host	Parasite	No. Specimens	Locality
PM28g	*Heteromunia pectoralis*	*Ptilonyssus emberizae*	1F, 2D	Anterior airsac
94-101A	"	"	1F	Nasal cavity
94-103A	"	"	4P, 4L	Lung
94-103B	"	"	26F, 2M, 2P	Mouth, Trachea, Syrinx, Lung, Anterior airsac, Thoracic airsac, Posterior airsac
94-103C	"	"	28F, 2M	"
94-103E	"	"	10F, 2M, 1P	"
94-104E	"	"	2F, 1P	Lung, Anterior airsac, Thoracic airsac
94-105A	"	"	4F	Lung, Posterior airsac
94-107B	"	"	10F	mouth, lung, anterior airsac, posterior airsac
NT5	*Melopsittacus undulatus*	*Sternostoma tracheacolum*	1F	"
NT6	"	"	"	Posterior airsac
NT12	"	"	"	Anterior airsac
NT21	"	"	"	Syrinx
NT22	"	"	"	Thoracic airsac
NT25	"	"	"	Syrinx
NT30	"	"	"	Anterior airsac
B138a	"	"	1F	Syrinx
B138b	"	"	1F, 1N	Lung
B137a	"	"	1M	Thoracic airsac
B137b	"	"	1F	Syrinx
B53	*Melopsittacus undulatus*	*Sternostoma tracheacolum*	2F	Thoracic airsac
B139	"	"	1F	Anterior airsac
94-82	"	"	2F	Trachea
94-108	"	"	2F	Thoracic airsac, Posterior airsac
94-115	"	"	2F	Thoracic airsac
NT9	*Poephila acuticauda*	*Ptilonyssus neochmiae*	"	Nasal cavity
NT14	"	"	"	"
NT23	"	"	2F, 1N	"
LT143	"	"	1F	"
LT107	"	"	2F	"
LT122	"	"	"	"
LT108	"	"	1F	"
LT123	"	*Ptilonyssus astridae*	1F, 1M	"
LT17	"	"	5F, 1M, 1N	"
LT71	"	"	9F, 2M	"
LT15	"	"	2F	"
LT102	"	"	3F, 1L	"
94-15A	"	"	1F	"
94-15B	"	"	1M	"
94-24	"	"	11F, 7M, 1P, 1L	"
94-25	"	"	6F, 1M, 1P	"
94-41	"	"	5F	"
94-125	"	"	4F, 2M	"
94-146	"	"	1M	"
NT13	"	*Sternostoma paddae*	1D	"
NT27	"	*Kytonyssus andrei*	1F	"
NT1	*Poephila personata*	*Ptilonyssus astridae*	2F, 1M, 1D	"
NT3	"	"	7F, 1M	"
NT4	"	"	3F, 1P	"
NT8	"	"	2F	"
NT26	"	"	1F, 1M	"
NT28	"	"	3F	"
NT29	"	"	1F	"

Table 1. Continued, Nasal mite reference collection from the nasal mite surveys (1992-1994) of the Gouldian Finch and some other co-occurring species in northern Australia.

Slide Reference No.	Host	Parasite	No. Specimens	Locality
NT32	*Poephila personata*	*Ptilonyssus astridae*	2F	"
NT33	"	"	"	"
NT34	"	"	7F, 2M, 1D	"
NT35	"	"	1F, 1M	"
M82	"	"	1F, 2M, 1N	"
M96	"	"	1F	"
M87	"	"	1F, 2M, 2N	"
M86	"	"	2F	"
M99	"	"	4F	"
M80	"	"	4F, 2M	"
M79	"	"	1M	"
M40	"	"	1F	"
M86	"	"	"	"
M130	"	"	"	"
M95	"	"	"	"
M142	"	"	1F	"
M94	"	"	4F, 2M, 2N	"
MF26	"	*Kytodites amandavae*	5F, 2M	Anterior airsac Posterior airsac Trachea
M142	"	"	3F	Lung
M24	"	"	1F	Trachea
94-23	"	"	11F, 3M	Lung, Posterior airsac, Anterior airsac
94-45A	"	"	2F	Posterior airsac
M130	"	*Sternostoma paddae*	3F	Nasal cavity
NT12	"	*Sternostoma tracheacolum*	1F	Anterior airsac
Z91	*Taeniopygia guttata*	*Ptilonyssus astridae*	1N	Nasal cavity
Z76	"	"	2F, 1D	"
Z60	"	"	1M	"
Z77	"	"	3F, 1M, 2N	"
94-33	"	"	1M	"
94-61	"	"	21F, 4M, 2P	"
94-63	*Taeniopygia bichenovii*	"	2F	"
94-145	"	"	3F, 1P	"

APPENDIX II.

Ptilonyssus neochmiae **Domrow 1969 in the captive Gouldian Finch and** ***Sternostoma paddae*** **Fain in the wild Gouldian Finch.**

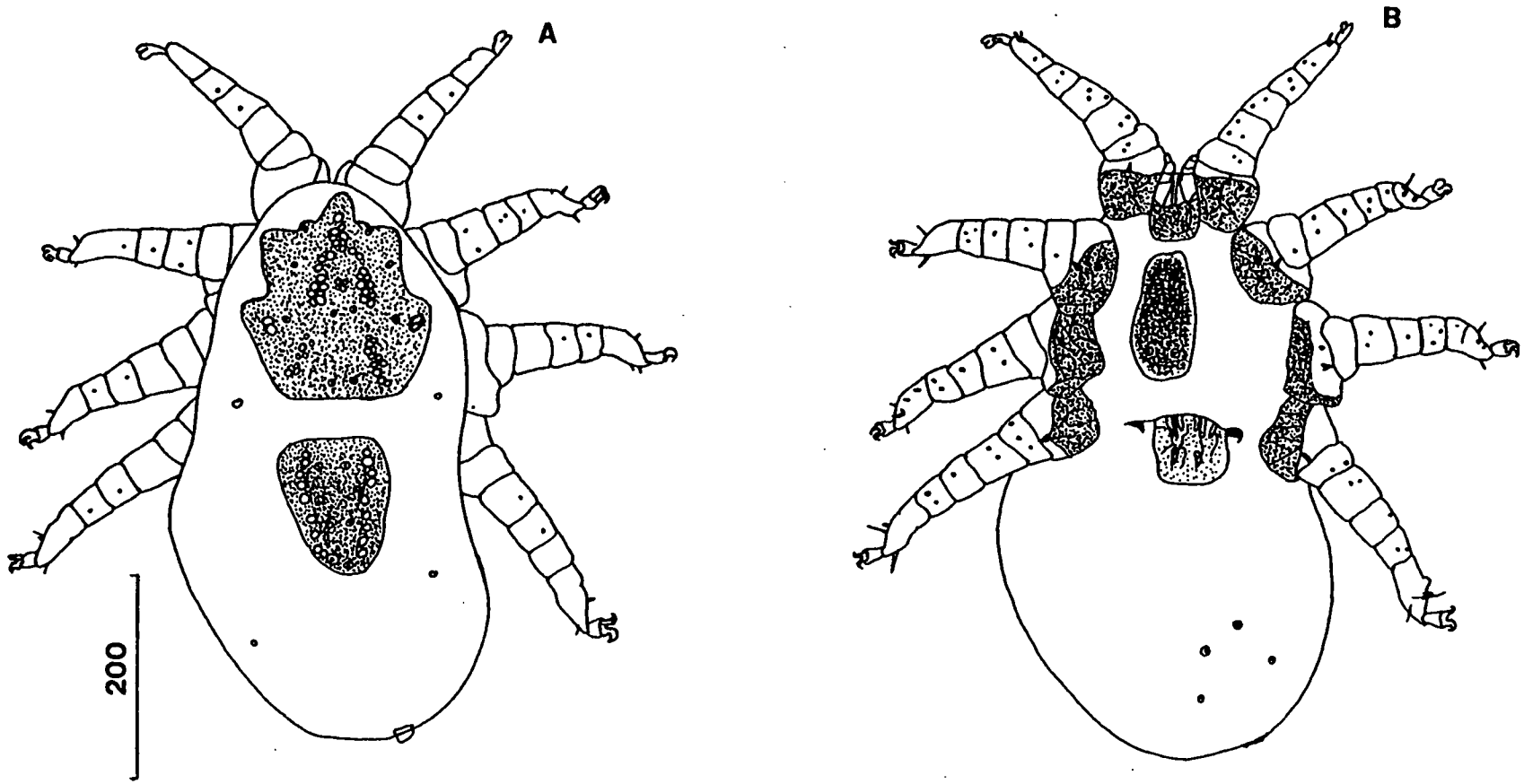

Figure 1. ***Sternostoma paddae*** **Faln** Female: A, dorsal view; B, ventral view.

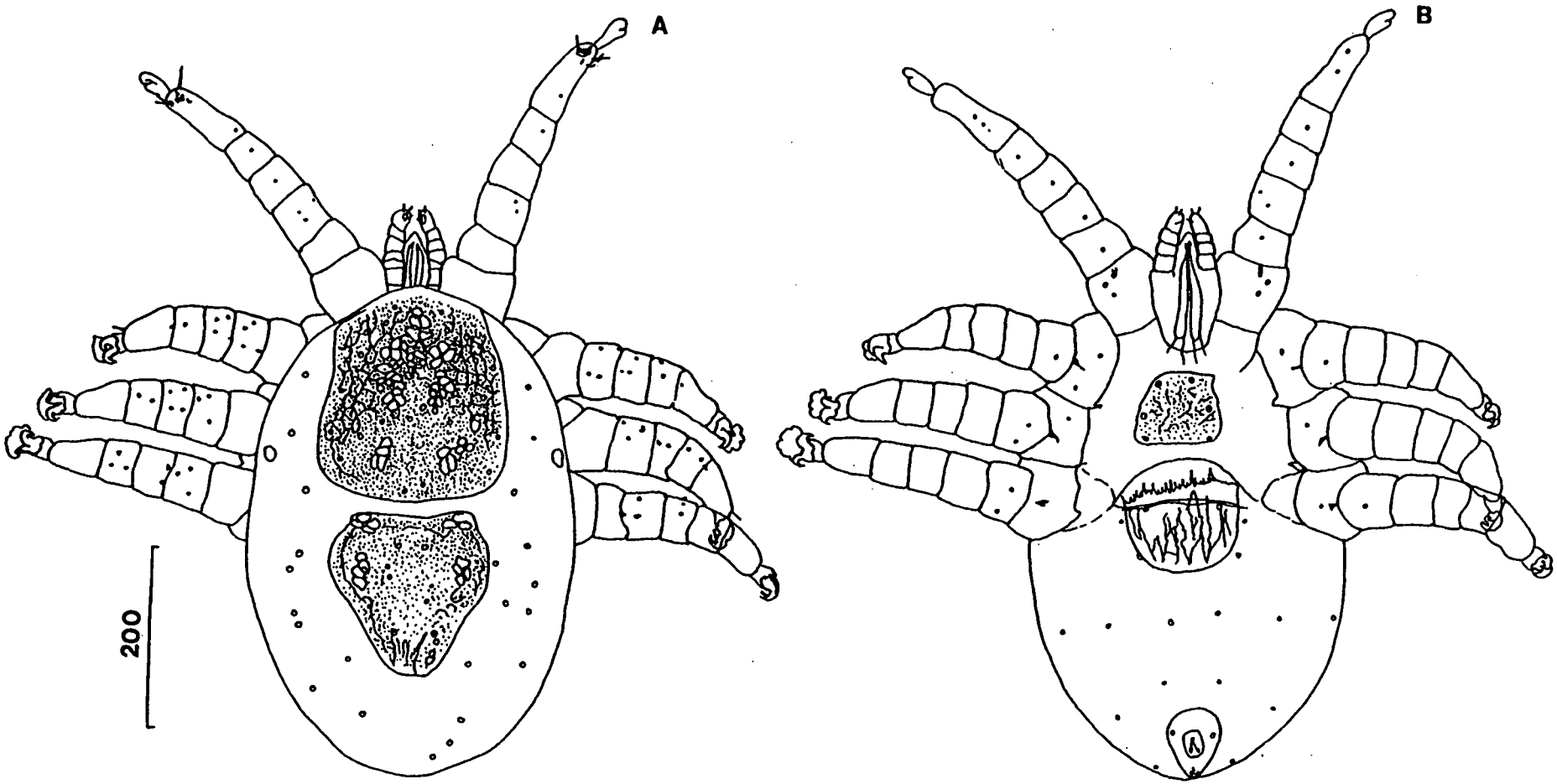

Figure 2. ***Ptilonyssus neochmiae*** **Domrow Female: A, dorsal view; B, ventral view.**

APPENDIX III.

Source, infection history and biological details for captive and wild caught Gouldian Finches examined during the present study.

Key to Table 1:

ID - All birds were given a unique number as an identifying reference. This number was subsequently used on microscope slides of mounted mites, bird tissue samples and preserved host carcases and as a tag in statistical data sets

Sex - Sex of host was determined by plumage initially and subsequently confirmed by examination of gonads during dissection. The sex of bird No. 112 was not determined:
M = male; **F** = female

Age - For the purposes of the present study three age categories were recognised. These were based on plumage colour:
J = juvenile; **I** = immature; **A** = adult.

HC - Three head colour types are known from wild Gouldian Finches (orange, red and black). Some variations were detected in captive reared birds used in the present study, however, the general colour of all birds conformed to the three recognised wild head colour types. Head colour for adult birds No. 56, No. 60 and No. 176 was not recorded. The head colour of juvenile birds was invariably green. Where head moult had begun, immature birds were identified according to adult head colour types:
R = red; **B** = black; **O** = orange; **G** = green

Source - Original source of birds used in experimental studies:
W = wild caught; **A** = captive reared; **TWP** = Territory Wildlife Park; **D** = Darwin;
UT = University of Tasmania; **NT** = Northern Territory; **QLD** = Queensland;
TAS = Tasmania

History - Details on the use of birds in biological studies and experiments.

Death - Indicates whether a host bird died in captivity (due to disease or accidental death) or was deliberately killed:
D = died naturally; **K** = killed by lethal anaesthetic injection.

