

**ASPECTS OF THE
POPULATION ECOLOGY OF THE LONG-NOSED POTOROO,
Potorous tridactylus (KERR, 1792),
IN SOUTHEASTERN TASMANIA.**

by

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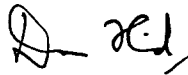
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March 1996.

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Don Hird.

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Abstract :

Aspects of the Population Ecology of the Long-Nosed Potoroo.

The aim of this study was to describe the population parameters of a natural population of the long-nosed potoroo. The study was designed to be longitudinal in order to collect data over the entire lifespans of at least some individuals. Parameters of special interest were body mass and its relation to seasonality and home-range, survivorship, female reproductive activity in relation to maternal age, seasonality and breeding interval, and capture rates in relation to microhabitat.

Capture / recapture data was systematically collected from a study area of approximately 35 ha at Porter Hill, five km southeast of Hobart. The study was designed to be longitudinal, potentially across generations of potoroos, and to also collect data for two syntopic species, the brown bandicoot and eastern bettong.

A grid of ten transects, each of 20 sites, was trapped. Each trapping session was comprised of a transect trapped on two successive nights, with distant transects being trapped at successive sessions to minimise potential trapping impact on individual animals. Data from 134 such sessions form the basis of the thesis, some subsidiary data was also collected to supplement individual longevity data.

Trappability of potoroos at Porter Hill was high compared with studies of potoroos on mainland Australia. Adult potoroos had a persistent male-biased sex ratio over time. Sexual dimorphism was evident, with males having significantly greater body mass (based on both mean adult and maximum body mass) than females. Captures in traps occupied at a trap site on a previous night were sex-biased, with intra-sex avoidance of traps. Breeding in potoroos was aseasonal. Mean population density based on known-to-be-alive data for each sex was estimated to be 0.7 individuals ha⁻¹. A life table and survivorship curve are presented. Longevity patterns indicated uneven survivorship, with first-year mortality of around 80%, and some individuals living to eight years of age.

Microhabitat selection was examined in relation to floristic diversity and vegetation structure. Sites were grouped on the basis of an agglomerative classification of floristic

data, and analysis of variance was used to determine whether significant between-group differences in capture rates occurred. Vegetation groups were described, and appeared to vary with physical attributes of the local area. Significantly higher potoroo capture rates were obtained from one of the ten groups; a group comprised of floristically depauperate sites of open vegetation structure.


Home range was examined using kernel analysis. A threshold number of captures which yielded a range asymptotic to the full home range area was determined by taking repeated random samples of differing sizes from individual capture-site data. Individuals with at least the threshold number of captures were examined further. Males had significantly larger home ranges than females, although considerable individual variation in home-range was also evident. Considerable overlap of both male and female home ranges occurred. The implications of these and related data for mating systems in the potoroo are discussed.

The results are discussed in terms of the imputed mating system and trophic ecology of potoroos. Poroos exploit a dispersed food resource, primarily hypogeal fungi. This, together with aseasonal breeding, is suggested to have led to a mating system where males have undergone sexual selection in body mass and home-range behaviour in order to search for and compete for access to receptive females. This social system is discussed in relation to that of other potoroids and comparable marsupials.

Don HIRD.

Statement of Responsibility

The material presented in this thesis has not been submitted for the award of any degree or diploma in any university. To the best of my knowledge and belief the thesis contains no material previously published or written by another person except where due reference is made in the text of the thesis.

A handwritten signature in black ink, appearing to read 'Don Hird', followed by a period.

Don Hird

Acknowledgements

My inspiration in natural history and science derives from parental guidance. An early introduction to the habitats such as Victoria's Grampians, Croajingalong and Wilson's Promontory was a great privilege. Further development of this interest was stimulated by explorers of earlier generations, amongst whom Charles Darwin, John Gould, Norman Wakefield, David Fleay, Jim Willis and Michael Sharland deserve mention. Their sense of value in interpreting the natural world is a continuing beacon.

More recently Tasmanian environments have been a source of both inspiration, and anguish as they disappear. Again it is fellow naturalists; they can't all be named here but they know who they are, who continue the flare of interest. A special mention is to the Tas FieldNats Wildlife Survey team.

This project was originally designed to be exploratory; of a marsupial community over time. This represents a less reductionist approach, in both the methodological and environmental senses, than many studies. Practical and interpretive difficulties are inherent but surmountable in this sort of approach, and I believe such studies are a necessary complement to more specialised biology. I take full responsibility for this aspect of the study.

Joan and the late Esmond Dorney, of Porter Hill, have encouraged ecological studies there over four decades. Their genuine interest as well as their essential permission to use the protected study area, have been vital to my work. The emergency baby-sitting and after dark assistance with flat batteries was a bonus !

This has been shoestring biology. University of Tasmania Zoology Department lent the traps and provided some ear tags, computing access and occasional desk space. All other expenses including the cost of transport, baits, and some of the tags were borne by our family budget.

Othmar Buchmann encouraged the study at its inception, following his earlier work and that of Dr Eric Guiler, at Porter Hill. More recently Dr Mark Hindell supervised the writing up and interpretation of results, with considerable skill and patience. Dr Peter McQuillan, University of Tasmania Geography and Environmental Studies Department, assisted over the years with ideas on integrating and articulating different threads of Tasmanian ecology, and its often urgent need for protection. For earlier academic inspiration I mention Drs Tony Lee and Gordon Sanson (Monash), and Ric How, Bill Humphries and Richard Zann (LaTrobe). The Tasmanian Land Information Bureau provided a digitised map of the study area region.

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Lastly I thank those marsupial dark horses, the potoroos. Their outrageous gall at not being rare, endangered, pests to humans, extinct like thylacines, cuddly like koalas or Disneyesque like Tasmanian Devils, makes them quiet achievers in the modern wreck of marsupial conservation. Long may they bound !

Don Hird.

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Chapter One.

Biology of the Long-nosed Potoroo, *Potorous tridactylus* (Kerr, 1792)

Introduction.

This study is of a Tasmanian population of the long-nosed potoroo, *Potorous tridactylus* (Kerr, 1792). Sometimes known as rat-kangaroos from their general body form, potoroos are small marsupials with adults weighing from 0.7 to 1.4 kg. Body mass varies over the wide geographic range of the species which, as well as including most of lowland Tasmania, includes coastal eastern Australia from Victoria to southern Queensland. A small disjunct population, known as Gilbert's potoroo, *Potorous tridactylus gilberti* occurs in south-western Western Australia.

Potoroos are generally dark rufous brown to grey, sometimes with paler fur underneath the body and with a white tail tip. They have a long, tapering snout and robust forelimbs with spathulate claws adapted for digging for plant and invertebrate food, their predominant diet. The tail is short in comparison with that of kangaroos and wallabies generally. Potoroos use a fast gait consisting of short hops with the body held close to the ground, and a slower quadrupedal shuffle. Potoroo behaviour is generally nocturnal and secretive, especially since their usual habitats often include dense heathy or scrubby vegetation.

Prior studies on potoroos have provided estimates of population parameters such as population density, home range and seasonality of breeding. Most of these studies, however, have been based on small datasets, both in terms of numbers of individuals from which data was obtained and from the number of observations on each individual. This study applied similar techniques to those of prior studies, but with the express intention of obtaining larger datasets and thus more rigorous estimates of population parameters.

1.1 Potoroos in History.

The *Poto Roo* of the Port Jackson aborigines is one of relatively few Australian mammals to be honoured with a form of its aboriginal name in its binomial nomenclature and common name (Strahan 1981). First described and illustrated for a European audience by Surgeon-General White in 1790 (White 1790), potoroos were amongst the biological curios of the early settlement of Australia, even though it was the only new macropodoid species described in the early years of settlement (Frith and Calaby 1969). The first description known of an Australian marsupial, a tammar wallaby, had arisen from Pelsaert's *Batavia* journal of 1629, while the first

description of a kangaroo had aroused even greater attention in Europe after the return of Cook's expedition of 1773 (Frith and Calaby 1969).

The species described by White, *Potorous tridactylus* (Kerr, 1792), is now regarded as including the Tasmanian population of the potoroo. The specific name applied by Kerr (1792) was a misnomer based on lack of recognition of the syndactylous second and third toes from White's (1790) illustration. In Tasmania, the first formal recognition of the potoroo was apparently by Waterhouse (1841) (Calaby and Richardson 1989) as *Hypsiprymnus murinus* or the rat-tailed hypsiprymnus.

Waterhouse (1841) also separated the potoroos and bettongs as a family (now known as the Potoroidae) from the kangaroos and wallabies (Macropodidae), on dental characters. The two families of kangaroo-like marsupials are now classified as comprising the superfamily Macropodoidea. Potoroids were clearly known to early settlers in Van Dieman's Land (later Tasmania), e.g. within the first year of settlement the Reverend Robert Knopwood recorded the shooting of "Kangaroo Rabbits" (Nicholls 1977), amongst larger wallabies and kangaroos (Barker and Caughley 1990), for food. Knopwood's animals may have been or included bettongs, *Bettongia gaimardii*, the other potoroid indigenous to Tasmania (including the lower Derwent valley) in historical time.

Distribution of modern potoroids at European settlement in Australia extended over much of Tasmania, and most of the Australian mainland excluding the far north, (Seebeck, Bennett and Scotts 1989). Although the two Tasmanian potoroids also had wide geographic ranges in mesic habitats, species other than the long-nosed potoroo and bettong occupied more arid and subtropical rainforest habitats.

In Tasmania, imputed identification of potoroids by Labillardiere of the D'Entrecasteaux expedition, 1792-3 by Plomley and Piard-Bernier (1993) seem doubtful as the animals in question were consistently described as inhabiting deep burrows; it seems probable that the term kangaroo was interpreted as marsupial and that the animals described may have been confused with either brushtail possum, *Trichosurus vulpecula*, or wombats, *Vombatus ursinus*, both of which would usually be common in the habitats visited, but were not mentioned in the accounts. Without museum specimens the record seems equivocal at best. Although kangaroos and wallabies had been collected by French naturalists on the Baudin expedition in 1802, potoroos (or potoroids, to include the bettong) were not (Plomley 1983).