Infected - Date of experimental infection or:
nil = bird not experimentally infected (i.e. either naturally infected or for experimental purposes, maintained free of infection); **wild** = naturally infected in the wild

Total - Total size of *S. tracheacolum* infrapopulation (including live and dead mites of all stages)

Dead - Total number of *S. tracheacolum* mites of all stages found dead

Life History, Population Biology, Pathology, Haematology, Behaviour - Indicates the specific use of each bird in the provision of data or observations in the current study:
***** = transmission (Chapter 2: Section 2.7, Transmission); **+** = feeding (Chapter 2: Section 2.4, Feeding); **#** = life history and locality (Chapter 2: Section 2.3, Locality); **A** = birds sampled at 3, 6, 9 and 12 months following experimental infection (Chapter 3: Section 3.32, Population growth of *S. tracheacolum*; Chapter 4: Section 4.3, Pathology and duration of infection and Section 4.4, Pathology and intensity of infection; Chapter 5: Section 5.3.1, Comparisons between *S. tracheacolum* infected and uninfected hosts); **B** = all birds with a known period of infection (Chapter 3: Section 3.3.2, Population Growth of *S. tracheacolum*); **C** = behaviour and symptoms (Chapter 6: Section 6.3.1, Weight, Section 6.3.2, Respiratory symptoms, Section 6.3.3, Activity level and respiratory ability and Section 6.34, Other symptoms of *S. tracheacolum* infection); **D** = all birds examined between 12 months and 2 years following experimental infection; **E** = birds contributing data for the calculation of estimates of host population and mite infrapopulation parameters.

Table 1. Source, infection history and biological details for captive and wild caught Gouldian Finches examined during the present study.

ID	Sex	Age	HC	Source	History	Death	Infested	Date	Total	Dead	Life History	Pop. Biology	Pathology	Haem.	Behaviour
1	M	A	R	W/Y, NT	Predated by snake	P	wild	7/6/91	9	3	.* #	.E			
2	M	A	R	A/QLD	Treatment experiment control	K	nil	31/5/91	90	8	.* #	.E			.C
10	M	A	R	A/QLD	Treatment experiment control	K	nil	29/5/91	6	1	.* #	.E			.C
11	F	A	B	A/QLD	Treatment experiment control	K	nil	29/5/91	36	1	.* #	.E			.C
12	F	A	B	A/QLD	Treatment experiment control	K	nil	31/5/91	147	3	.* #	.E			.C
13	M	A	R	A/QLD	Treatment experiment control	K	nil	4/6/91	55	1	.* #	.E			.C
14	F	A	B	A/QLD	Treatment experiment control	K	nil	4/6/91	25	3	.* #	.E			.C
16	F	A	R	A/TWP, NT	Zoo Exhibit	D	nil	19/5/91	5	0	.* #	.E			
17	M	A	R	A/QLD	Experimental stock at TWP, NT	D	nil	20/5/91	120	21	.* #	.E			.C
18	F	A	B	A/QLD	Experimental stock at TWP, NT	D	nil	20/6/91	1	0	.* #	.E			.C
19	M	A	O	A/QLD	Experimental stock at TWP, NT	D	nil	19/6/91	65	10	.* #	.E			.C
20	M	J	G	A/QLD	Experimental stock at CSRIO, NT	D	nil	24/6/91	103	2	.* #	.E			.C
21	F	A	B	A/QLD	Experimental stock at TWP, NT	D	nil	18/6/91	28	12	.* #	.E			.C
22	M	A	O	A/QLD	Experimental stock at TWP, NT	D	nil	19/6/91	58	5	.* #	.E			.C
23	F	A	R	A/QLD	Experimental stock at TWP, NT	D	nil	21/6/91	104	4	.* #	.E			.C
24	M	A	O	A/QLD	Experimental stock at TWP, NT	D	nil	18/6/91	4	2	.* #	.E			.C
27	F	I	B	A/QLD	Experimental stock at CSRIO, NT	D	nil	25/6/91	142	18	.* #	.E			.C
28	M	I	G	W/Y, NT	Collected from wild for mite stock	K	wild	4/10/91	178	38	.* #	.E			
29	M	I	G	W/Y, NT	Collected from wild for mite stock	K	wild	3/10/90	55	5	.* #	.E			
30	M	I	G	W/Y, NT	Collected from wild for mite stock	K	wild	15/10/90	76	22	.* #	.E			
31	F	I	B	W/Y, NT	Collected from wild for mite stock	K	wild	20/12/90	79	10	.* #	.E			
33	M	I	G	W/Y, NT	Collected from wild for mite stock	K	wild	13/11/90	59	1	.* #	.E			
34	F	I	B	W/Y, NT	Collected from wild for mite stock	K	wild	3/5/91	42	9	.* #	.E			

Table 1. Continued, Source, infection history and biological details for captive and wild caught Gouldian Finches examined in this study.

ID	Sex	Age	HC	Source	History	Death	Infested	Date	Total	Dead	Life History	Pop. Biology	Pathology	Haem.	Behaviour
35	F	I	G	W/Y, NT	Collected from wild for mite stock	K	wild	1/5/91	65	12	.* #	.E			
36	F	I	B	W/Y, NT	Collected from wild for mite stock	D	wild	22/4/91	56	10	.* #	.E			
56	M	A		W/N, NT	Accidental death at time of capture	K	wild	10/7/89	26	2	.* #	.E			
60	F	A		W/Y, NT	Accidental death at time of capture	K	wild	12/7/90	49	6	.* #	.E			
68	M	I	R	A/D, NT	Experimental stock at TWP, NT	D	nil	26/6/91	23	3	.* #	.E			.C
102	M	A	R	A/D, NT	Experimental stock at TWP, NT	D	nil	27/6/91	74	13	.* #	.E			.C
103	F	A	O	A/A, SA	Experimental stock at UT, TAS	D	nil	28/8/91	265	1	.* #	.E			.C
106	F	J	G	A/D, NT	Experimental stock at UT, TAS	D	nil	16/9/91	88	7	.* #	.E			.C
112		J	G	A/D, NT	Experimental stock at UT, TAS	D	nil	27/9/91	52	4	.* #	.E			.C
113	F	I	B	A/D, NT	Experimental stock at UT, TAS	D	nil	6/10/91	184	13	.* #	.E			.C
120	M	A	O	A/D, NT	Treatment experiment control	K	nil	28/4/92	63	12	.* #	.E			.C
121	M	A	O	A/QLD	Monitoring experiment 1992	D	12/2/92	11/5/92	11	0	.* + #	.E B			.C
123	F	A	R	A/QLD	Treatment experiment control	D	nil	29/4/92	2	1	.* #	.E			
125	M	A	O	A/QLD	Monitoring experiment 1992	K	12/2/92	18/5/92	13	2	.* + #	.E B A	.A	.A	.C
127	M	A	O	A/QLD	Monitoring experiment 1992	D	12/2/92	10/5/92	13	0	.* + #	.E B			.C
128	M	A	O	A/D, NT	Experimental stock UT, TAS	D	17/1/92	23/4/92	10	1	.* + #	.E			
129	F	A	O	A/D, NT	Treatment experiment control	K	nil	13/5/92	5	4	.* + #	.E			
130	M	A	O	A/QLD	Monitoring experiment 1992	K	12/2/92	18/5/92	168	9	.* + #	.E B A	.A	.A	.C
131	M	A	O	A/QLD	Monitoring experiment 1992	K	12/2/92	21/5/92	31	4	.* + #	.E B A	.A	.A	.C
132	F	A	B	A/QLD	Monitoring experiment 1992	D	12/2/92	22/4/92	28	4	.* + #	.E B			.C
133	F	A	B	A/QLD	Experimental stock at UT,TAS	D	17/1/92	22/4/92	17	1	.* + #	.E			
134	F	A	B	A/QLD	Monitoring experiment 1992	K	12/2/92	25/5/92	215	10	.* + #	.E B A	.A	.A	.C
135	M	A	O	A/QLD	Monitoring experiment 1992	K	12/2/92	20/5/92	30	6	.* + #	.E B A	.A	.A	.C

Table 1. Continued, Source, infection history and biological details for captive and wild caught Gouldian Finches examined in this study.

ID	Sex	Age	HC	Source	History	Death	Infested	Date	Total	Dead	Life History	Pop. Biology	Pathology	Haem.	Behaviour
137	F	A	B	A/QLD	Monitoring experiment 1992	D	12/2/92	30/5/92	7	0	.* + #	.E B			.C
138	F	A	O	A/D, NT	Experimental stock at UT, TAS	D	17/1/92	30/1/92	1	0	.* + #	.E			
139	M	A	O	A/D, NT	Experimental stock at UT, TAS	D	17/1/92	31/1/92	3	1	.* #	.E			
140	M	A	R	A/D, NT	Experimental stock at UT, TAS	D	17/1/92	3/2/92	3	0	.* + #	.E			
141	F	J	G	A/D, NT	Experimental stock at UT, TAS	D	17/1/92	9/2/92	2	0	.* + #	.E			
142	M	A	R	A/QLD	Experimental stock at UT, TAS	D	17/1/92	11/2/92	2	0	.* #	.E			
143	M	I	I	A/D, NT	Experimental stock at UT, TAS	D	17/1/92	3/3/92	1	0	.* #	.E			
144	M	A	O	A/QLD	Experimental stock at UT, TAS	D	17/1/92	5/3/92	2	0	.* #	.E			
145	M	J	G	A/D, NT	Experimental stock at UT, TAS	D	17/1/92	9/3/92	8	2	.* #	.E			
146	M	I	O	A/D, NT	Experimental stock at UT, TAS	D	17/1/92	11/3/92	4	0	.* #	.E			
147	F	A	B	A/QLD	Monitoring experiment 1992	D	12/2/92	17/3/92	1	0	.* #	.E B			.C
148	M	A	O	A/QLD	Monitoring experiment 1992	D	12/2/92	12/2/92	1	0	.* #	.E B			.C
160	F	A	B	A/QLD	Monitoring experiment 1992	K	12/2/92	27/7/92	257	59	.* + #	.E B A	.A	.A	.C A
161	F	A	B	A/QLD	Monitoring experiment 1992	K	12/2/92	28/7/92	273	14	.* + #	.E B A	.A	.A	.C A
162	M	A	R	A/QLD	Monitoring experiment 1992	K	12/2/92	30/7/92	185	24	.* + #	.E B A	.A	.A	.C A
163	M	A	O	A/QLD	Monitoring experiment 1992	K	12/2/92	31/7/92	178	21	.* + #	.E B A	.A	.A	.C A
164	F	A	B	A/QLD	Monitoring experiment 1992	D	12/2/92	14/7/92	224	43	.* + #	.E B A	.A	.A	.C A
165	M	A	O	A/QLD	Monitoring experiment 1992	D	12/2/92	31/7/92	216	30	.* + #	.E B A	.A	.A	.C A
166	F	A	B	A/QLD	Monitoring experiment 1992	K	12/2/92	22/10/92	77	2	.* #	.E B			.C
167	F	A	R	A/QLD	Monitoring experiment 1992	D	12/2/92	2/9/92	41	1	.* #	.E B			.C
170	M	I	G	A/UT, TAS	Monitoring experiment 1992	D	nil	18/8/92	57	10	.* #	.E			.C
171	F	I	G	A/D, NT	Experimental stock at UT, TAS	D	22/10/92	30/11/92	9	0	.* #	.E			
173	F	A	B	A/D, NT	Experimental stock at UT, TAS	D	22/10/92	3/12/92	7	0	.* #	.E			

Table 1. Continued, Source, infection history and biological details for captive and wild caught Gouldian Finches examined in this study.

ID	Sex	Age	HC	Source	History	Death	Infested	Date	Total	Dead	Life History	Pop. Biology	Pathology	Haem.	Behaviour
174	F	A	B	A/D, NT	Experimental stock at UT, TAS	D	22/10/92	21/11/92	27	1	.* #	.E			
175	F	J	G	A/D, NT	Experimental stock at UT, TAS	D	22/10/92	21/11/92	5	0	.* #	.E			
176	M	A		A/D, NT	Experimental stock at UT, TAS	D	22/10/92	24/11/92	20	0	.* #	.E			
180	F	A	O	A/D, NT	Experimental stock at UT, TAS	K	22/10/93	3/3/93	371	12	.* #	.E			
181	M	A	R	A/D, NT	Experimental stock at UT, TAS	K	22/10/92	19/3/93	217	9	.* #	.E			
182	F	A	R	A/D, NT	Experimental stock at UT, TAS	K	22/10/93	17/3/93	274	35	.* #	.E			
188	F	A	B	A/QLD	Monitoring experiment 1993	D	2/3/93	25/4/93	23	0	.* #	.E B			.C
189	F	A	B	A/QLD	Monitoring experiment 1993	D	2/3/93	4/5/93	9	0	.* #	.E B			.C
190	M	A	B	A/QLD	Monitoring experiment 1993	D	2/3/93	17/5/93	73	1	.* #	.E B			.C
191	M	A	R	A/QLD	Monitoring experiment 1993	D	2/3/93	2/6/93	41	0	.* #	.E B			.C
192	F	A	B	A/QLD	Monitoring experiment 1993	D	2/3/93	30/7/93	175	3	.* #	.E B			.C
193	F	A	B	A/QLD	Monitoring experiment 1993	D	2/3/93	15/8/93	27	0	.* #	.E			.C
194	F	A	B	A/QLD	Monitoring experiment 1993	D	2/3/93	7/9/93	25	3	.* #	.E			.C
195	F	A	B	A/QLD	Monitoring experiment 1993	D	2/3/93	11/9/93	160	18	.* #	.E B			.C
196	F	A	R	A/QLD	Monitoring experiment 1993	D	2/3/93	12/9/93	162	28	.* #	.E B			.C
401	M	A	O	A/QLD	Monitoring experiment 1993	D	2/3/93	18/10/93	285	43		.E B			.C
402	F	A	B	A/QLD	Monitoring experiment 1993	D	2/3/93	21/10/93	91	27		.E B			.C
403	M	A	B	A/QLD	Monitoring experiment 1993	D	2/3/93	29/10/93	42	8		.E B			.C
405	M	A	B	A/QLD	Monitoring experiment 1993	K	2/3/93	6/12/93	8	5		.E B	.A	.A	.C A
406	M	A	O	A/QLD	Monitoring experiment 1993	K	2/3/93	6/12/93	35	4		.E B	.A	.A	.C A
407	F	A	B	A/QLD	Monitoring experiment 1993	K	2/3/93	6/12/93	73	11		.E B	.A	.A	.C A
408	M	A	O	A/QLD	Monitoring experiment 1993	D	2/3/93	30/12/93	19	3		.E B			.C
412	M	A	O	A/QLD	Monitoring experiment 1993	K	2/3/93	6/12/93	31	7		.E B A	.A	.A	.C A

Table 1. Continued, Source, infection history and biological details for captive and wild caught Gouldian Finches examined in this study.

ID	Sex	Age	HC	Source	History	Death	Infested	Date	Total	Dead	Life History	Pop. Biology	Pathology	Haem.	Behaviour
413	M	A	R	A/QLD	Monitoring experiment 1993	K	2/3/93	6/12/93	22	12		.E B A	.A	.A	.C A
414	F	A	O	A/QLD	Monitoring experiment 1993	K	2/3/93	6/12/93	192	60		.E B A	.A	.A	.C A
415	F	A	B	A/QLD	Monitoring experiment 1993 control	K	nil	17/2/94	0	-		.E A	.A	.A	.C A
416	M	A	R	A/QLD	Monitoring experiment 1993 control	K	nil	17/2/93	0	-		.E A	.A	.A	.C A
417	M	A	R	A/QLD	Monitoring experiment 1993 control	K	nil	17/2/93	0	-		.E A	.A	.A	.C A
418	M	A	B	A/QLD	Monitoring experiment 1993 control	K	nil	17/2/93	0	-		.E A	.A	.A	.C A
419	F	A	B	A/QLD	Monitoring experiment 1993 control	K	nil	17/2/93	0	-		.E A	.A	.A	.C A
452	M	A	O	A/QLD	Monitoring experiment 1992	K	12/2/92	24/2/94	5	4		.E D			.C
453	F	A	B	A/QLD	Monitoring experiment 1993	K	2/3/93	6/12/93	79	2		.E A	.A	.A	.C A
460	M	A	O	A/QLD	Monitoring experiment 1992	K	12/2/92	16/4/93	29	NR		.E D			.C
461	M	A	B	A/QLD	Monitoring experiment 1992	K	12/2/92	13/4/93	13	NR		.E D			.C
462	M	A	B	A/QLD	Monitoring experiment 1992	K	12/2/92	1/9/93	23	NR		.E D			.C
1001	F	A	B	A/QLD	Monitoring experiment 1992 control	D	nil	11/2/92	0	-		.E			.C
1002	M	A	B	A/QLD	Monitoring experiment 1992 control	D	nil	30/5/92	0	-		.E			.C
1003	M	A	O	A/QLD	Monitoring experiment 1992	D	12/2/92	3/6/92	0	-		.E			.C
1004	F	A	B	A/QLD	Monitoring experiment 1992 control	D	nil	20/2/92	0	-		.E			.C
1005	F	A	B	A/QLD	Monitoring experiment 1992 control	D	nil	22/3/92	0	-		.E			.C
1006	F	A	B	A/QLD	Monitoring experiment 1992 control	D	nil	22/2/92	0	-		.E			.C
1007	F	A	B	A/QLD	Monitoring experiment 1992 control	D	nil	17/3/92	0	-		.E			.C
1008	F	A	B	A/QLD	Monitoring experiment 1992 control	D	nil	17/3/92	0	-		.E			.C
1009	M	A	O	A/QLD	Monitoring experiment 1992 control	D	nil	6/3/92	0	-		.E			.C
1010	M	A	O	A/QLD	Monitoring experiment 1992 control	D	nil	31/3/92	0	-		.E			.C
1011	F	A	B	A/QLD	Monitoring experiment 1992 control	D	nil	2/4/92	0	-		.E			.C

Table 1. Continued, Source, infection history and biological details for captive and wild caught Gouldian Finches examined in this study.

ID	Sex	Age	HC	Source	History	Death	Infested	Date	Total	Dead	Life History	Pop. Biology	Pathology	Haem.	Behaviour
1012	M	A	O	A/QLD	Monitoring experiment 1992 control	D	nil	18/4/92	0	-		.E			.C
1013	F	A	R	A/QLD	Monitoring experiment 1992 control	D	nil	24/4/92	0	-		.E			.C
1014	M	A	O	A/QLD	Monitoring experiment 1992 control	D	nil	27/4/92	0	-		.E			.C
1015	M	A	B	A/QLD	Monitoring experiment 1992 control	D	nil	27/4/92	0	-		.E			.C
1016	M	A	O	A/QLD	Monitoring experiment 1992 control	D	nil	10/5/92	0	-		.E			.C
1017	M	A	B	A/QLD	Monitoring experiment 1992 control	D	nil	14/5/92	0	-		.E			.C
1018	M	A	O	A/QLD	Monitoring experiment 1992 control	K	nil	19/5/92	0	-		.E			.C
1019	M	A	O	A/QLD	Monitoring experiment 1992 control	K	nil	15/5/92	0	-		.E	.A	.A	.C A
1020	M	A	O	A/QLD	Monitoring experiment 1992 control	K	nil	25/5/92	0	-		.E	.A	.A	.C A
1021	F	A	B	A/QLD	Monitoring experiment 1992 control	K	nil	20/5/92	0	-		.E	.A	.A	.C A
1022	M	A	B	A/QLD	Monitoring experiment 1992 control	K	nil	22/5/92	0	-		.E	.A	.A	.C A
1023	M	A	O	A/QLD	Monitoring experiment 1992 control	K	nil	27/7/92	0	-		.E	.A	.A	.C A
1024	F	A	B	A/QLD	Monitoring experiment 1992 control	K	nil	31/7/92	0	-		.E	.A	.A	.C A
1025	F	A	B	A/QLD	Monitoring experiment 1992 control	K	nil	28/7/92	0	-		.E	.A	.A	.C A
1026	M	A	B	A/QLD	Monitoring experiment 1992 control	K	nil	30/7/92	0	-		.E	.A	.A	.C A
1027	F	A	B	A/QLD	Monitoring experiment 1992 control	K	nil	28/7/92	0	-		.E	.A	.A	.C A
1028	M	A	O	A/QLD	Monitoring experiment 1992 control	K	nil	27/7/92	0	-		.E	.A	.A	.C A
1029	M	A	B	A/QLD	Monitoring experiment 1992	D	12/2/92	25/3/92	0	-		.E			.C
1030	M	A	O	A/QLD	Monitoring experiment 1992	D	12/2/92	27/4/92	0	-		.E			.C
1031	F	A	B	A/QLD	Monitoring experiment 1992	D	12/2/92	23/3/92	0	-		.E			.C
1032	F	A	B	A/QLD	Monitoring experiment 1992	D	12/2/92	9/3/92	0	-		.E			.C
1033	F	A	B	A/QLD	Monitoring experiment 1992	D	12/2/92	19/2/92	0	-		.E			.C
1034	M	A	O	A/QLD	Monitoring experiment 1992	D	12/2/92	12/2/92	0	-		.E			.C

Table 1. Continued, Source, infection history and biological details for captive and wild caught Gouldian Finches examined in this study.

ID	Sex	Age	HC	Source	History	Death	Infested	Date	Total	Dead	Life History	Pop. Biology	Pathology	Haem.	Behaviour
1035	F	A	B	A/QLD	Monitoring experiment 1992	D	12/2/92	16/2/92	0	-		.E			.C
1036	F	A	B	A/QLD	Monitoring experiment 1992	D	12/2/92	20/2/92	0	-		.E			.C
1037	F	A	B	A/QLD	Monitoring experiment 1992	D	12/2/92	12/2/92	1	0		.E			.C
1038	M	A	B	A/QLD	Monitoring experiment 1992	D	12/2/92	23/3/93	8	0		.E			.C
1039	F	A	B	A/QLD	Monitoring experiment 1992 control	D	nil	25/2/92	0	-		.E			.C
1040	F	A	O	A/QLD	Monitoring experiment 1992 control	D	nil	22/2/92	0	-		.E			.C
1041	F	A	O	A/QLD	Monitoring experiment 1992 control	D	nil	25/2/92	0	-		.E			.C
1042	M	A	B	A/QLD	Monitoring experiment 1992 control	D	nil	25/2/92	0	-		.E			.C
1043	M	A	O	A/QLD	Monitoring experiment 1992 control	D	nil	26/2/92	0	-		.E			.C
1044	M	A	O	A/QLD	Monitoring experiment 1992 control	D	nil	20/3/92	0	-		.E			.C
1045	F	A	B	A/QLD	Monitoring experiment 1992 control	D	nil	18/4/93	0	-		.E			.C
1046	F	A	B	A/QLD	Monitoring experiment 1992	D	12/2/92	20/2/92	0	-		.E			.C
1047	F	A	O	A/QLD	Monitoring experiment 1992	D	12/2/92	26/2/92	0	-		.E			.C
1048	M	A	B	A/QLD	Monitoring experiment 1992	D	12/2/92	12/3/92	0	-		.E			.C
1049	M	A	O	A/QLD	Monitoring experiment 1993 control	D	nil	24/3/93	0	-		.E			.C
1050	F	A	B	A/QLD	Monitoring experiment 1993	D	2/3/93	31/3/93	0	-		.E			.C
1051	F	A	B	A/QLD	Monitoring experiment 1993 control	D	nil	12/4/93	0	-		.E			.C
1052	F	A	B	A/QLD	Monitoring experiment 1993	D	2/3/93	10/4/93	0	-		.E			.C
1053	M	A	O	A/QLD	Monitoring experiment 1993	D	2/3/93	12/4/93	0	-		.E			.C
1054	M	A	O	A/QLD	Monitoring experiment 1993	D	2/3/93	20/4/93	2	-		.E			.C
1055	M	A	O	A/QLD	Monitoring experiment 1993	D	2/3/93	22/4/93	0	-		.E			.C
1056	M	A	B	A/QLD	Monitoring experiment 1993	D	2/3/93	29/4/93	0	-		.E			.C
1057	F	A	B	A/QLD	Monitoring experiment 1993 control	D	nil	4/5/93	0	-		.E			.C

Table 1. Continued, Source, infection history and biological details for captive and wild caught Gouldian Finches examined in this study.

ID	Sex	Age	HC	Source	History	Death	Infested	Date	Total	Dead	Life History	Pop. Biology		Pathology		Haem.	Behaviour
1058	M	A	B	A/QLD	Monitoring experiment 1993 control	D	nil	4/5/93	0	-		.E					.C
1059	F	A	O	A/QLD	Monitoring experiment 1993 control	D	nil	5/5/93	0	-		.E					.C
1060	M	A	R	A/QLD	Monitoring experiment 1993 control	D	nil	2/6/92	0	-		.E					.C
1061	F	A	B	A/QLD	Monitoring experiment 1993 control	D	nil	22/6/93	0	-		.E					.C
1062	M	A	O	A/QLD	Monitoring experiment 1993 control	D	nil	24/6/93	0	-		.E					.C
1063	F	A	B	A/QLD	Monitoring experiment 1993 control	D	nil	21/10/93	0	-		.E					.C
1064	M	A	O	A/QLD	Monitoring experiment 1993 control	D	nil	21/10/93	0	-		.E					.C
1065	M	A	O	A/QLD	Monitoring experiment 1993 control	D	nil	7/7/93	0	-		.E					.C
1066	F	A	B	A/QLD	Monitoring experiment 1993 control	D	nil	4/10/93	0	-		.E					.C
1067	M	A	R	A/QLD	Monitoring experiment 1993 control	D	nil	5/10/93	0	-		.E					.C
1068	F	A	R	A/QLD	Monitoring experiment 1993 control	D	nil	27/9/93	0	-		.E					.C
2001	M	A	O	A/QLD	Monitoring experiment 1993 control	K	nil	6/12/93	0	-		.E	B	.A		.A	.C A
2002	F	A	B	A/QLD	Monitoring experiment 1993 control	K	nil	6/12/93	0	-		.E	B	.A		.A	.C A
2003	M	A	O	A/QLD	Monitoring experiment 1993 control	K	nil	6/12/93	0	-		.E	B	.A		.A	.C A
2004	F	A	B	A/QLD	Monitoring experiment 1993 control	K	nil	6/12/93	0	-		.E	B	.A		.A	.C A

APPENDIX IV.

Source and biological details for wild caught birds examined during nasal mite surveys between 1992 and 1994 in the Northern Territory.

Key to Table 1:

Identity - Unique identifying number for each bird used in referencing of preserved tissues and slide mounted nasal mites

Host Species - common name of host species

Locality - Birds were collected on **Newry** Station, NT (16^{o} 08' S 120^{o} 05' E) or **Yinberrie** Hills, NT (14^{o} 08' S 132^{o} 05' E)

Date - Date of collection of bird specimen

Age - Age of bird: **A** = Adult; **I** = Immature; **J** = Juvenile

Sex - Sex of bird: **M** = Male; **F** = Female

Weight - Weight of bird at the time of capture

Moult - Primary and secondary feather moult in progress at time of bird capture

Nasal Mites - **no** = no evidence of nasal mites from the families Rhinonyssidae, Speleognathidae, Turbinoptidae or Kytoditidae; species of nasal mite are indicated

Total mites - Total number of mites in infrapopulation of each nasal mite species present

F - Number of live adult non-gravid female mites
FE - Number of live gravid female mites
M - Number of live adult males
D - Number of immature mites (i.e larvae, protonymphs, deutonymphs, nymphs)
DF - Number of dead adult non-gravid female mites
DFE - Number of dead gravid female mites
DM - Number of dead adult males
DD - Number of dead immature mites

Table 1. Source and biological details of wild caught birds examined during nasal mite surveys between 1992 and 1994 in the Northern Territory.