With the release of Gould's (1863) *Mammals of Australia : Kangaroos*, the Tasmanian potoroo was accorded specific status as *Hypsiprymnus apicalis*, the

Tasmanian rat-kangaroo, and a first hand field description of habitat and diet appeared. The diet attributed to potoroos by Gould (1863), and typical in early accounts, was of "roots, herbage, grass and leaves" largely based on the gross anatomical likeness of potoroids to larger macropodoids.

Human focus on kangaroos and wallabies, whether in the wild or displayed in zoos, is in contrast with that of the more cryptic and poorly known potoroids. The utility of kangaroos as a human food source has been another reason for continuing disparate attention, as has the potential of larger kangaroos and wallabies for dietary competition as grazers or browsers with introduced domestic stock. Potoroids have occasionally been cited as agricultural pests (e.g. for the potaroo and the rufous bettong, *Aepyprymnus rufescens* (Schlager 1981); and for the burrowing bettong, *Bettongia lesueur* (Frith 1973)), but macropodids are ecologically dominant both generally and in the human economy. No use of potoroids as food by Tasmanian aboriginals is known but archaeological studies indicate that while macropods, particularly Bennett's wallaby, had been of major importance to some tribes, and other mammals such as platypus were occasionally utilised as food, potoroid bones were absent from thousands of individual prey of other species (Marshall 1992), despite the probable presence of potoroids in the local fauna.

An important ecological theme during the European history of potoroid populations is the decline of many distributional ranges and populations. The monotypic potoroid *Caloprymnus campestris* or desert rat-kangaroo is probably extinct, as is the broad-faced potaroo, *Potorous platyops*. The ranges of mainland Australian potoroids, especially bettongs (*Bettongia* spp) are greatly reduced or fragmented, as are those of many smaller macropodids within the Critical Weight Range (CWR), of body mass less than 5.5 kg (Johnson, Burbidge, and McKenzie 1989) that has been correlated with extinction or massive geographic range-reduction of many marsupial species in Australia.

1.2 Development of Knowledge of Potoroo Ecology.

Knowledge of potoroids and other Australian mammals expanded in the mid-nineteenth century, particularly through the efforts of John Gould and his principal collector John Gilbert. Indeed, only one potoroid was discovered in the nineteenth century after publication of Gould's (1863) monograph, the musky rat kangaroo *Hysiprymnodon moschatus* (Frith and Calaby 1969). The century following publication of Gould (1863) saw the sparsely documented demise of many

species, especially those on mainland Australia and within the CWR (Calaby and Grigg 1989).

Body mass in modern potoroids ranges from 0.5 kg for the musky rat-kangaroo to around 3.5 kg for the rufous bettong. In this respect they overlap with the smallest of the macropodids (e.g. the warabi, *Petrogale burbidgei*, at around 1.2 kg), but, with the larger macropodids ranging up to 66 kg in body mass, potoroids are clearly of relatively small body size. The extinct Pleistocene *Propleopus oscillans*, the giant rat-kangaroo, known only as a rare fossil, weighed around 70 kg, but is probably most closely related to the smallest modern potoroid, the musky rat-kangaroo (Flannery 1985, 1989).

1.2.1 Reproductive biology of potoroos.

Reproductive biology of potoroos has been investigated in detail by Hughes (1962, 1964), Shaw and Rose (1979), Tyndale-Biscoe and Renfree (1987), Rose (1989) and Bryant (1989). Many similarities between potoroids and macropodids are evident, especially in the predominantly monovular pattern of female reproduction, and embryonic diapause represented by a quiescent blastocyst stage that is known throughout both families. Potoroids are nonetheless distinguished by typically higher annual fecundity of 2.5 to three young usually achieved through continuous breeding, compared to macropodids typically producing one to 1.8 young per year, especially in temperate regions through seasonal breeding (Lee and Cockburn 1985). Pouch life duration is also significantly shorter in potoroids, 14 to 21 weeks (Rose 1989), compared to 28 to 50 weeks in macropodids (Stuart-Dick and Higginbotham 1989). Reproductive anatomy of potoroids *vis a vis* macropodids led Pearson (1950) to conclude that the groups were distinct (on the basis of a unique anterior vaginal caecum in potoroids), in agreement with earlier separation of the families (or subfamilies).

1.2.2 Behavioural biology.

Cryptic and secretive are adjectives often invoked to describe potoroid behaviour, and reflect a lack of thorough, albeit difficult, investigation. Some studies of behaviours have been conducted, often in laboratory situations (agonistic behaviour (Kitchener 1967); maternal behaviour (Johnson 1988); incidental social behaviour (Veselovsky 1969)), summarised for Macropodoidea at large by Johnson (1989); Jarman and Coulson (1989), Coulson (1989), and Croft (1989). Potoroid behavioural repertoires have been suggested to support a putative phylogeny within the family (Ganslosser 1992). Most potoroid behavioural studies published are based on captive

animals, a reflection of the practical difficulties often inherent in field studies. As much as potoroid behaviour is poorly known, that of some macropodids, particularly the larger, open-country species, have been relatively well documented. Some basic social acts such as maternal pouch-young grooming and maternal-offspring allogrooming, appear to be distributed throughout the Macropodoidea and are apparently universal and primitive (Coulson 1989).

1.2.3 Ecology of potoroos.

The sparse development of ecological information on Australian mammals following the publication of Gould (1863) is at least as evident in Tasmania, where Gould was based for approximately twelve months (Sauer 1982), as in Australia generally. Only in the 1950's and 1960's did detailed autecological and population studies of marsupials gain momentum. In Tasmania Guiler (1958, 1960a, 1960b, 1971), Kitchener (1967, 1973) and Heinsohn (1966, 1968) studied the potoroo and other small marsupials in the same generalised trophic niche (the southern brown bandicoot, *Isodon obesulus*, and eastern barred bandicoot, *Perameles gunnii*). Habitat preferences, population density, home range and breeding parameters were the main focii of these studies, but their short or sporadic duration and consequent small datasets limit their usefulness.

Dietary studies indicated the importance of fungal sporocarps together with other plant and invertebrate food items for potoroos Guiler (1971). Estimates of home-range, detailed in Chapter Four, varied widely (Seebeck *et al* 1989), but were often based on inadequate data and non-comparable methodologies. Individual home-ranges were reported as overlapping within and between sexes. Breeding was variously reported to be continuous, or continuous with seasonal peaks (Guiler 1960b). Longevity was reported as exceeding seven years, although detailed survivorship was not reported. Potoroos were reported to be frequently sympatric with brown and sometimes barred bandicoots, with bettongs inhabiting drier more open habitats.

Related to these ecological studies were those of Hughes (1962, 1964) and Shaw and Rose (1979) into reproductive biology, and Hope (1974) and Johnston and Sharman (1976, 1977) into morphological and genetic variation and taxonomy of the potoroo. The latter authors assigned all of the eastern Australian populations of the long-nosed potoroo to a single species, *Potorous tridactylus*, on the basis of breeding experiments and morphometric and protein similarities. Potoroos nonetheless exhibit considerable morphological variation, both latitudinally in eastern Australia

generally, and in a longitudinal cline of increasing body mass from west to east across northern Tasmania (Johnston and Sharman 1976).

A significant taxonomic development was the identification of a new potoroo species, previously presumed to be within *Potorous tridactylus*, from eastern and east-central Victoria and south-eastern NSW. The long-footed potoroo, *Potorous longipes*, has hind feet longer than head length, a greater body mass, and a distinctive karyotype to that of the long-nosed potoroo (Seebeck and Johnston 1980). It occurs in mixed open eucalypt forest in close proximity to populations of the long-nosed potoroo, in areas of rainfall above 1100 mm (Seebeck 1983).

An overall review of potoroid ecology (Seebeck *et al* 1989), has provided a summary of the known ecology of each of the ten modern potoroid species. Recent studies in Tasmania have included studies on maternal behaviour and population biology (Johnson 1988). Although Seebeck *et al* (1989) and other authors have commented on the imputed similarity of Tasmanian potoroo habitat to that of mainland Australia based on the density of vegetation in studied habitats (e.g. of Heinsohn 1966; Guiler 1958 *et seq*), some Tasmanian potoroo populations occupy relatively open habitat (e.g. Hird 1992). Surveys of modern distribution and habitat preference on mainland Australia have been undertaken by Seebeck (1981) for Victoria, and Schlager (1981) for NSW and southern Queensland populations.

Other significant studies include a population study in fragmented relic habitat patches in western Victoria (Bennett 1987, 1993), and population studies in the same general region (e.g. Seebeck 1995b). Guiler (1971) suggested that fungi were significant in the diet of potoroos. Subsequent faecal analysis studies indicate that potoroos include up to 50 local species of mostly hypogaeal (truffle-like) fungi in their diet (Bennett and Baxter 1989; Claridge, Tanton and Cunningham 1993), with mycophagy in Australian mammals summarised by Claridge and May (1994). Bandicoots exhibit partial overlap with potoroos in diet, although fungi generally comprise a smaller dietary component than in potoroos (Claridge 1993).

Life history strategies of macropodoid marsupials have been summarised by Lee and Cockburn (1985) and Norbury, Sanson and Lee (1989). While macropodoids in general have a prolonged pouch life and a relatively high mass of young at weaning compared to other marsupials, within the Macropodoidea the potoroids have relatively brief pouch life compared to that of macropodids. Annual fecundity tends to be constrained by the litter size of a single young in all macropodoids except the musky rat-kangaroo (with litters of two), but the frequency of continuous (or

near-continuous) breeding in potoroids leads to higher overall annual fecundity. Data on longevity and survivorship patterns is lacking for most macropodoid species.