Identity	Host Species	Locality	Date	Age	Sex	Weight	Moult	Nasal Mites	Total mites	F	FE	M	D	DF	DFE	DM	DD
B1	Budgerigar	Newry	13/7/93	I	F	32		no	0	0	0	0	0	0	0	0	0
B11	Budgerigar	Newry	16/7/93	A	F	25		no	0	0	0	0	0	0	0	0	0
B12	Budgerigar	Newry	16/7/93	A	M	28.5		no	0	0	0	0	0	0	0	0	0
B13	Budgerigar	Newry	16/7/93	A	M	27.5		no	0	0	0	0	0	0	0	0	0
B131	Budgerigar	Newry	20/7/93	A	M	32.5	no	no	0	0	0	0	0	0	0	0	0
B132	Budgerigar	Newry	20/7/93	A	M	31	yes	no	0	0	0	0	0	0	0	0	0
B133	Budgerigar	Newry	20/7/93	A	F	27	no	no	0	0	0	0	0	0	0	0	0
B134	Budgerigar	Newry	20/7/93	A	M	28	yes	no	0	0	0	0	0	0	0	0	0
B135	Budgerigar	Newry	20/7/93	A	M	29	no	no	0	0	0	0	0	0	0	0	0
B136	Budgerigar	Newry	20/7/93	A	F	29.5	no	no	0	0	0	0	0	0	0	0	0
B137	Budgerigar	Newry	20/7/93	A	M	26	no	S. tracheacolum	2	1	0	1	0	0	0	0	0
B138	Budgerigar	Newry	20/7/93	A	M	29	no	S. tracheacolum	3	1	0	0	0	1	0	0	1
B139	Budgerigar	Newry	20/7/93	A	M	27.5	yes	S. tracheacolum	1	1	0	0	0	0	0	0	0
B14	Budgerigar	Newry	16/7/93	A	F	31		no	0	0	0	0	0	0	0	0	0
B51	Budgerigar	Newry	30/6/93	A	M	31	no	no	0	0	0	0	0	0	0	0	0
B52	Budgerigar	Newry	30/6/93	I	M	26.5	no	no	0	0	0	0	0	0	0	0	0
B53	Budgerigar	Newry	30/6/93	I	M	27	no	S. tracheacolum	2	1	1	0	0	0	0	0	0
B54	Budgerigar	Newry	30/6/93	I	M	27.5	no	no	0	0	0	0	0	0	0	0	0
B55	Budgerigar	Newry	30/6/93	A	F	27	no	no	0	0	0	0	0	0	0	0	0
B61	Budgerigar	Newry	20/7/93	A	M	28	no	no	0	0	0	0	0	0	0	0	0
B62	Budgerigar	Newry	20/7/93	A	F	29	no	no	0	0	0	0	0	0	0	0	0
B63	Budgerigar	Newry	20/7/93	A	M	27	no	no	0	0	0	0	0	0	0	0	0
B65	Budgerigar	Newry	20/7/93	A	M	26.5	no	no	0	0	0	0	0	0	0	0	0

Table 1. Continued, Source and biological details of wild caught birds examined during nasal mite surveys between 1992 and 1994 in the Northern Territory.

Identity	Host Species	Locality	Date	Age	Sex	Weight	Moult	Nasal Mites	Total mites	F	FE	M	D	DF	DFE	DM	DD
B66	Budgerigar	Newry	20/7/93	A	M	27.5	no	no	0	0	0	0	0	0	0	0	0
B67	Budgerigar	Newry	20/7/93	A	M	28	no	no	0	0	0	0	0	0	0	0	0
B8	Budgerigar	Newry	17/7/93	A	F	27.5		no	0	0	0	0	0	0	0	0	0
BUDG1	Budgerigar	Newry	16/8/92	A	M			no	0	0	0	0	0	0	0	0	0
BUDG10	Budgerigar	Newry	16/8/92	A	F			no	0	0	0	0	0	0	0	0	0
BUDG11	Budgerigar	Newry	18/8/92	A	M			no	0	0	0	0	0	0	0	0	0
BUDG12	Budgerigar	Newry	18/8/92	A	F			no	0	0	0	0	0	0	0	0	0
BUDG13	Budgerigar	Newry	19/8/92	A	M			no	0	0	0	0	0	0	0	0	0
BUDG14	Budgerigar	Newry	19/8/92	A	M			no	0	0	0	0	0	0	0	0	0
BUDG15	Budgerigar	Newry	19/8/92	A	M			no	0	0	0	0	0	0	0	0	0
BUDG16	Budgerigar	Newry	19/8/92	A	F			no	0	0	0	0	0	0	0	0	0
BUDG17	Budgerigar	Newry	19/8/92	A	F			S. tracheacolum	1	0	0	0	0	1	0	0	0
BUDG18	Budgerigar	Newry	19/8/92	A	F			S. tracheacolum	1	0	1	0	0	0	0	0	0
BUDG19	Budgerigar	Newry	20/8/92	A	F			no	0	0	0	0	0	0	0	0	0
BUDG2	Budgerigar	Newry	16/8/92	I	M			S. tracheacolum	1	0	0	0	0	1	0	0	0
BUDG20	Budgerigar	Newry	15/8/92	A	F			S. tracheacolum	1	1	0	0	0	0	0	0	0
BUDG21	Budgerigar	Newry	15/8/92	A	F			no	0	0	0	0	0	0	0	0	0
BUDG22	Budgerigar	Newry	15/8/92	A	M			no	0	0	0	0	0	0	0	0	0
BUDG23	Budgerigar	Newry	15/8/92	A	M			no	0	0	0	0	0	0	0	0	0
BUDG24	Budgerigar	Newry	15/8/92	A	F			S. tracheacolum	1	0	0	0	0	1	0	0	0
BUDG25	Budgerigar	Newry	15/8/92	A	F			no	0	0	0	0	0	0	0	0	0
BUDG26	Budgerigar	Newry	15/8/92	A	M			no	0	0	0	0	0	0	0	0	0
BUDG27	Budgerigar	Newry	15/8/92	A	F			no	0	0	0	0	0	0	0	0	0

Table 1. Continued, Source and biological details of wild caught birds examined during nasal mite surveys between 1992 and 1994 in the Northern Territory.

Identity	Host Species	Locality	Date	Age	Sex	Weight	Moult	Nasal Mites	Total mites	F	FE	M	D	DF	DFE	DM	DD
BUDG3	Budgerigar	Newry	16/8/92	A	M			no	0	0	0	0	0	0	0	0	0
BUDG4	Budgerigar	Newry	16/8/92	A	M			no	0	0	0	0	0	0	0	0	0
BUDG5	Budgerigar	Newry	16/8/92	A	M			no	0	0	0	0	0	0	0	0	0
BUDG6	Budgerigar	Newry	16/8/92	A	F			S. tracheacolum	1	1	0	0	0	0	0	0	0
BUDG7	Budgerigar	Newry	16/8/92	A	M			no	0	0	0	0	0	0	0	0	0
BUDG8	Budgerigar	Newry	16/8/92	A	F			no	0	0	0	0	0	0	0	0	0
BUDG9	Budgerigar	Newry	16/8/92	A	F			no	0	0	0	0	0	0	0	0	0
94-53	Budgerigar	Newry	24/7/94	A	M	31	no	no	0	0	0	0	0	0	0	0	0
94-54	Budgerigar	Newry	24/7/94	A	M	23	yes	no	0	0	0	0	0	0	0	0	0
94-55	Budgerigar	Newry	24/7/94	A	F	28.5	no	no	0	0	0	0	0	0	0	0	0
94-56	Budgerigar	Newry	24/7/94	A	F	25.5	no	no	0	0	0	0	0	0	0	0	0
94-57	Budgerigar	Newry	24/7/94	A	F	29.5	yes	no	0	0	0	0	0	0	0	0	0
94-58	Budgerigar	Newry	24/7/94	A	F	31	yes	no	0	0	0	0	0	0	0	0	0
94-59	Budgerigar	Newry	24/7/94	I	M	26	no	no	0	0	0	0	0	0	0	0	0
94-64	Budgerigar	Newry	27/7/94	A	M	29	no	no	0	0	0	0	0	0	0	0	0
94-65	Budgerigar	Newry	27/7/94	I	F	23.5	no	no	0	0	0	0	0	0	0	0	0
94-78	Budgerigar	Newry	31/7/94	A	M	29	no	S. tracheacolum	1	1	0	0	0	0	0	0	0
94-79	Budgerigar	Newry	31/7/94	A	M	28.5	yes	no	0	0	0	0	0	0	0	0	0
94-80	Budgerigar	Newry	31/7/94	A	M	30	yes	no	0	0	0	0	0	0	0	0	0
94-81	Budgerigar	Newry	31/7/94	A	M	27.5	yes	no	0	0	0	0	0	0	0	0	0
94-82	Budgerigar	Newry	31/7/94	A	M	29.5	no	S. tracheacolum	2	2	0	0	0	0	0	0	0
94-83	Budgerigar	Newry	31/7/94	A	F	28.5	no	no	0	0	0	0	0	0	0	0	0
94-84	Budgerigar	Newry	31/7/94	A	M	28.5	no	no	0	0	0	0	0	0	0	0	0

Table 1. Continued, Source and biological details of wild caught birds examined during nasal mite surveys between 1992 and 1994 in the Northern Territory.

Identity	Host Species	Locality	Date	Age	Sex	Weight	Moult	Nasal Mites	Total mites	F	FE	M	D	DF	DFE	DM	DD
94-85	Budgerigar	Newry	31/7/94	A	M	30	yes	no	0	0	0	0	0	0	0	0	0
94-86	Budgerigar	Newry	8/03/94	A	F	29	no	no	0	0	0	0	0	0	0	0	0
94-87	Budgerigar	Newry	8/04/94	A	M	28.5	yes	no	0	0	0	0	0	0	0	0	0
94-88	Budgerigar	Newry	8/03/94	A	F	26.5	yes	no	0	0	0	0	0	0	0	0	0
94-89	Budgerigar	Newry	8/04/94	A	M	26	no	no	0	0	0	0	0	0	0	0	0
94-108	Budgerigar	Newry	8/12/94	I	F	26	no	S. tracheacolum	2	0	1	0	0	1	0	0	0
94-112	Budgerigar	Newry	13/8/94	A	M	27	no	no	0	0	0	0	0	0	0	0	0
94-113	Budgerigar	Newry	13/8/94	I	M	26	no	no	0	0	0	0	0	0	0	0	0
94-114	Budgerigar	Newry	13/8/94	I	M	25	no	no	0	0	0	0	0	0	0	0	0
94-115	Budgerigar	Newry	13/8/94	I	F	26	no	S. tracheacolum	2	0	0	0	0	1	1	0	0
94-116	Budgerigar	Newry	13/8/94	J	M	25	no	no	0	0	0	0	0	0	0	0	0
94-117	Budgerigar	Newry	13/8/94	A	M	29.5	no	no	0	0	0	0	0	0	0	0	0
94-118	Budgerigar	Newry	13/8/94	J	F	27	no	no	0	0	0	0	0	0	0	0	0
94-119	Budgerigar	Newry	13/8/94	J	M	26	no	no	0	0	0	0	0	0	0	0	0
94-120	Budgerigar	Newry	13/8/94	J	M	27	no	no	0	0	0	0	0	0	0	0	0
94-121	Budgerigar	Newry	13/8/94	J	F	26	no	no	0	0	0	0	0	0	0	0	0
94-122	Budgerigar	Newry	13/8/94	I	M	25.5	no	no	0	0	0	0	0	0	0	0	0
DB73	Double-barred Finch	Newry	23/7/93	A	F	9.5	yes	no	0	0	0	0	0	0	0	0	0
DOUB1	Double-barred Finch	Newry	20/8/92	A	F			no	0	0	0	0	0	0	0	0	0
94-62	Double-barred Finch	Newry	25/7/94	A	F	6.5	no	no	0	0	0	0	0	0	0	0	0
94-63	Double-barred Finch	Newry	25/7/94	A	F	8	yes	P. astridae	2	2	0	0	0	0	0	0	0
94-123	Double-barred Finch	Newry	20.8.94	A	M	7.5	yes	no	0	0	0	0	0	0	0	0	0
94-124	Double-barred Finch	Newry	20/8/94	A	F	7	no	no	0	0	0	0	0	0	0	0	0

Table 1. Continued, Source and biological details of wild caught birds examined during nasal mite surveys between 1992 and 1994 in the Northern Territory.

Identity	Host Species	Locality	Date	Age	Sex	Weight	Moult	Nasal Mites	Total mites	F	FE	M	D	DF	DFE	DM	DD
94-142	Double-barred Finch	Timber Creek		A	F	7	no	no	0	0	0	0	0	0	0	0	0
94-144	Double-barred Finch	Timber Creek		A	F	8	no	no	0	0	0	0	0	0	0	0	0
94-145	Double-barred Finch	Timber Creek		A	F	8.5	no	P. astridae	4	3	0	0	1	0	0	0	0
GF146	Gouldian Finch	Newry	8/10/93	J	F	10.5	no	S. tracheacolum	53	38	8	1	6	0	0	0	0
GF18	Gouldian Finch	Newry	20/7/93	I	M	10.5	no	no	0	0	0	0	0	0	0	0	0
GF2	Gouldian Finch	Newry	15/7/93	I	F	11.5	no	S. tracheacolum	6	0	3	0	3	0	0	0	0
94-140	Gouldian Finch	Timber Creek		J	F	13.5	no	no	0	0	0	0	0	0	0	0	0
GF109	Gouldian Finch	Yinberrie	20/7/93	J		130	no	no	0	0	0	0	0	0	0	0	0
GF110	Gouldian Finch	Yinberrie	16/8/92	A	M	14	yes	S. tracheacolum	2	1	0	0	1	0	0	0	0
GF111	Gouldian Finch	Yinberrie	16/8/92	J	F	13	yes	S. tracheacolum	46	26	7	0	3	10	0	0	0
GF111	Gouldian Finch	Yinberrie	16/8/92	J	F	13	yes	S. paddae	1	0	0	0	1	0	0	0	0
GF112	Gouldian Finch	Yinberrie	16/8/92	J	M	11	yes	S. tracheacolum	51	34	13	0	1	1	0	0	2
GF147	Gouldian Finch	Yinberrie	8/04/93	J		11	no	no	0	0	0	0	0	0	0	0	0
GF41	Gouldian Finch	Yinberrie	29/6/93	I	M	13.5	no	no	0	0	0	0	0	0	0	0	0
GF42	Gouldian Finch	Yinberrie	29/6/93	I	M	14.5	yes	no	0	0	0	0	0	0	0	0	0
GF43	Gouldian Finch	Yinberrie	29/6/93	I	F	17	no	no	0	0	0	0	0	0	0	0	0
GF44	Gouldian Finch	Yinberrie	29/6/93	I	M	14.5	no	no	0	0	0	0	0	0	0	0	0
GF45	Gouldian Finch	Yinberrie	29/6/93	I	M	15.5	yes	S. tracheacolum	4	0	4	0	0	0	0	0	0
GF46	Gouldian Finch	Yinberrie	29/6/93	I	M	16	no	S. tracheacolum	14	6	7	0	1	0	0	0	0
GF47	Gouldian Finch	Yinberrie	29/6/93	I	M	17.5	no	no	0	0	0	0	0	0	0	0	0
GF48	Gouldian Finch	Yinberrie	29/6/93	I	M	14.5	no	S. tracheacolum	56	20	27	0	9	0	0	0	0
GF49	Gouldian Finch	Yinberrie	29/6/93	I	F	14	no	no	0	0	0	0	0	0	0	0	0
GF50	Gouldian Finch	Yinberrie	29/6/93	I	M	14	no	S. tracheacolum	2	2	0	0	0	0	0	0	0

Table 1. Continued, Source and biological details of wild caught birds examined during nasal mite surveys between 1992 and 1994 in the Northern Territory.

Identity	Host Species	Locality	Date	Age	Sex	Weight	Moult	Nasal Mites	Total mites	F	FE	M	D	DF	DFE	DM	DD
GF19	Gouldian Finch	Newry	23/7/93	J	M	14.5	no	no	0	0	0	0	0	0	0	0	0
LONG1	Long-tailed Finch	Newry	13/8/92	A				no	0	0	0	0	0	0	0	0	0
LONG11	Long-tailed Finch	Newry	20/8/92	A	F			no	0	0	0	0	0	0	0	0	0
LONG12	Long-tailed Finch	Newry	21/8/92	A	M			no	0	0	0	0	0	0	0	0	0
LONG13	Long-tailed Finch	Newry	14/8/92	A	M			K. andrei	1	1	0	0	0	0	0	0	0
LONG14	Long-tailed Finch	Newry	16/8/92	A	F			no	0	0	0	0	0	0	0	0	0
LONG15	Long-tailed Finch	Newry	16/8/92	A	M			no	0	0	0	0	0	0	0	0	0
LONG16	Long-tailed Finch	Newry	16/8/92	A	M			no	0	0	0	0	0	0	0	0	0
LONG2	Long-tailed Finch	Newry	16/8/92	A	F			no	0	0	0	0	0	0	0	0	0
LONG3	Long-tailed Finch	Newry	19/8/92	A	F			no	0	0	0	0	0	0	0	0	0
LT10	Long-tailed Finch	Newry	17/7/93	A	M	14		no	0	0	0	0	0	0	0	0	0
LT100	Long-tailed Finch	Newry	22/7/93	A	F	13.5	yes	no	0	0	0	0	0	0	0	0	0
LT101	Long-tailed Finch	Newry	22/7/93	A	F	13	no	no	0	0	0	0	0	0	0	0	0
LT102	Long-tailed Finch	Newry	22/7/93	A	F	12.5	no	P. astridae	4	1	2	0	1	0	0	0	0
LT103	Long-tailed Finch	Newry	22/7/93	A	F	13.5	yes	no	0	0	0	0	0	0	0	0	0
LT104	Long-tailed Finch	Newry	22/7/93	A	F	13.5	yes	no	0	0	0	0	0	0	0	0	0
LT105	Long-tailed Finch	Newry	22/7/93	A	M	13	no	no	0	0	0	0	0	0	0	0	0
LT106	Long-tailed Finch	Newry	22/7/93	A	M	13.5	yes	no	0	0	0	0	0	0	0	0	0
LT144	Long-tailed Finch	Newry	8/11/93	A	M	13	yes	no	0	0	0	0	0	0	0	0	0
LT15	Long-tailed Finch	Newry	20/7/93	A	F	13.5	yes	P. astridae	2	0	2	0	0	0	0	0	0
LT16	Long-tailed Finch	Newry	19/7/93	A	M	15	no	no	0	0	0	0	0	0	0	0	0
LT17	Long-tailed Finch	Newry	19/7/93	A	M	16.5	no	P. astridae	7	5	0	1	1	0	0	0	0
LT23	Long-tailed Finch	Newry	25/7/93	A	F	14.5	no	no	0	0	0	0	0	0	0	0	0

Table 1. Continued, Source and biological details of wild caught birds examined during nasal mite surveys between 1992 and 1994 in the Northern Territory.

Identity	Host Species	Locality	Date	Age	Sex	Weight	Moult	Nasal Mites	Total mites	F	FE	M	D	DF	DFE	DM	DD
LT3	Long-tailed Finch	Newry	15/7/93	A	M	14		no	0	0	0	0	0	0	0	0	0
LT32	Long-tailed Finch	Newry	20/7/93	A	F	13.5	yes	no	0	0	0	0	0	0	0	0	0
LT33	Long-tailed Finch	Newry	19/7/93	A	M	15	yes	no	0	0	0	0	0	0	0	0	0
LT38	Long-tailed Finch	Newry	23/7/93	A	M	14.5	yes	no	0	0	0	0	0	0	0	0	0
LT39	Long-tailed Finch	Newry	23/7/93	A	M	13	yes	no	0	0	0	0	0	0	0	0	0
LT57	Long-tailed Finch	Newry	21/7/93	A	F	13.5	yes	no	0	0	0	0	0	0	0	0	0
LT58	Long-tailed Finch	Newry	28/7/93	I	M	15.5	no	no	0	0	0	0	0	0	0	0	0
LT69	Long-tailed Finch	Newry	27/7/93	A	F	13	yes	no	0	0	0	0	0	0	0	0	0
LT70	Long-tailed Finch	Newry	27/7/93	A	M	14.5	yes	no	0	0	0	0	0	0	0	0	0
LT71	Long-tailed Finch	Newry	29/7/93	A	F	15.5	yes	P. astridae	12	1	9	1	0	1	0	0	0
LT72	Long-tailed Finch	Newry	23/7/93	A	M	12	yes	no	0	0	0	0	0	0	0	0	0
LT74	Long-tailed Finch	Newry	23/7/93	A	M	14	yes	no	0	0	0	0	0	0	0	0	0
LT88	Long-tailed Finch	Newry	22/7/93	A	M	13.5	yes	no	0	0	0	0	0	0	0	0	0
LT89	Long-tailed Finch	Newry	22/7/93	A	M	13.5	no	no	0	0	0	0	0	0	0	0	0
LT9	Long-tailed Finch	Newry	17/7/93	A	M	14.5		no	0	0	0	0	0	0	0	0	0
LT90	Long-tailed Finch	Newry	22/7/93	A	F	14.5	yes	no	0	0	0	0	0	0	0	0	0
94-17	Long-tailed Finch	Newry	17/7/94	A	M	12.5	yes	no	0	0	0	0	0	0	0	0	0
94-9	Long-tailed Finch	Newry	17/7/94	A	M	14	no	no	0	0	0	0	0	0	0	0	0
94-5	Long-tailed Finch	Newry	17/7/94	A	F	11	no	no	0	0	0	0	0	0	0	0	0
94-1	Long-tailed Finch	Newry	18/7/94	A	F	14	yes	no	0	0	0	0	0	0	0	0	0
94-2	Long-tailed Finch	Newry	18/7/94	A	M	14.5	no	no	0	0	0	0	0	0	0	0	0
94-3	Long-tailed Finch	Newry	17/7/94	A	M	13.5	yes	no	0	0	0	0	0	0	0	0	0
94-4	Long-tailed Finch	Newry	17/7/94	A	F	12.5	yes	no	0	0	0	0	0	0	0	0	0

Table 1. Continued, Source and biological details of wild caught birds examined during nasal mite surveys between 1992 and 1994 in the Northern Territory.

Identity	Host Species	Locality	Date	Age	Sex	Weight	Moult	Nasal Mites	Total mites	F	FE	M	D	DF	DFE	$\overline{DM}$	DD
94-6	Long-tailed Finch	Newry	17/7/94	A	F	15	yes	no	0	0	0	0	0	0	0	0	0
94-7	Long-tailed Finch	Newry	17/7/94	A	F	15	yes	no	0	0	0	0	0	0	0	0	0
94-8	Long-tailed Finch	Newry	17/7/94	A	F	15.5	no	no	0	0	0	0	0	0	0	0	0
94-12	Long-tailed Finch	Newry	17/7/94	A	F	13.5	no	no	0	0	0	0	0	0	0	0	0
94-13	Long-tailed Finch	Newry	17/7/94	A	M	15	no	no	0	0	0	0	0	0	0	0	0
94-14	Long-tailed Finch	Newry	17/7/94	I	F	12	no	no	0	0	0	0	0	0	0	0	0
94-15	Long-tailed Finch	Newry	17/7/94	A	M	14	no	P. astridae	1	1	0	0	0	0	0	0	0
94-16	Long-tailed Finch	Newry	17/7/94	A	F	13	no	no	0	0	0	0	0	0	0	0	0
94-18	Long-tailed Finch	Newry	17/7/94	A	F	13.5	yes	no	0	0	0	0	0	0	0	0	0
94-24	Long-tailed Finch	Newry	21/7/94	A	M	13	yes	P. astridae	20	8	3	7	2	0	0	0	0
94-25	Long-tailed Finch	Newry	21/7/94	A	M	13	yes	P. astridae	8	5	1	1	1	0	0	0	0
94-26	Long-tailed Finch	Newry	21/7/94	A	M	16	yes	no	0	0	0	0	0	0	0	0	0
94-27	Long-tailed Finch	Newry	21/7/94	A	F	14	no	no	0	0	0	0	0	0	0	0	0
94-34	Long-tailed Finch	Newry	22/7/94	A	M	13.5	no	no	0	0	0	0	0	0	0	0	0
94-35	Long-tailed Finch	Newry	22/7/94	A	F	14.5	yes	no	0	0	0	0	0	0	0	0	0
94-36	Long-tailed Finch	Newry	22/7/94	A	F	13.5	yes	no	0	0	0	0	0	0	0	0	0
94-37	Long-tailed Finch	Newry	22/7/94	A	F	15	yes	no	0	0	0	0	0	0	0	0	0
94-38	Long-tailed Finch	Newry	22/7/94	A	F	14.5	no	no	0	0	0	0	0	0	0	0	0
94-39	Long-tailed Finch	Newry	22/7/94	A	M	14	yes	no	0	0	0	0	0	0	0	0	0
94-41	Long-tailed Finch	Newry	22/7/94	A	M	13	yes	P. astridae	5	3	2	0	0	0	0	0	0
94-46	Long-tailed Finch	Newry	22/7/94	A	M	12.5	yes	no	0	0	0	0	0	0	0	0	0
94-48	Long-tailed Finch	Newry	22/7/94	A	F	13	no	no	0	0	0	0	0	0	0	0	0
94-49	Long-tailed Finch	Newry	22/7/94	A	M	14	yes	no	0	0	0	0	0	0	0	0	0

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Identity	Host Species	Locality	Date	Age	Sex	Weight	Moult	Nasal Mites	Total mites	F	FE	M	D	DF	DFE	DM	DD
94-50	Long-tailed Finch	Newry	22/7/94	A	F	13.5	no	no	0	0	0	0	0	0	0	0	0
94-125	Long-tailed Finch	Newry	20/8/94	A	F	11.5	no	P. astridae	6	4	0	2	0	0	0	0	0
94-131	Long-tailed Finch	Newry	22/8/94	A	M	13.5	yes	no	0	0	0	0	0	0	0	0	0
94-141	Long-tailed Finch	Timber Creek		A	F	13.5	no	no	0	0	0	0	0	0	0	0	0
94-146	Long-tailed Finch	Timber Creek		I	F	12.5	no	P. astridae	1	0	0	1	0	0	0	0	0
LONG10	Long-tailed Finch	Yinberrie	16/8/92	A	M			P. neochmiae	3	1	1	1	0	0	0	0	0
LONG5	Long-tailed Finch	Yinberrie	16/8/92	A	F			P. neochmiae	1	1	0	0	0	0	0	0	0
LONG6	Long-tailed Finch	Yinberrie	16/8/92	A	F			P. neochmiae	1	1	0	0	0	0	0	0	0
LONG7	Long-tailed Finch	Yinberrie	16/8/92	A	M			S. paddae	1	0	0	0	1	0	0	0	0
LONG8	Long-tailed Finch	Yinberrie	16/8/92	A	F			no	0	0	0	0	0	0	0	0	0
LONG9	Long-tailed Finch	Yinberrie	16/8/92	A	M			no	0	0	0	0	0	0	0	0	0
LT107	Long-tailed Finch	Yinberrie	20/7/93	A	M	12.5	yes	P. neochmiae	2	2	0	0	0	0	0	0	0
LT108	Long-tailed Finch	Yinberrie	20/7/93	I	M	12.5	no	P. neochmiae	1	1	0	0	0	0	0	0	0
LT113	Long-tailed Finch	Yinberrie	25/7/93	A	M	11.5	yes	no	0	0	0	0	0	0	0	0	0
LT114	Long-tailed Finch	Yinberrie	25/7/93	A	F	14	yes	no	0	0	0	0	0	0	0	0	0
LT119	Long-tailed Finch	Yinberrie	25/7/93	A	F	12	yes	no	0	0	0	0	0	0	0	0	0
LT121	Long-tailed Finch	Yinberrie	25/7/93	A	F	13.5	yes	no	0	0	0	0	0	0	0	0	0
LT123	Long-tailed Finch	Yinberrie	25/7/93	A	M	11	yes	P. astridae	2	0	1	1	0	0	0	0	0
LT124	Long-tailed Finch	Yinberrie	25/9/93	A	M	13	yes	no	0	0	0	0	0	0	0	0	0
LT127	Long-tailed Finch	Yinberrie	30/7/93	A	F	11.5	yes	no	0	0	0	0	0	0	0	0	0
LT128	Long-tailed Finch	Yinberrie	30/7/93	A	F	14	yes	no	0	0	0	0	0	0	0	0	0
LT129	Long-tailed Finch	Yinberrie	30/7/93	I	M	10.5	yes	no	0	0	0	0	0	0	0	0	0
LT143	Long-tailed Finch	Yinberrie	8/10/93	A	F	14	yes	P. neochmiae	1	1	0	0	0	0	0	0	0

Table 1. Continued, Source and biological details of wild caught birds examined during nasal mite surveys between 1992 and 1994 in the Northern Territory.