1.3 Aims Of This Study.

The limitations of surveys of natural communities based on single-samples or limited spatial or temporal scales have been highlighted by Wiens (1981) who showed that, in bird communities, significant year-to-year and concurrent variation between nearby plots in contiguous vegetation types occurs in parameters such as species density. The variability included differences in the direction and magnitude of trends. Such variability is difficult to elucidate and the use of longer-term studies such as this may be a valuable method to overcome some of the inherent difficulties involved. Although not explicitly designed to explore year-to-year trends, this study was intended to collect population data which would overcome some of the vagaries of shorter-term studies.

The principal aim of this study was, therefore, to obtain longitudinal population data from a natural population of the long-nosed potoroo. While some population parameters such as estimates of the mean adult longevity can be relatively easily derived from data on a species' reproductive potential (assuming population stability), longitudinal studies are of special interest in that they can enable quantification of differential life history contributions of individuals to population demographics.

Description of microhabitat usage, individual home range data, and female reproductive outcomes, again including a temporal dimension to the data, were also principal objectives of the study. Dispersal and philopatry data were also of interest, especially since amongst terrestrial mammals juvenile marsupials may often be identified with both their mother and maternal home-range.

A secondary but important component of the study was the mammalian community ecology of the study area, particularly for mammals in the generalised fungivore / omnivore trophic niche (Lee and Cockburn 1985) and thus potential competitors of potoroos. Marsupial community ecology has been examined in some arboreal (e.g. Davey 1984) and larger macropodid groups (e.g. Calaby and Grigg 1989; Fox, 1989), but is poorly known for the range of Tasmanian mammalian habitats (see, e.g., Rounsevell, Taylor and Hocking (1991) for an outline of the extent of systematic survey effort).

1.4 Format Of This Thesis.

This introductory chapter is followed by an outline of the survey methods of the study and a broad overview of results. Chapter Three provides an analysis of the use by potoroos, and other species, of microhabitats on the study area. A detailed investigation of home-range for resident potoroos comprises Chapter Four. Finally, Chapter Five details conclusions drawn from this study in the context of the known biology of potoroos and related species.

Chapter Two.

General Methods and Demographic Overview.

Longitudinal studies of marsupial populations are uncommon and often difficult to interpret due to temporal variation in environmental conditions and stochastic variation in the population under study. This complexity is amplified when the study species is cryptic and major aspects of its biology such as behavioural repertoires are poorly known.

This chapter details information with respect to overall capture results, primarily of mammals, and some analysis of general demographic trends, with the principal purpose of providing an overview of results from the study as a whole. Trapping results are presented together with an interpretation of results not intensively examined in subsequent chapters, i.e. demographic data, community ecology of all mammal species trapped, seasonality of breeding and evidence for sex-based body mass dimorphism. More detailed analysis of potoroo microhabitat utilisation and home-range parameters appears in following chapters.

2.1 Methods.

2.1.1 Study Area and Trapping Grid Design.

Fieldwork for this study commenced in 1987. The location of the 35 ha study area was approximately five km southeast of Hobart in southern Tasmania, at Porter Hill on the eastern slopes of Mount Nelson (Figure 2.1). Porter Hill was the site of previous significant potoroo studies (e.g. Guiler 1958; Kitchener 1967) and allowed both accessibility and habitat security. Detailed habitat description of Porter Hill is provided in Chapter Three.

After pilot studies, ten transects of 20 trapsites were selected for their accessibility, compact distribution and representation of relatively intact natural habitats (Figure 2.2). Transects were usually comprised of two roughly parallel lines of ten trapsites, or of a single line of 20 trapsites (sites 401-420). Transects were approximately 50 metres apart, with trap spacing along transect lines of approximately 20 metres. Trapping was designed to be regular over time (two trapping sessions per month) and to eliminate undue impact on individuals through overly frequent capture.

Figure 2.1

Location of the 35 ha study area, situated approximately five km southeast of Hobart on the eastern slopes of Mount Nelson in southern Tasmania.

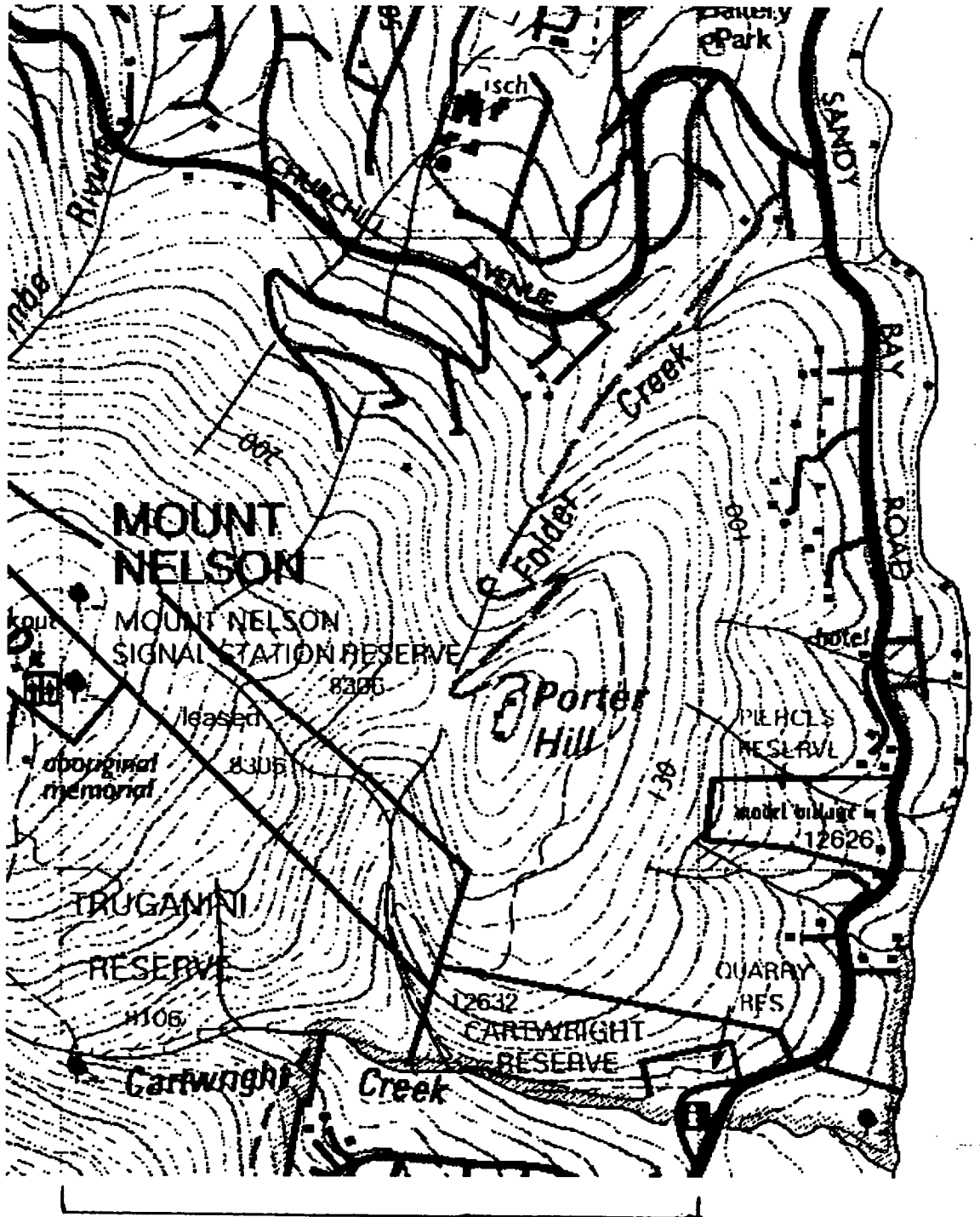
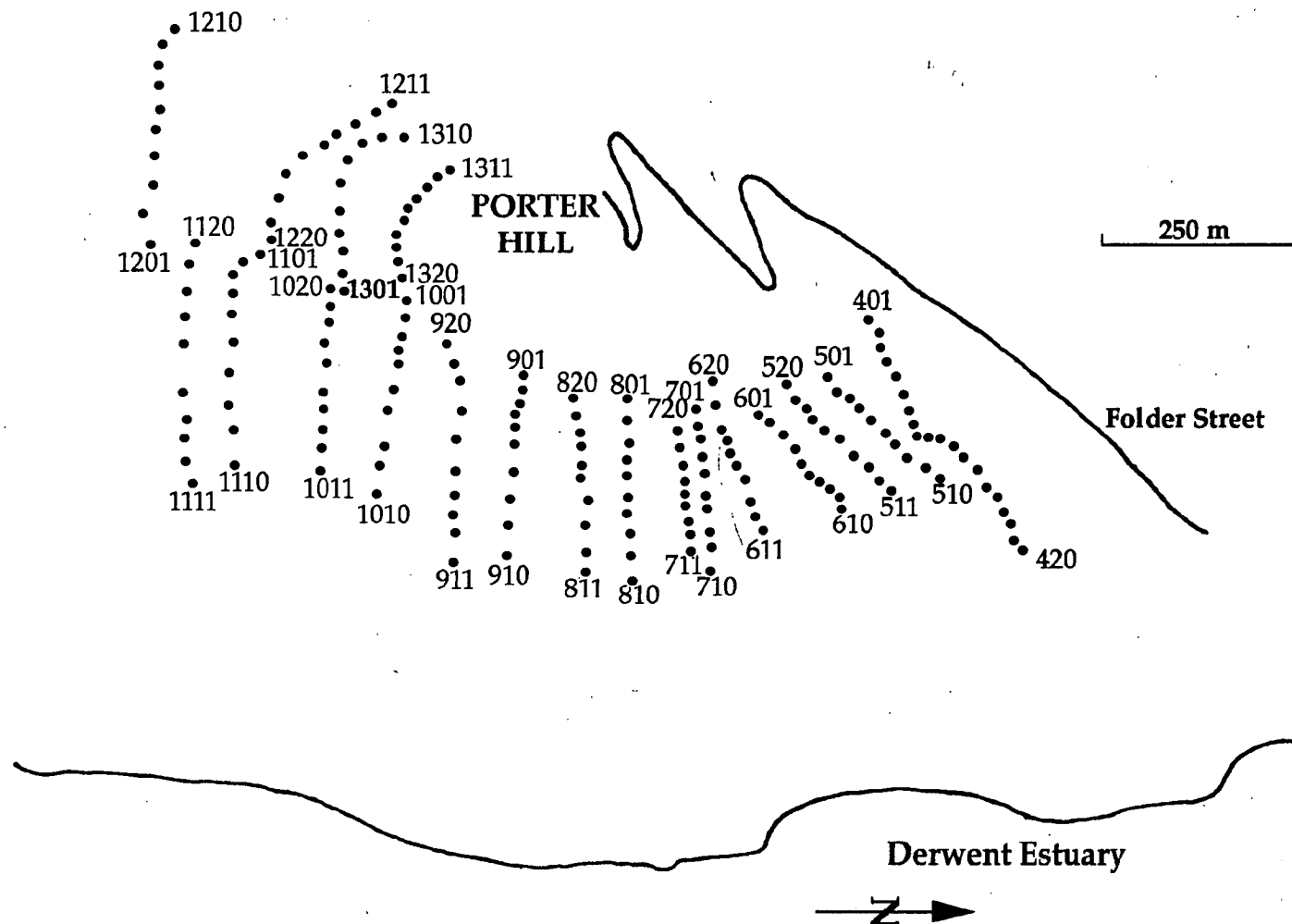