Identity	Host Species	Locality	Date	Age	Sex	Weight	Moult	Nasal Mites	Total mites	F	FE	M	D	DF	DFE	DM	DD
LT145	Long-tailed Finch	Yinberrie	8/02/93	A	F	14.5	yes	no	0	0	0	0	0	0	0	0	0
94-132	Long-tailed Finch	Yinberrie		A	F		yes	no	0	0	0	0	0	0	0	0	0
94-134	Long-tailed Finch	Yinberrie		A	M		yes	no	0	0	0	0	0	0	0	0	0
94-135	Long-tailed Finch	Yinberrie		A	M		no	no	0	0	0	0	0	0	0	0	0
94-136	Long-tailed Finch	Yinberrie	8/02/94	A	M	13.5	yes	no	0	0	0	0	0	0	0	0	0
94-137	Long-tailed Finch	Yinberrie	8/05/94	A	M	14.5	yes	no	0	0	0	0	0	0	0	0	0
94-138	Long-tailed Finch	Yinberrie	8/03/94	A	F	12.5	no	no	0	0	0	0	0	0	0	0	0
94-139	Long-tailed Finch	Yinberrie	31/8/94	A	M	13.5	no	no	0	0	0	0	0	0	0	0	0
LT122	Long-tailed Finch	Yinberrie	25/7/93	A	M	12.5	yes	P. neochmiae	4	2	2	0	0	0	0	0	0
M142	Masked Finch	Newry	8/09/93	A	M	12	no	K. amandavae	3	3	0	0	0	0	0	0	0
M142	Masked Finch	Newry	8/09/93	A	M	12	no	P. astridae	1	1	0	0	0	0	0	0	0
M24	Masked Finch	Newry	23/7/93	A	M	13	no	K. amandavae	1	1	0	0	0	0	0	0	0
M25	Masked Finch	Newry	23/7/93	A	M	13.5	no	no	0	0	0	0	0	0	0	0	0
M26	Masked Finch	Newry	23/7/93	A	F	13.5	no	K. amandavae	7	5	0	2	0	0	0	0	0
M27	Masked Finch	Newry	22/7/93	A	F	13.5	no	no	0	0	0	0	0	0	0	0	0
M40	Masked Finch	Newry	23/7/93	A	M	12.5	no	P. astridae	1	1	0	0	0	0	0	0	0
M56	Masked Finch	Newry	21/7/93	A	M	15	no	no	0	0	0	0	0	0	0	0	0
M6	Masked Finch	Newry	15/7/93	A	M	12		no	0	0	0	0	0	0	0	0	0
M7	Masked Finch	Newry	15/7/93	A	F	12		no	0	0	0	0	0	0	0	0	0
M79	Masked Finch	Newry	22/7/93	A	M	13.5	no	P. astridae	1	0	0	1	0	0	0	0	0
M80	Masked Finch	Newry	22/7/93	A	M	13	yes	P. astridae	6	2	2	2	0	0	0	0	0
M81	Masked Finch	Newry	22/7/93	A	M	11.5	no	no	0	0	0	0	0	0	0	0	0
M82	Masked Finch	Newry	22/7/93	I	F	12.5	no	P. astridae	4	1	0	2	1	0	0	0	0

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Identity	Host Species	Locality	Date	Age	Sex	Weight	Moult	Nasal Mites	Total mites	F	FE	M	D	DF	DFE	DM	DD
M83	Masked Finch	Newry	22/7/93	A	M	13	no	no	0	0	0	0	0	0	0	0	0
M85	Masked Finch	Newry	25/7/93	A	F	11.5	yes	no	0	0	0	0	0	0	0	0	0
M86	Masked Finch	Newry	25/7/93	A	F	12.5	no	P. astridae	3	3	0	0	0	0	0	0	0
M87	Masked Finch	Newry	25/7/93	A	F	12	yes	P. astridae	5	1	0	2	2	0	0	0	0
M93	Masked Finch	Newry	22/7/93	I	F	12.5	no	no	0	0	0	0	0	0	0	0	0
M94	Masked Finch	Newry	22/7/93	A	M	12.5	no	P. astridae	8	4	0	2	2	0	0	0	0
M95	Masked Finch	Newry	22/7/93	A	M	12	no	P. astridae	2	1	0	0	0	1	0	0	0
M96	Masked Finch	Newry	22/7/93	A	M	12.5	0	P. astridae	1	1	0	0	0	0	0	0	0
M97	Masked Finch	Newry	22/7/93	A	M	13	no	no	0	0	0	0	0	0	0	0	0
M98	Masked Finch	Newry	22/7/93	A	F	12	no	no	0	0	0	0	0	0	0	0	0
M99	Masked Finch	Newry	22/7/93	I	M	12.5	no	P. astridae	4	2	1	0	0	1	0	0	0
MASK1	Masked Finch	Newry	13/8/92	A	F			no	0	0	0	0	0	0	0	0	0
MASK10	Masked Finch	Newry	19/8/92	A	M			no	0	0	0	0	0	0	0	0	0
MASK11	Masked Finch	Newry	19/8/92	A	M			no	0	0	0	0	0	0	0	0	0
MASK12	Masked Finch	Newry	19/8/92	A	M			S. tracheacolum	1	0	0	0	0	1	0	0	0
MASK13	Masked Finch	Newry	19/8/92	A	F			no	0	0	0	0	0	0	0	0	0
MASK14	Masked Finch	Newry	19/8/92	A	F			P. astridae	4	3	0	0	1	0	0	0	0
MASK17	Masked Finch	Newry	21/8/92	A	M			P. astridae	2	2	0	0	0	0	0	0	0
MASK18	Masked Finch	Newry	21/8/92	A	M			no	0	0	0	0	0	0	0	0	0
MASK19	Masked Finch	Newry	21/8/92	A	M			no	0	0	0	0	0	0	0	0	0
MASK2	Masked Finch	Newry	13/8/92	A	F			P. astridae	4	2	0	1	1	0	0	0	0
MASK20	Masked Finch	Newry	14/8/92	A	M			no	0	0	0	0	0	0	0	0	0
MASK21	Masked Finch	Newry	14/8/92	A	M			P. astridae	11	6	2	2	1	0	0	0	0

Table 1. Continued, Source and biological details of wild caught birds examined during nasal mite surveys between 1992 and 1994 in the Northern Territory.

Identity	Host Species	Locality	Date	Age	Sex	Weight	Moult	Nasal Mites	Total mites	F	FE	M	D	DF	DFE	DM	DD
MASK22	Masked Finch	Newry	15/8/92	A	F			P. astridae	2	1	0	1	0	0	0	0	0
MASK23	Masked Finch	Newry	15/8/92	A	M			no	0	0	0	0	0	0	0	0	0
MASK24	Masked Finch	Newry	16/8/92	A	F			no	0	0	0	0	0	0	0	0	0
MASK25	Masked Finch	Newry	16/8/92	A	F			no	0	0	0	0	0	0	0	0	0
MASK26	Masked Finch	Newry	16/8/92	A	F			no	0	0	0	0	0	0	0	0	0
MASK27	Masked Finch	Newry	16/8/92	A	F			no	0	0	0	0	0	0	0	0	0
MASK28	Masked Finch	Newry	15/8/92	A	F			no	0	0	0	0	0	0	0	0	0
MASK29	Masked Finch	Newry	16/8/92	A	M			no	0	0	0	0	0	0	0	0	0
MASK3	Masked Finch	Newry	16/8/92	A	M			P. astridae	1	1	0	0	0	0	0	0	0
MASK30	Masked Finch	Newry	16/8/92	A	F			no	0	0	0	0	0	0	0	0	0
MASK31	Masked Finch	Newry	16/8/92	A	M			no	0	0	0	0	0	0	0	0	0
MASK4	Masked Finch	Newry	16/8/92	A	F			no	0	0	0	0	0	0	0	0	0
MASK5	Masked Finch	Newry	16/8/92	A	M			P. astridae	3	3	0	0	0	0	0	0	0
MASK6	Masked Finch	Newry	16/8/92	A	M			no	0	0	0	0	0	0	0	0	0
MASK7	Masked Finch	Newry	16/8/92	A	F			no	0	0	0	0	0	0	0	0	0
MASK8	Masked Finch	Newry	18/8/92	A	M			no	0	0	0	0	0	0	0	0	0
MASK9	Masked Finch	Newry	20/8/92	A	F			P. astridae	8	4	3	1	0	0	0	0	0
94-10	Masked Finch	Newry	17/7/94	A	M	13.5	no	no	0	0	0	0	0	0	0	0	0
94-11	Masked Finch	Newry	17/7/94	I	M	12.5	no	P. astridae	5	2	1	1	1	0	0	0	0
94-19	Masked Finch	Newry	21/7/94	A	M	12.5	no	P. astridae	1	1	0	0	0	0	0	0	0
94-20	Masked Finch	Newry	21/7/94	A	M	13	no	no	0	0	0	0	0	0	0	0	0
94-21	Masked Finch	Newry	21/7/94	A	M	13.5	no	no	0	0	0	0	0	0	0	0	0
94-22	Masked Finch	Newry	21/7/94	A	M	13	no	no	0	0	0	0	0	0	0	0	0

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Identity	Host Species	Locality	Date	Age	Sex	Weight	Moult	Nasal Mites	Total mites	F	FE	M	D	DF	DFE	DM	DD
94-23	Masked Finch	Newry	21/7/94	A	F	12.5	no	K. amandavae	14	11	3	0	0	0	0	0	0
94-40	Masked Finch	Newry	22/7/94	A	M	12.5	no	no	0	0	0	0	0	0	0	0	0
94-45	Masked Finch	Newry	22/7/94	A	F	12.5	no	P. astridae	1	1	0	0	0	0	0	0	0
94-45	Masked Finch	Newry	22/7/94	A	F	12.5	no	K. amandavae	2	2	0	0	0	0	0	0	0
94-47	Masked Finch	Newry	22/7/94	A	F	11.5	no	no	0	0	0	0	0	0	0	0	0
94-51	Masked Finch	Newry	22/7/94	A	M	12	no	P. astridae	3	1	0	2	0	0	0	0	0
94-52	Masked Finch	Newry	22/7/94	A	F	12	no	P. astridae	4	1	1	0	2	0	0	0	0
94-66	Masked Finch	Newry	8/01/94	A	M	13.5	no	no	0	0	0	0	0	0	0	0	0
94-86A	Masked Finch	Newry	8/03/94	A	F	13	no	no	0	0	0	0	0	0	0	0	0
94-109	Masked Finch	Newry	8/12/94	A	F	12.5	no	P. astridae	2	2	0	0	0	0	0	0	0
94-110	Masked Finch	Newry	13/8/94	A	M	12.5	no	no	0	0	0	0	0	0	0	0	0
94-111	Masked Finch	Newry	13/8/94	A	F	15	no	no	0	0	0	0	0	0	0	0	0
94-128	Masked Finch	Newry	21/8/94	A	M	14	no	no	0	0	0	0	0	0	0	0	0
94-129	Masked Finch	Newry	21/8/94	A	M	14	no	no	0	0	0	0	0	0	0	0	0
94-130	Masked Finch	Newry	21/8/94	A	F	13	yes	P. astridae	2	1	0	1	0	0	0	0	0
94-143	Masked Finch	Timber Creek		A	M	11	yes	no	0	0	0	0	0	0	0	0	0
94-147	Masked Finch	Timber Creek		A		10	no	P. astridae	3	2	0	0	1	0	0	0	0
M115	Masked Finch	Yinberrie	25/7/93	A	F	10	no	no	0	0	0	0	0	0	0	0	0
M116	Masked Finch	Yinberrie	25/7/93	A	M	10.5	no	no	0	0	0	0	0	0	0	0	0
M117	Masked Finch	Yinberrie	30/7/93	I	M	11	no	no	0	0	0	0	0	0	0	0	0
M118	Masked Finch	Yinberrie	25/7/93	A	M	12.5	yes	no	0	0	0	0	0	0	0	0	0
M120	Masked Finch	Yinberrie	25/7/93	A	M	12	no	no	0	0	0	0	0	0	0	0	0
M125	Masked Finch	Yinberrie	25/7/93	A	M	11.5	yes	no	0	0	0	0	0	0	0	0	0