Figure 2.2

Layout of the ten transects, each of 20 trappingsites, within the study area. Numbers represent outermost trappingsites (transects are numbered four to 13).

Transect Sites at Porter Hill



2.1.2 Trapping Frequency and Coverage.

Each trapping session consisted of one transect being trapped on two sequential nights and then left for two to three months. The next trapping session was usually undertaken one to four weeks later (124 of the 134 trapping sessions), but for ten sessions another non-adjacent transect was trapped on the next two nights. A non-adjacent transect (and usually one separated by two intervening transects) was trapped at the subsequent trapping session. Individuals could thus be trapped on subsequent nights within a transect but trapping sessions were separated temporally and spatially, minimising the likelihood of prolonged capture disturbance to individual animals. Distribution of all trapping sessions was random over transects and months (Figure 2.3).

For analysis of habitat and home-range utilisation, data from 134 transect trapping sessions, each of two nights and twenty trapsites (40 trapnights per session), was used (5360 trapnights in total). These data covered the period October 1987 to July 1994. Breaks in trapping were from December 1989 to April 1990 (due to theft of equipment) and from May 1993 to January 1994. For analysis of life-history data some additional trapping sessions were undertaken later to obtain additional data on marked individuals.

2.1.3 Trapping.

Cage traps were treadle-activated wire cages 20x20x80cm. Baits were of a slice of potato spread with peanut butter, a method known to be effective from pilot and prior surveys. Baits were suspended at the rear of the cage to minimise interference from ants. Soil around the entrance of the cage was also disturbed, usually by gouging or scratching soil with a knife. Soil disturbance is thought to be attractive to potoroos (S. Bennett; pers. communication).

2.1.4 Data Recording.

At capture, the species concerned was noted. Potoroos, bandicoots (*Isoodon obesulus* unless otherwise noted) and bettongs (*Bettongia gaimardii*) were placed in a canvas sack for further examination, while brushtail possums (*Trichosurus vulpecula*) were released. Potoroos, bandicoots and bettongs were ear-tagged (Salt Lake Stamp Co. monel fingerling tags) on both ears. Location, tag numbers if present, sex and body mass (Salter spring balance) were recorded. Any unusual body conditions (especially poor condition), extent of tail-albinism (for potoroids), presence of ectoparasites, injuries (especially including ear rips or perforations and

tail injuries), and any exceptional circumstances (such as lost tag status) were also noted.

Female reproductive status was based on the following criteria

- (i) whether a pouch young was present (in which case it's crown-rump length was estimated by palpation;
- (ii) whether pouch had ever been occupied (unused pouches were shallow and white, with non-distended teats), or;
- (iii) whether the pouch-sphincter was tightly closed (indicating imminent birth or presence of small pouch young (Bryant 1989; Rose 1989).

Pouch young were not extracted from the pouch as studies on some related species (e.g. Rose 1985, Taylor and Rose 1987; for the bettong) have found that losses of pouch young (and possibly inhibition of development pouch young) may occur in such circumstances. Where young at foot or larger pouch young out of the pouch were encountered, they were returned to the pouch where possible or tagged and released with the mother. When separation of mother and young occasionally occurred the young was released under nearby shelter.

Most young potoroos were not tagged at the pouch-young or young-at-foot stages because, due to the short time interval young spend as young-at-foot, the trapping regime meant that the likelihood of capturing a young suitable for tagging was not high. Sexual maturity of females was taken to occur at nine to ten months based on regular observation of females of 700 - 850 g body mass with pouch young in conjunction with the age : body mass curves of Bryant (1989). For male potoroos, young but mature animals are in the 800 - 1000 g body mass range (Hughes 1964).

Other species caught were noted and released. Cages with missing baits were noted, including whether or not the door was shut. Because much of the study data was collected under tight time constraints (due to the author's work and other commitments), extensive repeated measurements, such as of body dimensions, were not made; data on morphological variation in the potoroo (including Hobart specimens) has been recorded by Johnston and Sharman (1976) and Bryant (1989).

Field notes (based on trapping events from a trap disturbed for any reason or capture event) were entered into a SAS (SAS Institute, Cary NC, USA) database for further analysis. SAS software was subsequently used to summarise data and undertake some statistical analysis.

2.1.5 Potoroo Survivorship and Life-Table Analysis.

Two methods are available for compiling life-tables:

- (i) a segment approach which examines all individuals alive over a time period (a "vertical" approach), and;
- (ii) a cohort approach which follows individuals entering the population over a particular time period until they disappear from the population (a "horizontal" approach) (Begon and Mortimer 1981). The vertical approach requires an ability by the researcher to age individuals, but in this study no reliable method for aging adult individuals was available although young individuals weighed one kilogram or less and were subjectively recognisable. The duration of this study approximated the recorded maximum life span of wild potoroos, of seven years (Guiler and Kitchener 1967), and was thus more suited to the horizontal approach of Begon and Mortimer (1981), although the numbers of individuals sampled in some known-age classes were small.

The number of young born annually was estimated from the product of the known-to-be-alive estimate of adult females (section 2.2.4), and the estimated number of pouch young produced annually based on a mean time between births of 140 days (Lee and Cockburn 1985; Bryant 1989). Because no evidence for age-specific variation in fecundity of adult females was found in this study, mean annual production of pouch young was based on a 140 day interval between successive births.

The intrinsic rate of natural increase of a population, r_m , was calculated for the purpose of this study using the approximation cited in Pianka (1994), i.e. r_m is approximated by $\log_e R_0 / T$; where R_0 is the net reproductive rate and T is mean generation time, on the assumption that R_0 is close to 1.

2.1.6 Evidence for Sex-Based Individual Tolerance.

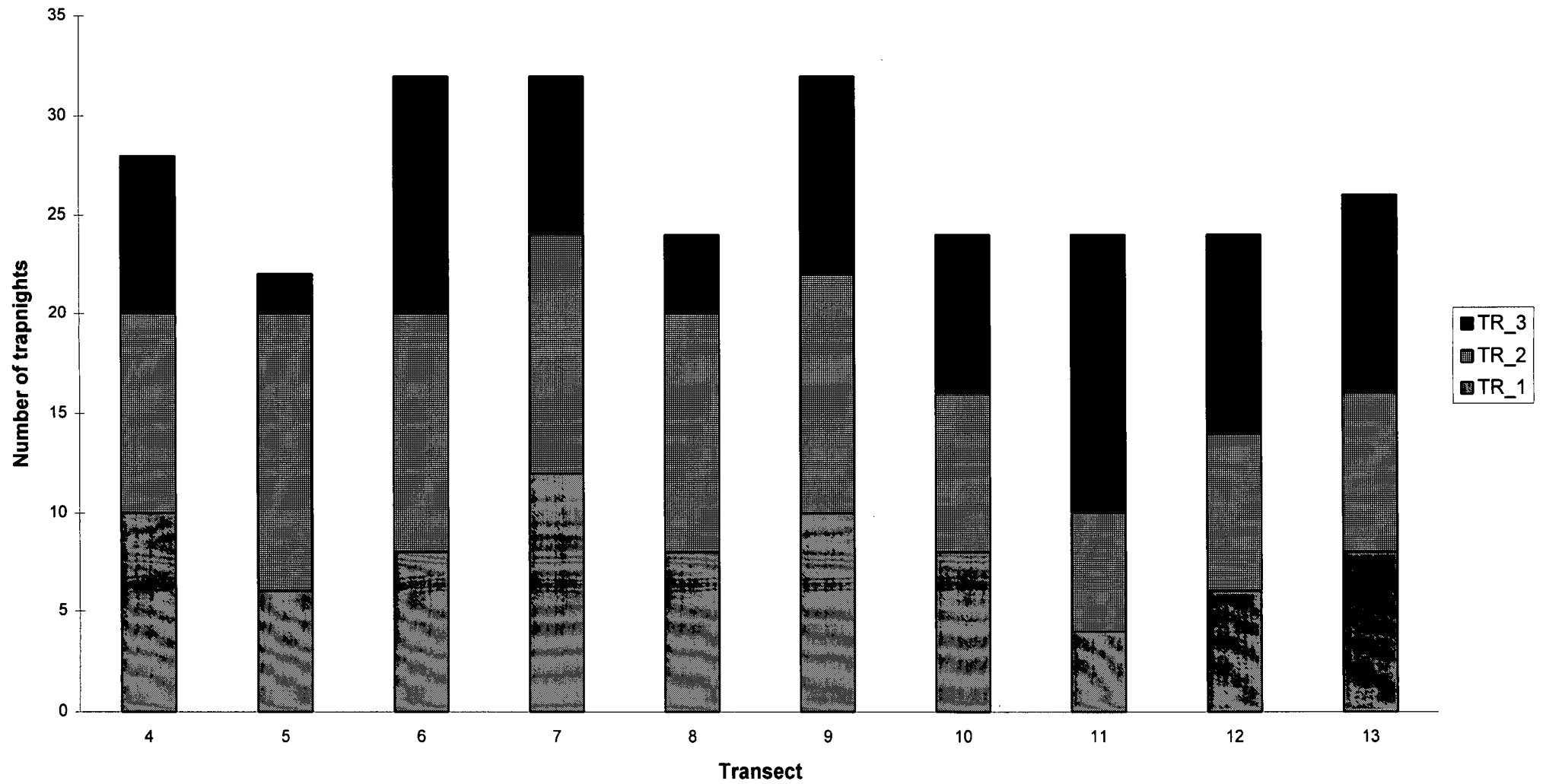
Sex-based tolerance was examined by use of a chi-square test on the sex of animals trapped on sequential nights at the same trap site. As residual scent on traps was inferred as the probable cause of any such sex difference in trappability, only captures of different individuals were included in this analysis.

Captured animals were also routinely inspected for obvious fighting injuries or scarring, as tail-bites and rips in ears have been reported in potoroos (Johnson 1988).

Figure 2.3

Trapping frequency of transects by season over the course of the study. Tr_1, Tr_2 and Tr_3 refer to the seasons used; January-April, May-August and September-December respectively, see text for explanation.

Transect Coverage by Season, 1987-94



2.1.7 Sexual Dimorphism in Potoroo Body Mass.

Body mass data was analysed for male and female resident potoroos (individuals with at least ten capture records). Possible sex differences were analysed on the basis of both the mean of all body mass observations and maximum individual body mass by using t-tests.

2.1.8 Seasonal Variation in Adult Potoroo Body Mass.

Seasons were defined as the periods January-April, May-August and September-December in order to minimise the disaggregation of the data and broadly reflect local seasonal patterns. Seasonal body mass variation for male and female potoroos was examined using one-way analysis of variance, using all body mass records of at least 750 g.

2.2 Results.

2.2.1 Total Capture Numbers and Capture Rates.

From the 5360 trapnights, 1278 potoroo, 264 bandicoot, 75 bettong and 232 brushtail possum capture events representing trap success rates of 23.8%, 4.9%, 1.4% and 4.3% respectively were recorded, a total of 1849 captures or a trap success of 34.5% were recorded for these four species. Capture rates are based on total trapnights; some traps were found shut but unoccupied. Total captures per four-month season over the principal trapping period (based on at least ten nights trapping, 200 trapnights per season) increased over the survey period (Figure 2.4). A noteworthy qualitative feature of the capture pattern is the “self-introduction” of the bettong, with their first appearance recorded about half way through the study and regular recaptures of several individuals thereafter.

Regression analysis of capture rates over time, for comparable seasons, (Table 2.1) indicates that the potoroo and bettong capture rates (captures per 100 trapnights) increased significantly, while that of the brown bandicoot decreased significantly over the course of the study. The capture rate for brushtail possums did not exhibit a temporal trend.

2.2.2 Individual Capture Numbers and Capture Rates.

In order to analyse long-term trappability rates, tagged individuals were only counted once in each season in which they were captured in this analysis. Thus the numbers of animals were smaller than for gross capture data. Numbers of captures of identified individual potoroos, bandicoots and bettongs per season are presented in figure 2.5.

Figure 2.4
Frequency of captures of potoroos, brown bandicoots, bettongs and
brushtail possums per season over the principal trapping period
(based on at least ten nights trapping, 200 trapnights per season).

Number of
Captures per
100 Trapnights

Capture Rate by Season

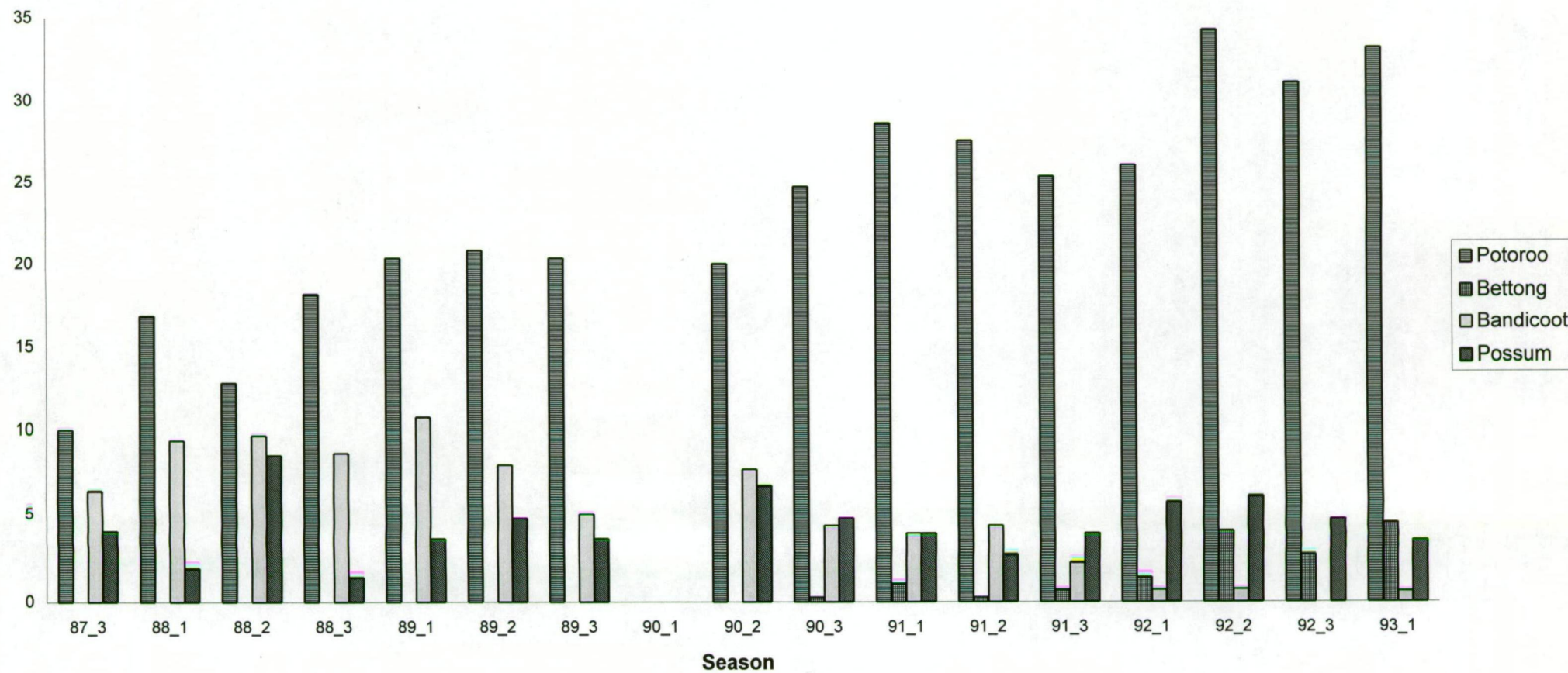


Table 2.1 Regression analysis of capture rates over time for potoroos, bandicoots, bettongs brushtail possum and the overall rate, for each season where at least eight trapnights were undertaken.

| | Regression Statistics | | |
|------------------|-----------------------|----------|-----------|
| | F Value | Prob > F | Direction |
| Potoroo | 106.26 | < 0.01 | increase |
| Bandicoot | 45.82 | < 0.01 | decrease |
| Bettong | 18.42 | < 0.01 | increase |
| Brushtail Possum | 0.21 | > 0.1 | n.a. |
| All Captures | 26.40 | < 0.01 | increase |

Regression analysis of captures over time of known individuals (Table 2.2) were undertaken as for all capture events, with the exception that the first ten four-month seasons of the study were omitted to allow time over the initial phase of the study for resident individuals to be captured and identified (see figure 2.7). On the basis of this analysis, only bandicoots exhibited a significant change in individual capture rate, with a decline in numbers over the period examined.

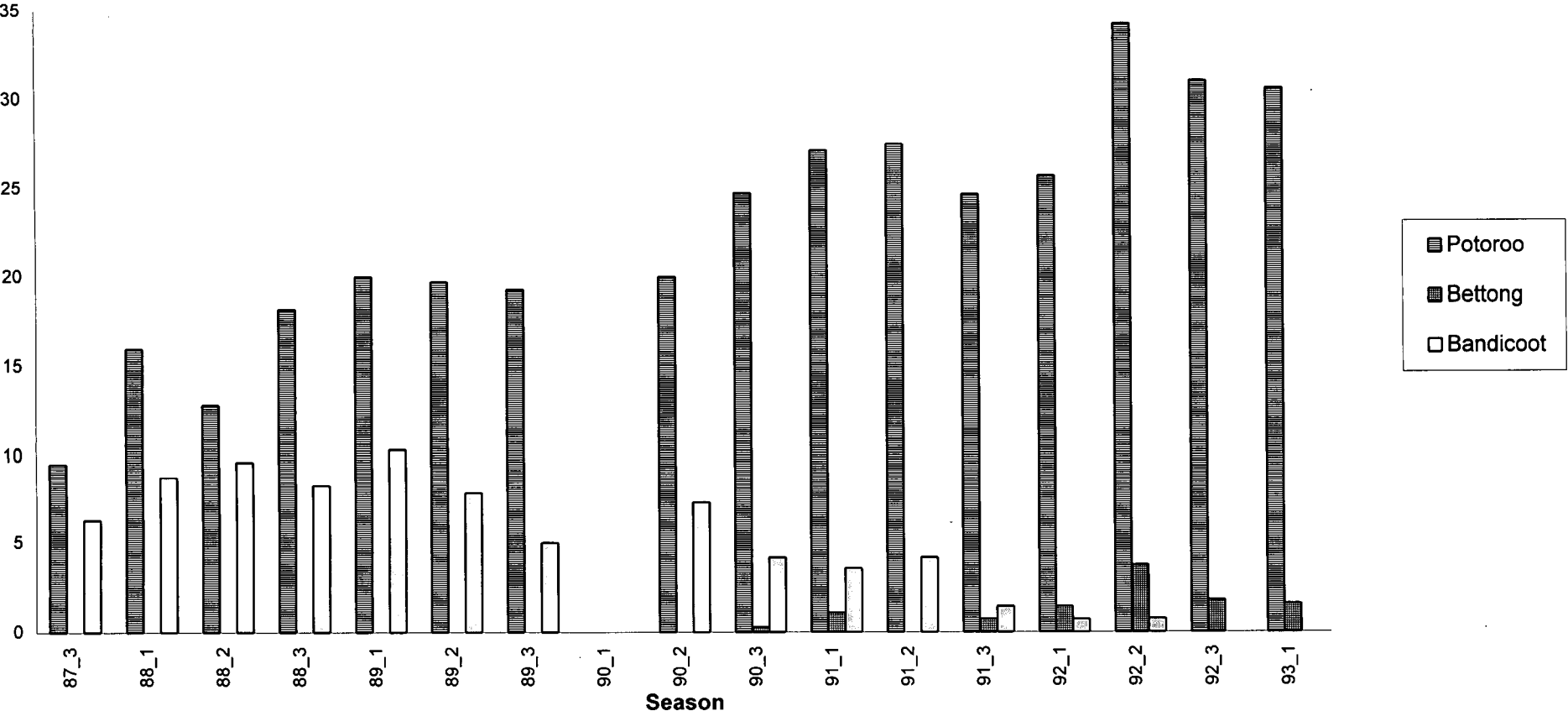
Table 2.2 Regression analysis of capture rates over time for individual potoroos, bandicoots and the overall rate, for each season where at least eight trapnights were undertaken..