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Identity	Host Species	Locality	Date	Age	Sex	Weight	Moult	Nasal Mites	Total mites	F	FE	M	D	DF	DFE	DM	DD
M126	Masked Finch	Yinberrie	25/7/93	I	F	11.5	no	no	0	0	0	0	0	0	0	0	0
M130	Masked Finch	Yinberrie	27/7/93	A	F	12.5	no	S. paddae	3	2	1	0	0	0	0	0	0
M130	Masked Finch	Yinberrie	27/7/93	A	F	12.5	no	P. astridae	1	1	0	0	0	0	0	0	0
MASK15	Masked Finch	Yinberrie	16/8/92	A	M			no	0	0	0	0	0	0	0	0	0
MASK16	Masked Finch	Yinberrie	16/8/92	I	M			no	0	0	0	0	0	0	0	0	0
94-133	Masked Finch	Yinberrie		A	M		yes	no	0	0	0	0	0	0	0	0	0
PIC1	Pictorella Mannikin	Newry	16/6/92	I	M			no	0	0	0	0	0	0	0	0	0
PIC10	Pictorella Mannikin	Newry	16/8/92	I	F			no	0	0	0	0	0	0	0	0	0
PIC11	Pictorella Mannikin	Newry	16/8/92	I	F			no	0	0	0	0	0	0	0	0	0
PIC12	Pictorella Mannikin	Newry	18/8/92	A	F			no	0	0	0	0	0	0	0	0	0
PIC13	Pictorella Mannikin	Newry	20/8/92	A	M			no	0	0	0	0	0	0	0	0	0
PIC14	Pictorella Mannikin	Newry	20/8/92	A	M			no	0	0	0	0	0	0	0	0	0
PIC15	Pictorella Mannikin	Newry	20/8/92	A	F			no	0	0	0	0	0	0	0	0	0
PIC16	Pictorella Mannikin	Newry	20/8/92	I	F			no	0	0	0	0	0	0	0	0	0
PIC17	Pictorella Mannikin	Newry	21/8/92	A	M			S. tracheacolum	1	0	0	0	0	1	0	0	0
PIC18	Pictorella Mannikin	Newry	21/8/92	A	M			no	0	0	0	0	0	0	0	0	0
PIC19	Pictorella Mannikin	Newry	21/8/92	A	M			no	0	0	0	0	0	0	0	0	0
PIC2	Pictorella Mannikin	Newry	16/6/92	A	M			S. tracheacolum	4	4	0	0	0	0	0	0	0
PIC20	Pictorella Mannikin	Newry	21/8/92	A	M			P. emberizae	2	1	1	0	0	0	0	0	0
PIC21	Pictorella Mannikin	Newry	21/8/92	A	F			P. emberizae	3	0	3	0	0	0	0	0	0
PIC22	Pictorella Mannikin	Newry	21/8/92	A	F			P. emberizae	3	1	1	1	0	0	0	0	0
PIC23	Pictorella Mannikin	Newry	21/8/92	A	M			no	0	0	0	0	0	0	0	0	0
PIC24	Pictorella Mannikin	Newry	21/8/92	A	M			P. emberizae	1	1	0	0	0	0	0	0	0

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Identity	Host Species	Locality	Date	Age	Sex	Weight	Moult	Nasal Mites	Total mites	F	FE	M	D	DF	DFE	DM	DD
PIC25	Pictorella Mannikin	Newry	21/8/92	I	M			no	0	0	0	0	0	0	0	0	0
PIC26	Pictorella Mannikin	Newry	20/8/92	A	M			P. emberizae	3	2	0	0	0	1	0	0	0
PIC27	Pictorella Mannikin	Newry	19/8/92	A	F			no	0	0	0	0	0	0	0	0	0
PIC28	Pictorella Mannikin	Newry	19/8/92	A	M			S. tracheacolum	1	1	0	0	0	0	0	0	0
PIC29	Pictorella Mannikin	Newry	18/8/92	A	F			no	0	0	0	0	0	0	0	0	0
PIC3	Pictorella Mannikin	Newry	13/8/92	A	F			S. tracheacolum	1	1	0	0	0	0	0	0	0
PIC30	Pictorella Mannikin	Newry	16/8/92	A	M			no	0	0	0	0	0	0	0	0	0
PIC4	Pictorella Mannikin	Newry	14/8/92	A	M			S. tracheacolum	3	2	0	0	0	1	0	0	0
PIC5	Pictorella Mannikin	Newry	14/8/92	A	F			S. tracheacolum	1	1	0	0	0	0	0	0	0
PIC6	Pictorella Mannikin	Newry	14/8/92	A	F			no	0	0	0	0	0	0	0	0	0
PIC7	Pictorella Mannikin	Newry	14/8/92	A	F			P. emberizae	22	14	3	2	3	0	0	0	0
PIC8	Pictorella Mannikin	Newry	14/8/92	A	M			no	0	0	0	0	0	0	0	0	0
PIC9	Pictorella Mannikin	Newry	16/8/92	A	M			no	0	0	0	0	0	0	0	0	0
PM140	Pictorella Mannikin	Newry	8/06/93	A	M	17	yes	S. tracheacolum	10	3	4	0	3	0	0	0	0
PM141	Pictorella Mannikin	Newry	8/06/93	A	F	15	yes	no	0	0	0	0	0	0	0	0	0
PM20	Pictorella Mannikin	Newry	21/7/93	A	F	14	yes	S. tracheacolum	20	11	5	3	0	1	0	0	0
PM21	Pictorella Mannikin	Newry	25/7/93	A	M	16	no	no	0	0	0	0	0	0	0	0	0
PM22	Pictorella Mannikin	Newry	26/7/93	I	M	14.5	yes	P. emberizae	7	3	3	1	0	0	0	0	0
PM28	Pictorella Mannikin	Newry	27/7/93	A	F	13.5	no	S. tracheacolum	17	4	9	0	2	2	0	0	0
PM29	Pictorella Mannikin	Newry	27/7/93	A	F	13	yes	no	0	0	0	0	0	0	0	0	0
PM30	Pictorella Mannikin	Newry	27/7/93	A	M	13	yes	S. tracheacolum	7	2	4	0	1	0	0	0	0
PM31	Pictorella Mannikin	Newry	27/7/93	I	F	13.5	yes	no	0	0	0	0	0	0	0	0	0
PM34	Pictorella Mannikin	Newry	19/7/93	A	F	15.5	no	no	0	0	0	0	0	0	0	0	0

Table 1. Continued, Source and biological details of wild caught birds examined during nasal mite surveys between 1992 and 1994 in the Northern Territory.

Identity	Host Species	Locality	Date	Age	Sex	Weight	Moult	Nasal Mites	Total mites	F	FE	M	D	DF	DFE	DM	DD
PM35	Pictorella Mannikin	Newry	22/7/93	A	M	13.5	yes	no	0	0	0	0	0	0	0	0	0
PM36	Pictorella Mannikin	Newry	22/7/93	I	F	13.5	no	no	0	0	0	0	0	0	0	0	0
PM37	Pictorella Mannikin	Newry	22/7/93	I	F	13	yes	P. emberizae	6	1	5	0	0	0	0	0	0
PM37	Pictorella Mannikin	Newry	22/7/93	I	F	13	yes	S. tracheacolum	2	2	0	0	0	0	0	0	0
PM68	Pictorella Mannikin	Newry	29/7/93	A	M	15	yes	S. tracheacolum	2	2	0	0	0	0	0	0	0
PM84	Pictorella Mannikin	Newry	25/7/93	I	M	13	yes	S. tracheacolum	22	16	1	0	4	1	0	0	0
94-67	Pictorella Mannikin	Newry	8/01/94	A	F	13.5	yes	S. tracheacolum	2	0	2	0	0	0	0	0	0
94-68	Pictorella Mannikin	Newry	8/01/94	A	M	14	yes	S. tracheacolum	1	1	0	0	0	0	0	0	0
94-69	Pictorella Mannikin	Newry	8/01/94	A	M	15.5	yes	no	0	0	0	0	0	0	0	0	0
94-70	Pictorella Mannikin	Newry	8/01/94	I	M	12.5	yes	P. emberizae	3	3	0	0	0	0	0	0	0
94-71	Pictorella Mannikin	Newry	8/01/94	A	F	16.5	yes	S. tracheacolum	8	6	1	0	0	0	0	0	1
94-72	Pictorella Mannikin	Newry	8/01/94	I	F	13	yes	P. emberizae	1	1	0	0	0	0	0	0	0
94-73	Pictorella Mannikin	Newry	8/01/94	I	M	13	yes	S. tracheacolum	22	9	6	0	5	2	0	0	0
94-73	Pictorella Mannikin	Newry	8/01/94	I	M	13	yes	P. emberizae	23	16	5	2	0	0	0	0	0
94-74	Pictorella Mannikin	Newry	8/01/94	I	F	13	yes	P. emberizae	13	7	5	0	1	0	0	0	0
94-75	Pictorella Mannikin	Newry	8/01/94	I	F	13	yes	P. emberizae	19	8	5	4	2	0	0	0	0
94-76	Pictorella Mannikin	Newry	8/01/94	I	M	13.5	no	P. emberizae	1	0	0	1	0	0	0	0	0
94-76	Pictorella Mannikin	Newry	8/01/94	I	M	13.5	no	S. tracheacolum	27	19	5	0	3	0	0	0	0
94-77	Pictorella Mannikin	Newry	8/01/94	I	M	13.5	yes	P. emberizae	143	67	33	25	18	0	0	0	0
94-90	Pictorella Mannikin	Newry	8/05/94	A	M	15	yes	P. emberizae	5	4	1	0	0	0	0	0	0
94-91	Pictorella Mannikin	Newry	8/05/94	A	M	14	yes	S. tracheacolum	4	4	0	0	0	0	0	0	0
94-92	Pictorella Mannikin	Newry	8/05/94	A	M	14.5	yes	P. emberizae	37	16	9	8	4	0	0	0	0
94-93	Pictorella Mannikin	Newry	8/05/94	A	M	14	yes	no	0	0	0	0	0	0	0	0	0

Table 1. Continued, Source and biological details of wild caught birds examined during nasal mite surveys between 1992 and 1994 in the Northern Territory.

Identity	Host Species	Locality	Date	Age	Sex	Weight	Moult	Nasal Mites	Total mites	F	FE	M	D	DF	DFE	DM	DD
94-94	Pictorella Mannikin	Newry	8/05/94	A	M	14	yes	no	0	0	0	0	0	0	0	0	0
94-95	Pictorella Mannikin	Newry	8/05/94	A	F	13.5	yes	P. emberizae	1	1	0	0	0	0	0	0	0
94-96	Pictorella Mannikin	Newry	8/05/94	I	M	14.5	yes	S. tracheacolum	1	1	0	0	0	0	0	0	0
94-96	Pictorella Mannikin	Newry	8/05/94	I	M	14.5	yes	P. emberizae	17								
94-97	Pictorella Mannikin	Newry	8/05/94	A	M	12.5	yes	no	0	0	0	0	0	0	0	0	0
94-98	Pictorella Mannikin	Newry	8/05/94	A	F	13.5	yes	P. emberizae	17	8	7	2	0	0	0	0	0
94-99	Pictorella Mannikin	Newry	8/05/94	J	F	13.5	yes	P. emberizae	24	8	11	1	4	0	0	0	0
94-100	Pictorella Mannikin	Newry	8/05/94	I	F	13.5	yes	P. emberizae	1	1	0	0	0	0	0	0	0
94-101	Pictorella Mannikin	Newry	8/05/94	I	M	13.5	yes	P. emberizae	46	27	14	3	2	0	0	0	0
94-101	Pictorella Mannikin	Newry	8/05/94	I	M	13.5	yes	S. tracheacolum	1	1	0	0	0	0	0	0	0
94-102	Pictorella Mannikin	Newry	8/05/94	J	M	13	no	P. emberizae	9	2	6	0	1	0	0	0	0
94-103	Pictorella Mannikin	Newry	8/05/94	I	F	13.5	yes	P. emberizae	9	5	4	0	0	0	0	0	0
94-103	Pictorella Mannikin	Newry	8/05/94	I	F	13.5	yes	S. tracheacolum	84	41	17	5	16	5	0	0	0
94-104	Pictorella Mannikin	Newry	8/05/94	J	F	13.5	yes	P. emberizae	129	73	28	11	17	0	0	0	0
94-104	Pictorella Mannikin	Newry	8/05/94	J	F	13.5	yes	S. tracheacolum	3	1	1	0	1	0	0	0	0
94-105	Pictorella Mannikin	Newry	8/05/94	I	M	13	yes	P. emberizae	8	3	3	1	1	0	0	0	0
94-105	Pictorella Mannikin	Newry	8/05/94	I	M	13	yes	S. tracheacolum	4	1	0	0	0	0	3	0	0
94-106	Pictorella Mannikin	Newry	8/05/94	J	M	12.5	yes	P. emberizae	44	21	11	6	6	0	0	0	0
94-107	Pictorella Mannikin	Newry	8/05/94	J		13.5	no	P. emberizae	1	1	0	0	0	0	0	0	0
94-107	Pictorella Mannikin	Newry	8/05/94	J		13.5	no	S. tracheacolum	10	5	3	0	0	1	1	0	0
Z4	Zebra Finch	Newry	15/7/93	A	F	11		no	0	0	0	0	0	0	0	0	0
Z5	Zebra Finch	Newry	15/7/93	A	M	11.5		no	0	0	0	0	0	0	0	0	0
Z59	Zebra Finch	Newry	21/7/93	A	M	12	no	no	0	0	0	0	0	0	0	0	0

Table 1. Continued, Source and biological details of wild caught birds examined during nasal mite surveys between 1992 and 1994 in the Northern Territory.