| | Regression Statistics | | |
|--------------|-----------------------|----------|-----------|
| | F Value | Prob > F | Direction |
| Potoroo | 0.45 | > 0.1 | n.a. |
| Bandicoot | 35.52 | < 0.01 | decrease |
| Bettong | 3.12 | > 0.1 | n.a. |
| All Captures | 0.08 | > 0.1 | n.a. |

Figure 2.5
Numbers of captures of identified individual potoroos, bandicoots
and bettongs per four-month season.

Individual Capture Rates by Season

Number of
Captures per
100 Trapnights



2.2.3 Individual Potoroo Capture Frequencies.

A frequency distribution of individual potoroo capture events is presented in figure 2.6. While many identified individuals (64 %) were captured five times or fewer, many were captured ten or more times, with one male being captured on over 90 nights. The median number of potoroo captures was 3.5.

2.2.4 Potoroo Numbers Known-to-be-Alive.

Individual potoroos were considered "known-to-be-alive" between their initial tagging and their final capture. As individuals were usually initially tagged as young or mature adults, and would usually have lived beyond their final capture, known-to-be-alive estimates are conservative with respect to numbers of individuals actually alive. Figure 2.7 presents numbers of individuals known-to-be-alive over the course of the study. The known-to-be-alive estimate is considered reliable only for the years 1990-1994 as individuals may have been alive but not captured due to insufficient trapping coverage at other times.

2.2.5 Probability of Captures on Sequential Nights.

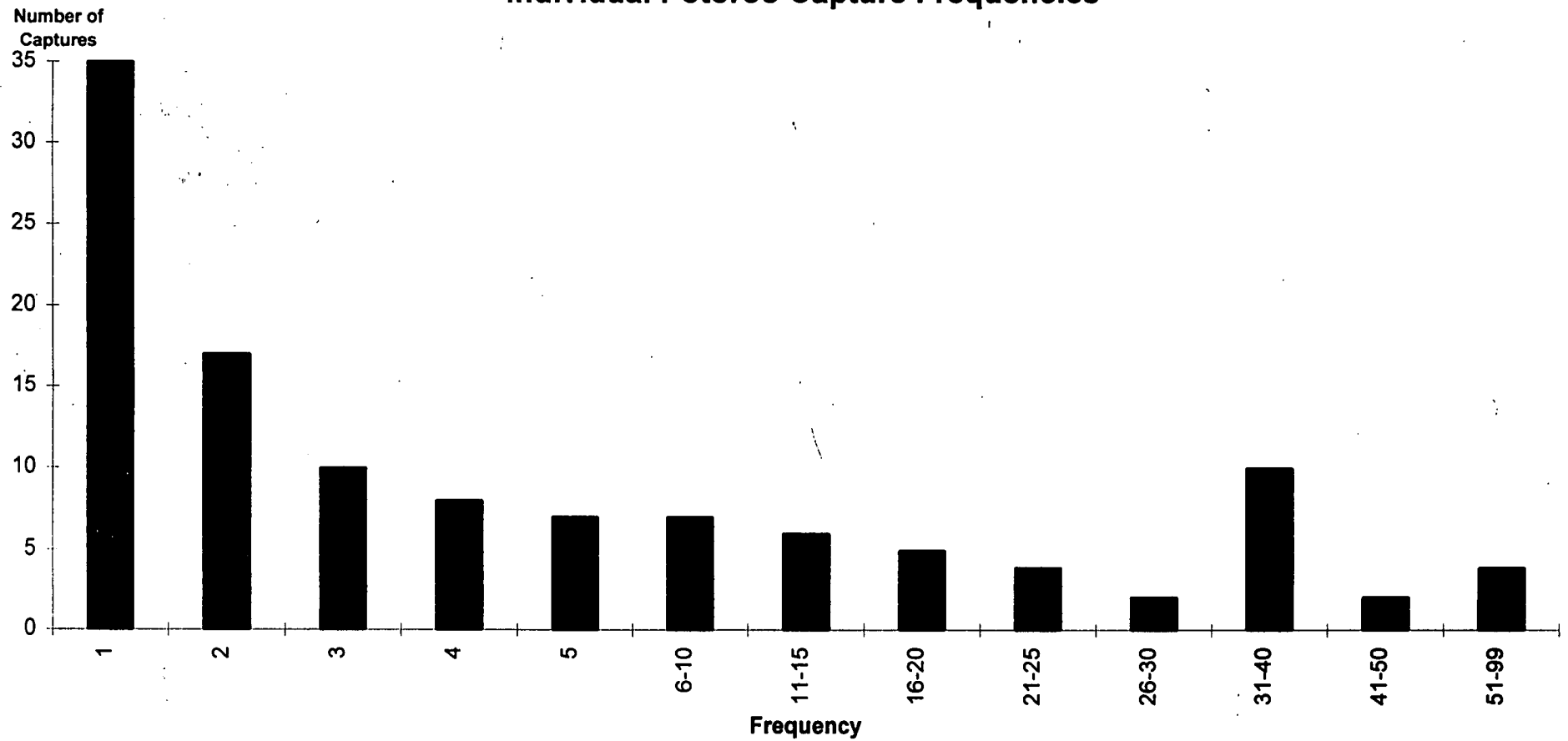
A paired t-test (Table 2.3) was used to examine numbers of each species caught on the first and second nights of trapping each transect. From the 134 available comparisons, only potoroos and the overall numbers of the four species exhibited a significant ($P < 0.05$) difference, with a lower number of animals caught on second nights.

Table 2.3. Paired t-test analysis of number of capture events between sequential nights (within transects) for potoroos, bandicoots, brushtail possum, and overall capture numbers. Mean difference is mean of number caught first night minus number caught next night.

| | T-test Statistics | | |
|------------------|-------------------|-----------|-----------------|
| | T:mean =0 | Prob > T | Mean Difference |
| Potoroo | 1.98 | < 0.05 | + 0.34 |
| Bandicoot | 1.61 | > 0.1 | + 0.17 |
| Bettong | 1.46 | > 0.1 | + 0.09 |
| Brushtail Possum | -1.18 | > 0.1 | - 0.11 |
| All Captures | 2.27 | < 0.05 | + 0.48 |

Figure 2.6
Frequency distribution of individual potoroo captures.

Individual Potoroo Capture Frequencies



2.2.6 Sex Ratios in Relation to Capture Rates.

The total number of captures of male potoroos from all sites (816) was significantly greater than that of females (430) (binomial $P < 0.001$: H_0 =male:female parity).

Similarly the number of individual males identified (82) was significantly greater than that of females (32) (binomial $P < 0.001$). Mean captures per individual for each sex were thus 10.0 and 13.4 for males and females respectively.

Bandicoots exhibited a significantly female-biassed sex ratio in terms of capture numbers (binomial $P < 0.001$), but not in terms of identified individuals (binomial $P > 0.1$) No sex differences in number of capture events or in numbers of identified individuals were detected for bettongs.

Table 2.4. Number of individuals captured, for potoroos, bandicoots and bettongs over the course of the study. P values are binomial probabilities based on (H_0 : parity between males and females in population).

| | Individuals Captured | | |
|-----------|----------------------|--------|---------|
| | Male | Female | P value |
| Potoroo | 82 | 32 | < 0.01 |
| Bandicoot | 33 | 42 | > 0.1 |
| Bettong | 10 | 9 | > 0.1 |

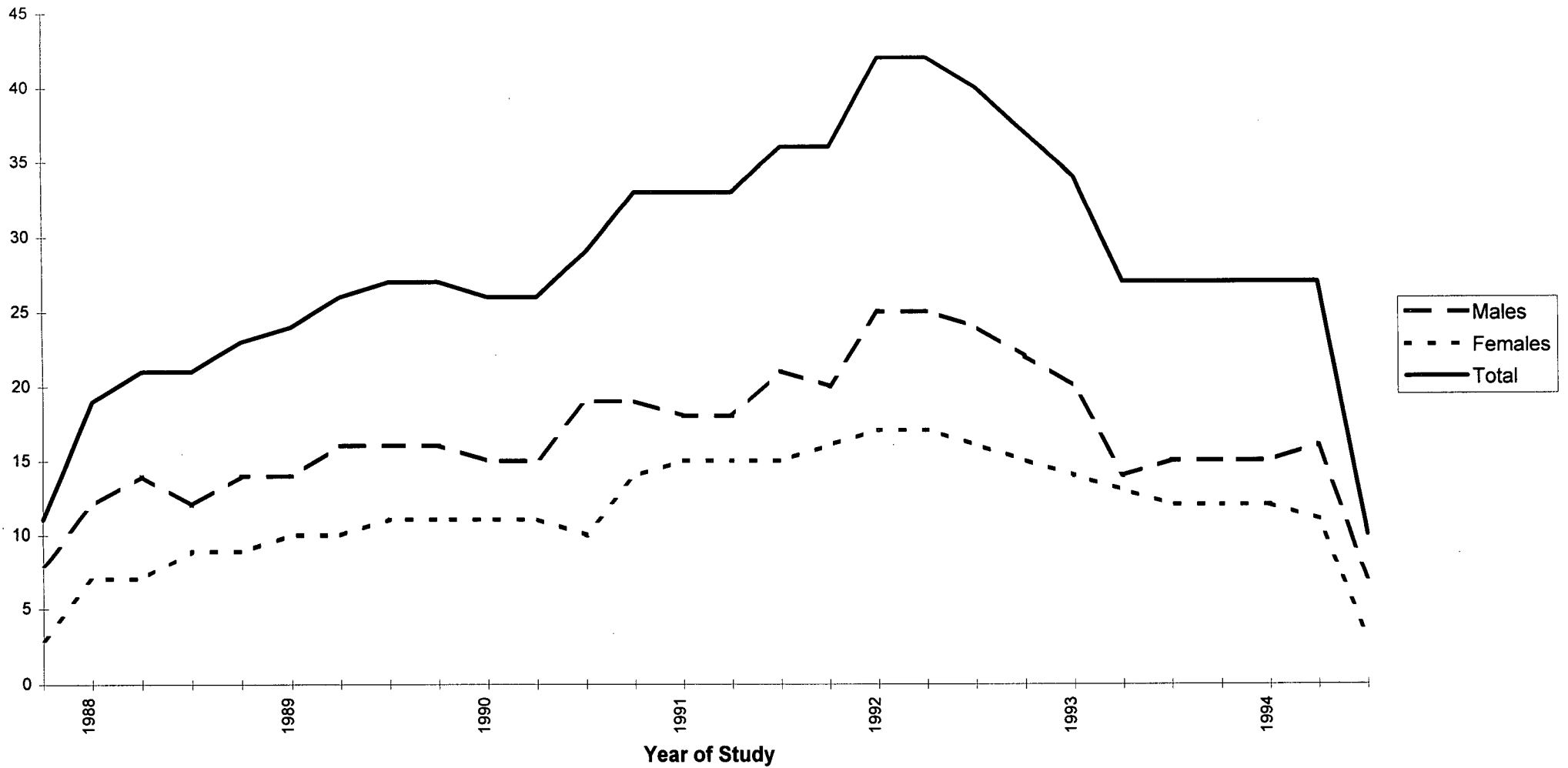
2.2.7 Evidence for Sex-Based Individual Tolerance.

Intrasexual tolerance was examined by testing for whether the sex of individuals trapped at the same trap site on sequential nights was randomly distributed.

Table 2.5 presents the results of the 92 occasions on which different individuals were captured on sequential nights at the same trap site. A chi square analysis yielded a significant chi-square statistic ($\chi^2_1 = 7.42$; $P < .01$), indicating that individuals entered traps occupied on the previous night by a potoroo of the same sex at a significantly lower frequency than would be expected from unbiased choice (the sex ratio of individuals captured in sequential pairs of nights reflected that of the population at large). Thus captures of opposite sex individuals on a subsequent night were more frequent than same sex captures, indicating intolerance within sexes.

Figure 2.7
Numbers of Individual Potoroos Known-to-be-Alive.

Potoroos Known to be Alive



Inspection of animals captured for injuries revealed apparent scarring from tail-bites and ear tearing, but their infrequency indicates substantive avoidance of injurious fighting amongst free-living individuals.

2.2.8. Seasonality of Breeding and Observed Longevity in Bandicoots and Bettongs.

The 42 female bandicoots identified in this study produced 36 observed litters of up to five pouch young between August and February. Some mortality of young during the ontogeny of individual litters occurred. A decline in numbers of breeding females on the study area was evident after the first three years of the study. Mean litter size, based on number of pouch young observed when a female was first trapped with a litter, was 2.94 (s.d. =1.15). Individual females with litters were trapped up to two years apart. Maximum observed lifespans were 785 days (mean 84, s.d. 162 days) for males, and 1002 days (mean 172, s.d. 246 days) for females.

Table 2.5 Sequential-Night Capture at Same Trapsite by Sex. Observed cell values are of a 2X2 contingency table for all captures of separate individuals at the same trapsite on two sequential nights. The higher number of male captures reflects the known-to-be-alive sex ratio.

Chi-square analysis provides strong evidence ($\chi^2_1 = 7.42$; $P < .01$) that the sexes enter traps differentially, tending to avoid traps in which an individual of the same sex was the occupant on the previous night.

| | | Second Night Capture | | Total |
|---------------------|----------|----------------------|------|-------|
| | | Female | Male | |
| First Night Capture | | | | |
| Female | Observed | 19 | 53 | 72 |
| | Expected | 27.8 | 44.2 | |
| Male | Observed | 52 | 60 | 112 |
| | Expected | 43.2 | 68.8 | |
| Total | Observed | 71 | 113 | 184 |

Nine bettong litters (of single pouch young) were observed throughout the year. Litters were observed up to 26 months apart (the observed lifespan for the individual concerned). Sequential litters were separated by a minimum of approximately 120 days. Maximum observed lifespans were 183 days (mean 55, s.d. 68 days) for males, and 828 days (mean 238, s.d. 339 days) for females.

2.2.9 Sexual Dimorphism in Potoroo Body Mass.

Body mass data for resident male and female potoroos are presented in table 2.6. Individuals with at least ten capture records (as a residency criterion) were included in the analysis, and both the mean of all body mass observations and maximum individual body mass were compared between sexes. On both measures males were significantly heavier than females ($P < 0.01$).

Table 2.6. Sexual dimorphism in body mass in the potoroo.

Only individuals with at least ten captures were included in the analyses. Two comparisons were made;

- (i), on the mean of mean individual body mass over all captures (Table 2.6a), and
- (ii), on the maximum individual body mass observed (Table 2.6b).

Table 2.6a

| Sex | Mean Body Mass (kg) | | | | |
|--------|---------------------|------|------|---------|-------------|
| | N | Mean | s.d. | P value | Range |
| Male | 237 | 1.42 | 0.17 | < 0.01 | 0.95 - 1.85 |
| Female | 414 | 1.19 | 0.19 | < 0.01 | 0.50 - 1.65 |

Table 2.6b

| Sex | Maximum Body Mass (kg) | | | | |
|--------|------------------------|------|------|---------|-------------|
| | N | Mean | s.d. | P value | Range |
| Male | 22 | 1.60 | 0.17 | < 0.05 | 1.40 - 1.85 |
| Female | 11 | 1.46 | 0.16 | < 0.05 | 1.25 - 1.85 |

2.2.10 Seasonal Variation in Adult Potoroo Body Mass.

Seasonal body mass data for male and female potoroos are presented in table 2.7. Individuals with a body mass of at least 750 g were included in the analysis, based on all body mass records. No significant seasonal variation in body mass was observed ($F=0.57$, 2d.f. $P > 0.5$).

2.2.11 Seasonality of Breeding in Potoroos.

Birth months for potoroo pouch young were estimated from the crown-rump length : age relationship of Bryant (1989). The annual distribution of births in this study is presented in Figure 2.8. Chi-square analysis of monthly birth totals indicates no significant departure from a random distribution across all months ($\chi^2_{11} = 8.83$; $P>0.5$).

Table 2.7 Seasonal analysis body mass variation.
No seasonal variation in body mass was evident :
(Females: $F=0.57$, 2d.f. $P > 0.5$),
(Males: $F=0.13$, 2d.f. $P > 0.8$).

| Season | Mean body mass (kg) | | | | s.d. (kg) | |
|---------|---------------------|--------|-----|------|-----------|------|
| | N | Female | N | Male | Female | Male |
| Jan-Apr | 79 | 1.21 | 154 | 1.41 | 0.23 | 0.20 |
| May-Aug | 131 | 1.20 | 269 | 1.41 | 0.15 | 0.18 |
| Sep-Dec | 87 | 1.19 | 185 | 1.40 | 0.16 | 0.17 |

2.2.12 Inception of Reproductive Maturity in Female Potoroos.

In this study six female potoroos with body mass between 500 and 800 g at first capture were observed. Additionally, five other females for which body mass was not initially recorded were classified as young on the basis of pouch condition or subjectively on size (with mean adult female potoroo body mass of 1190 g, such individuals are perceptibly small). From the potoroo growth curves of Bryant (1989; Figure 2), female potoroos in this size range would be approximately 180-240 days old, and, since they were observed with pouch young, indicate female reproductive maturity at approximately eight to nine months of age.

2.2.13 Potoroo Survivorship and Life-Table Analysis.

The ratio of young animals tagged to expected number of births in the study population was used as survivorship of the 0-1 year of age cohort, and subsequent survivorship of animals tagged while young (less than one year old) was used to construct a life table (Table 2.8) and semilogarithmic survivorship plot (Figure 2.9). Mortality of first-year young was considered to occur almost entirely in the independent phase (i.e. post young-at-heel stage), since inspection of pouch status of females caught more than once within a reproductive cycle indicated at most one mortality event within the first 130 days of life.

Because the methodology adopted here is not time-specific, assumptions as to the stability of age structure do not apply (Caughley 1966). Because knowledge of age of older individuals was contingent on capturing animals over all of their lifespans, however, numbers of animals sampled in the older age classes were low, and the age-class data should therefore be interpreted cautiously.