Identity	Host Species	Locality	Date	Age	Sex	Weight	Moult	Nasal Mites	Total mites	F	FE	M	D	DF	DFE	DM	DD
Z60	Zebra Finch	Newry	21/7/93	A	F	11.5	yes	P. astridae	1	0	0	1	0	0	0	0	0
Z64	Zebra Finch	Newry	21/7/93	A	F	12	yes	no	0	0	0	0	0	0	0	0	0
Z75	Zebra Finch	Newry	23/7/93	A	M	10.5	no	no	0	0	0	0	0	0	0	0	0
Z76	Zebra Finch	Newry	23/7/93	A	M	10.5	yes	P. astridae	3	1	1	0	1	0	0	0	0
Z77	Zebra Finch	Newry	23/7/93	A	F	10.5	yes	P. astridae	9	3	3	1	2	0	0	0	0
Z78	Zebra Finch	Newry	23/7/93	A	F	11.4	yes	no	0	0	0	0	0	0	0	0	0
Z91	Zebra Finch	Newry	22/7/93	A	M	10.5	yes	Sternostoma sp.	1	0	0	0	1	0	0	0	0
Z92	Zebra Finch	Newry	22/7/93	A	F	11.5	no	no	0	0	0	0	0	0	0	0	0
94-28	Zebra Finch	Newry	21/7/94	A	M	10.5	yes	no	0	0	0	0	0	0	0	0	0
94-29	Zebra Finch	Newry	21/7/94	A	M	10.5	yes	no	0	0	0	0	0	0	0	0	0
94-31	Zebra Finch	Newry	21/7/94	A	M	11.5	yes	no	0	0	0	0	0	0	0	0	0
94-32	Zebra Finch	Newry	21/7/94	A	M	10.5	yes	no	0	0	0	0	0	0	0	0	0
94-33	Zebra Finch	Newry	21/7/94	A	F	11	yes	P. astridae	1	0	0	1	0	0	0	0	0
94-42	Zebra Finch	Newry	22/7/94	A	M	10.5	no	no	0	0	0	0	0	0	0	0	0
94-43	Zebra Finch	Newry	22/7/94	A	F	11.5	no	no	0	0	0	0	0	0	0	0	0
94-44	Zebra Finch	Newry	22/7/94	A	F	10	no	no	0	0	0	0	0	0	0	0	0
94-60	Zebra Finch	Newry	25/7/94	A	F	11	no	no	0	0	0	0	0	0	0	0	0
94-61	Zebra Finch	Newry	25/7/94	A	F	11.5	no	P. astridae	27	13	8	4	2	0	0	0	0
94-126	Zebra Finch	Newry		J	M	10.5	yes	no	0	0	0	0	0	0	0	0	0
94-127	Zebra Finch	Newry	21/8/94	A	M	10.5	no	no	0	0	0	0	0	0	0	0	0
94-30	Zebre Finch	Newry	21/7/94	A	F	11.5	yes	no	0	0	0	0	0	0	0	0	0

APPENDIX V.

Table 1. Host specificity of *Sternostoma* in wild birds.

Parasite	Host Group	References
Sternostoma angrensis Castro	PASSERIFORMES Hirundinidae	Castro (1948)
Sternostoma augei Amaral	STRIGIFORMES Strigidae	Amaral (1962), Pence & Castro (1975)
Sternostoma batis (Fain)	PASSERIFORMES Muscicapidae	Fain (1962)
Sternostoma borceanum Feider & Mironescu	PASSERIFORMES Sturnidae	Feider & Mironescu (1968), Feider & Mironescu (1978)
Sternostoma boydi Strandtmann	CHARADRIIFORMES Laridae Scolopacidae	Strandtmann (1951), Strandtmann (1957), Spicer (1978), Fain (1956), Pence (1973c)
Sternostoma chlidoniadis Butenko	CHARADRIIFORMES Laridae	Butenko (1974)
Sternostoma christinae Guevara-Benitez, Lopez-Roman & Ubeda-Ontiveros	PASSERIFORMES Muscicapidae	Guevara-Benitez, Lopez-Roman & Ubeda-Ontiveros (1974)
Sternostoma clementei Amaral	PASSERIFORMES Tyrannidae	Amaral (1968)
Sternostoma colii Fain	COLIIFORMES Coliidae	Furman (1957)
Sternostoma cooremani Fain	CORACIIFORMES Alcedinidae	Fain (1956), Domrow (1965), Domrow (1966), Domrow (1987)
Sternostoma crotophagae Pence & Castro	CUCULIFORMES Cuculidae	
Sternostoma cryptorhynchum Berlese & Trouessart	PASSERIFORMES Passeridae	Furman (1957)
Sternostoma cuculorum Fain	CUCULIFORMES Cuculidae Meropidae	Fain (1956), Domrow (1965), Domrow (1969)
Sternostoma darlingi Spicer	PASSERIFORMES Tyrannidae	Spicer (1984)
Sternostoma dumetellae Pence	PASSERIFORMES Mimidae	Pence (1972)
Sternostoma dureni Fain	PASSERIFORMES Muscicapidae	Fain (1956), Domrow (1969)
Sternostoma epistomata Feider & Mironescu	CHARADRIIFORMES Laridae	Feider & Mironescu (1973)
Sternostoma eurocephali Fain		Fain (1960b)
Sternostoma francolini Fain		Fain (1960c)
Sternostoma fulicae Fain & Bafort	GRUIFORMES Rallidae	Fain & Bafort (1963), Guevara-Benitez & Ubeda-Ontiveros (1975), Butenko (1976)
Sternostoma furmani Strandtmann	GALLIFORMES Phasianidae	Strandtmann (1960)
Sternostoma giganteum Fain	PASSERIFORMES Muscicapidae	Fain (1962)
Sternostoma gliciphilae Domrow	PASSERIFORMES Meliphagidae	Domrow (1966)
Sternostoma guevarai Guevara-Benitez, Ubeda-Ontiveros & Cutillas-Barrios	GALLIFORMES Phasianidae	Guevara-Benitez, Ubeda-Ontiveros & Cutillas-Barrios (1979)
Sternostoma hedonophilum Fain & Aitken		Fain & Aitken (1969b)
Sternostoma hirundinis Fain	PASSERIFORMES Hirundinidae Bombycillidae	Fain (1956), Pence (1972), Pence (1973a)
Sternostoma hutsoni Furman	PASSERIFORMES Muscicapidae	Furman (1957)
Sternostoma hylandi Fain & Johnston	PASSERIFORMES Hirundinidae PICIFORMES Picidae	Hyland (1962), Fain & Johnston (1966)
Sternostoma hirundinis Fain	PASSERIFORMES Hirundinidae	Fain, Herin & Puylaert (1977)

Table 1. Continued, Host specificity of *Sternostoma* in wild birds.

Parasite	Host Group	References
Sternostoma isabelae Ubeda-Ontiveros & Guevara-Benitez	PASSERIFORMES Alaudidae	Ubeda-Ontiveros & Guevara-Benitez (1980)
Sternostoma kelloggi Hyland & Clark	PASSERIFORMES Mimidae	Cerný & Dusbábek (1970), Hyland & Clark (1959), Pence (1972)
Sternostoma kodrensis Shumilo & Lunkashu		Shumilo & Lunkashu (1970)
Sternostoma lagonostictae Fain	PASSERIFORMES Estrildidae	Fain (1956)
Sternostoma laniorum Fain	PASSERIFORMES Laniidae Muscicapidae	Fain (1956), Fain (1957), Feider & Mironescu (1969), Strandtmann (1960), Domrow (1965), Domrow (1966), Pence (1973b),
Sternostoma longisetosa Hyland	PASSERIFORMES Tyrannidae	Hyland (1961), Hyland & Moorhouse (1970), Fain & Aitken (1969)
Sternostoma loxiae Fain	PASSERIFORMES Fringillidae	Fain (1965)
Sternostoma minutus (Bregetova)	CHARADRIIFORMES Charadriidae	Furman (1957)
Sternostoma motacilli Pence	PASSERIFORMES Motocillidae	Pence (1972)
Sternostoma nectarinia Fain	PASSERIFORMES Nectariniidae Dicaeidae	Fain (1956), Strandtmann (1960)
Sternostoma neosittae Domrow	PASSERIFORMES Sittidae	Domrow (1969)
Sternostoma pastor Fain	PASSERIFORMES Sturnidae	Fain (1967), Feider & Mironescu (1978)
Sternostoma pencei Spicer	PASSERIFORMES Tyrannidae	Spicer (1984)
Sternostoma pirangae Pence	PASSERIFORMES Emberizidae	Pence (1973b), Pence & Castro (1975)
Sternostoma porteri Hyland	PICIFORMES Picidae	Hyland (1962), Fain & Johnston (1966) Pence (1972), Pence & Castro (1975),
Sternostoma quiscalis Fain & Aitken	PASSERIFORMES Emberizae	Fain & Aitken (1967)
Sternostoma sayornis Pence and Castro	PASSERIFORMES Tyrannidae	Pence & Castro (1975)
Sternostoma sialiphilus Hyland & Ford	PASSERIFORMES Muscicapidae	Hyland & Ford (1961), Pence (1972)
Sternostoma sinense Fain & Bafort		Fain & Bafort (1963)
Sternostoma sternahirundo Butenko	CHARADRIIFORMES Laridae	Butenko (1974)
Sternostoma stigitis Butenko	STRIGIFORMES Strigidae	Butenko (1976)
Sternostoma straeleni Fain	PASSERIFORMES Sturnidae	Fain (1958), Fain (1962)
Sternostoma strandtmanni Furman	PASSERIFORMES Emberizidae	Furman (1957), Pence (1972)
Sternostoma sturnicola Fain	PASSERIFORMES Sturnidae	Fain (1956)
Sternostoma tangarae Fain & Aitkin	PASSERIFORMES Emberizidae	Fain & Aitkin (1967), Pence (1972)
Sternostoma technaui Vitzthum	PASSERIFORMES Muscicapidae	Vitzthum (1935), Zumpt & Till (1955), Furman (1957), Domrow (1969), Pence (1972), Kadosaka, Kaneko & Asanuma (1987)
Sternostoma thienponti Fain	PASSERIFORMES Cracticidae Dicruridae	Fain (1956), Strandtmann (1960), Domrow (1965), Domrow (1966)
Sternostoma tyrannus Brooks & Strandtmann	PASSERIFORMES Tyrannidae	Brooks & Strandtmann (1960)

Table 1. Continued, Host specificity of *Sternostoma* in wild birds.

Parasite	Host group	References
Sternostoma tracheacolum Lawrence	PSITTACIFORMES Psittacidae PASSERIFORMES Tyrannidae Hirundinidae Sturnidae Motocillidae Muscicapidae Nectarinidae Emberizidae Fringillidae Passeridae Estrildidae	Cumming (1959), Fain & Hyland (1962), Černý (1969), Hyland & Moorhouse (1970), Pence (1972), Tidemann *et al.* (1992), Domrow (1992)
Sternostoma ubedai Ubeda-Ontíveros & Guevara-Benítez	PASSERIFORMES Muscicapidae	Ubeda-Ontíveros & Guevara-Benítez (1981)
Sternostoma zosteropus Domrow	PASSERIFORMES Zosteropidae	Domrow (1966)
Sternostoma sp.	CHARADRIIFORMES Laridae	Černý & Dusbábek (1970)

APPENDIX VI.

Survey of Budgerigar and Pictorella Mannikin museum spirit specimens for *S. tracheacolum*

In an attempt to gain historical evidence on the duration of the *S. tracheacolum*/ wild Gouldian Finch association Tidemann *et al.* (1992) sought to examine Gouldian Finch spirit specimens held in Australian and overseas collections. Although the 'World Inventory of Avian Spirit Specimens' listed 127 specimens (Wood, Zusi & Jenkinson, 1982), inquiries revealed all specimens to be either from captive bred stock or of unknown history.

Following the discovery of *S. tracheacolum* in the Budgerigar and a high prevalence of the same parasite in the Pictorella Mannikin in the present study, alcoholic specimens of these species were sought for examination. Wood *et al.* (1982) lists 128 Budgerigar and 15 Pictorella Mannikin spirit specimens held in various collections throughout the world.

The majority of Pictorella Mannikin and Budgerigar spirit specimens held in museums come from captive reared stock. However, in addition to the specimens examined here (see Table 1), the following wild caught specimens are confirmed by inquiry to be held in Australian and overseas collections.

The British Museum (Natural History) Tring, Hertfordshire holds 8 wild caught specimens of Pictorella Mannikin collected from Mount Anderson, Kimberley, WA in 1969 and 7 wild caught specimens of Budgerigar collected from Prarie, North Qld. in 1925 (5 specimens), Chichester Range, WA in 1966 (1 specimen) and Quilpie, South Qld. in 1964 (1 specimen).

The American Museum of Natural History, New York holds 5 spirit specimens of Budgerigar collected from Broadhurst Range, WA in 1972 (1 specimen), Birdsville Track, SA in 1974 (1 specimen) and Lyndhurst, SA in 1974 (3 specimens).

The Queensland Museum, South Brisbane holds 3 spirit specimens of Budgerigar collected from Dynevor Downs, Qld. in 1975 (2 specimens) and Taroom, Qld. in 1978 (1 specimen).

The South Australian Museum, Adelaide holds 13 wild caught Budgerigars collected from Koolunga, SA in 1983 (1 specimen), Etadunna Homestead, SA in 1984 and 1985 (5 specimens), Mabel Creek Station, SA in 1984 (5 specimens), Cooper Creek Crossing, SA in 1985 (1 specimen) and Point Bell, SA in 1986 (1 specimen).

No evidence of *S. tracheacolum* infection was found in 12 Budgerigars and 2 Pictorella Mannikins examined (see Table 1). To maintain the integrity of the spirit specimens, only the airsacs, trachea syrinx and bronchi were examined. The nasal cavity, buccal cavity and the lungs were not dissected.

Table 1. Spirit specimens of Pictorella Mannikin and Budgerigar examined for the presence of *S. tracheacolum*

Collection	Species/ Specimen No.	Sex	Date of collection	Locality of capture
	Budgerigar			
Museums and Art Galleries of the NT, Darwin, NT	T2874 (B30)	not known	4 July 1972	Alice Springs, NT
"	T2881 (5129)	"	14 January 1970	Hamilton River, Qld.
C.S.I.R.O., Canberra, ACT	14488	female	26 January 1972	Lake Cowal, NSW
	17489	male	26 January 1972	Lake Cowal, NSW
"	17481	female	June 1974	Barkly Tableland, NT
Australian Museum, Sydney, NSW	AM58138	not known	14 November 1984	Willandra Lakes, NSW
"	AM58137	"	"	"
"	AM57813	male	5 February 1984	Carrathool, NSW
National Museum of Natural History, Smithsonian Institute, USA	227083	male	5 January 1920	Farina, SA
"	227084	female	"	"
Museum of Victoria, Abbotsford, Vic	B12351	male	12 October 1974	Cockburn, SA
"	B12352	female	12 October 1974	"
	Pictorella Mannikin			
C.S.I.R.O., Canberra, ACT	17476	female	June 1974	Barkly Tableland, NT
"	17182	male	2 June 1974	Gulf district, Qld.