Figure 2.8

Birth months of potoroo pouch young at Porter Hill, estimated from the crown-rump length : age relationship of Bryant (1989).

Potoroo Births by Month

Number
of Births

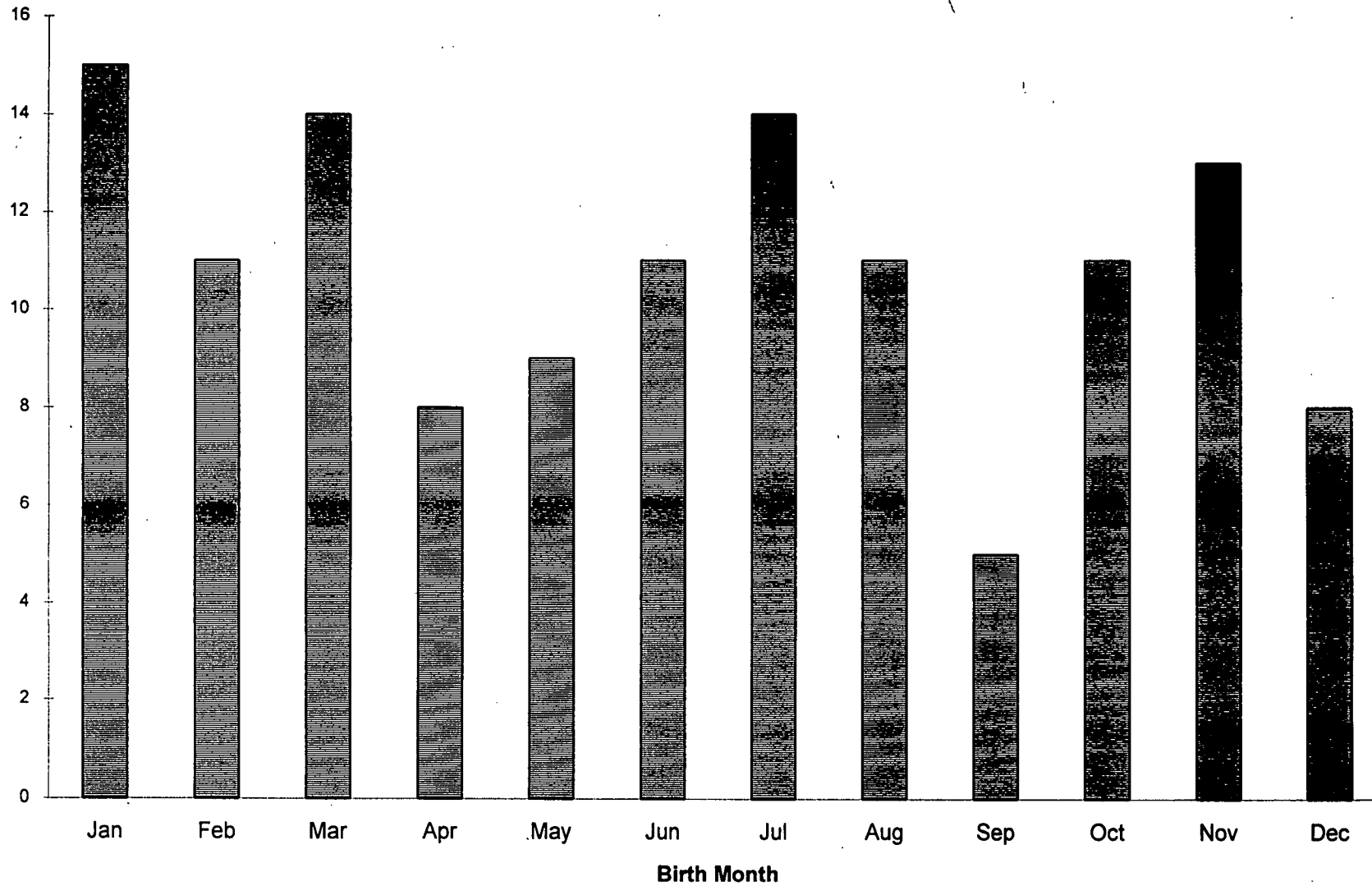


Table 2.8

Life table for *Potorous tridactylus* at Porter Hill. Compilation is based on cohort analysis.

| | |
|-------------|--|
| l_x | : Proportional survivorship from age $x - 1$. |
| m_x | : Age-specific fecundity. |
| $l_x m_x$ | : Realized fecundity. |
| $x l_x m_x$ | : Age weighted by realized fecundity. |
| E_x | : Expectation of life. |
| v_x | : Reproductive value. |
| GRR | : Gross reproductive rate. |
| R_0 | : Net reproductive rate. |
| T | : Mean generation time. |

| Age in years (x) | l_x | $\ln(l_x * 1000)$ | m_x | $l_x m_x$ | $x l_x m_x$ | E_x | v_x |
|------------------|-------|-------------------|-------|-----------|-------------|-------|-------|
| 0 | 1 | 6.91 | 0 | 0 | 0 | 1.92 | 0.99 |
| 1 | 0.2 | 5.30 | 0.27 | 0.05 | 0.054 | 4.60 | 4.95 |
| 2 | 0.19 | 5.25 | 1.3 | 0.25 | 0.494 | 3.79 | 4.93 |
| 3 | 0.17 | 5.14 | 1.3 | 0.22 | 0.663 | 3.12 | 4.05 |
| 4 | 0.14 | 4.94 | 1.3 | 0.18 | 0.728 | 2.57 | 3.34 |
| 5 | 0.1 | 4.61 | 1.3 | 0.13 | 0.65 | 2.20 | 2.86 |
| 6 | 0.06 | 4.09 | 1.3 | 0.08 | 0.468 | 2.00 | 2.60 |
| 7 | 0.04 | 3.69 | 1.3 | 0.05 | 0.364 | 1.50 | 1.95 |
| 8 | 0.02 | 3.00 | 1.3 | 0.03 | 0.208 | 1.00 | 1.30 |
| 9 | 0 | 0 | 1.3 | 0.00 | 0 | | |
| | | | 10.67 | 0.99 | 3.63 | | |
| | | | (GRR) | (R_0) | (T) | | |

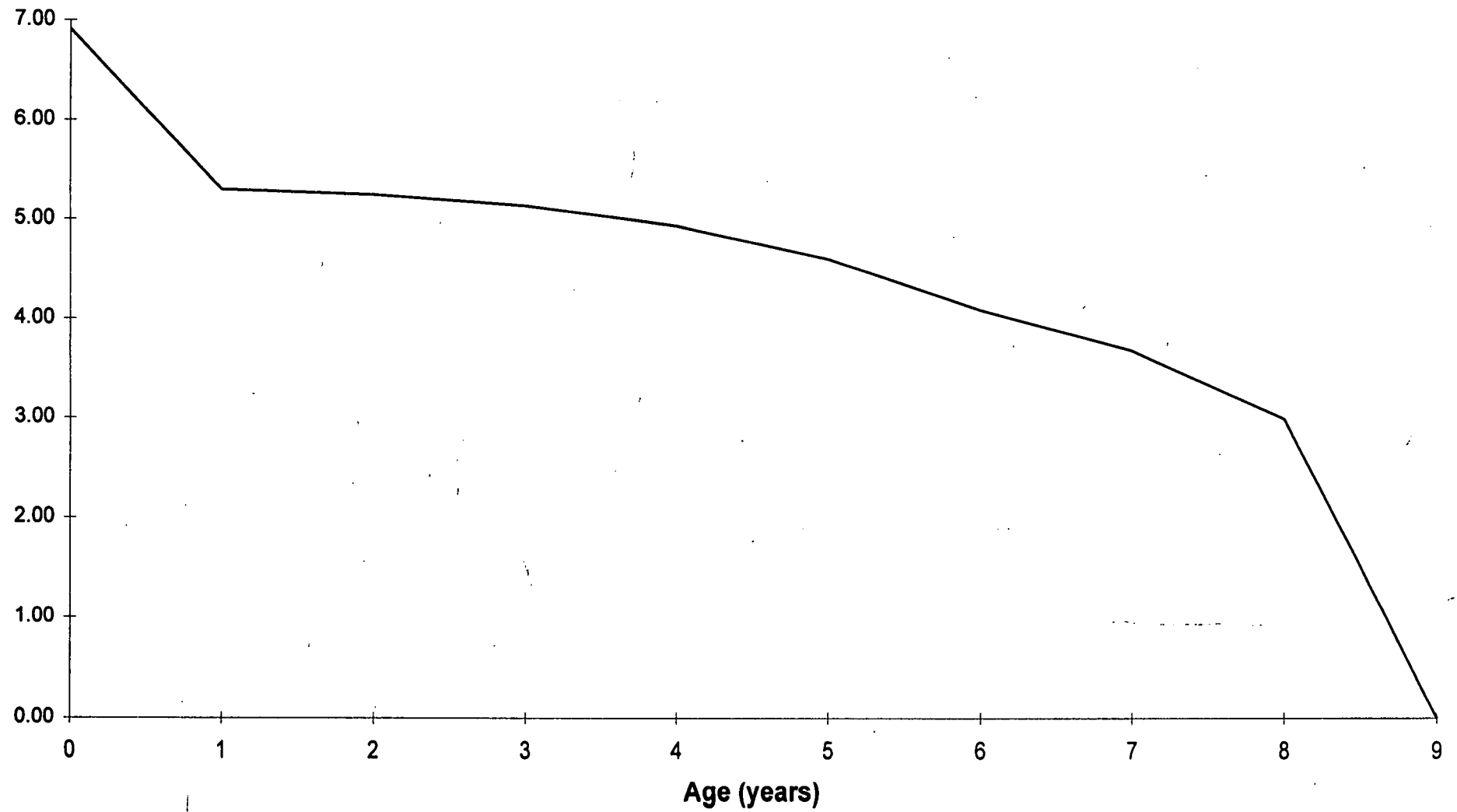
Direct evidence for senescent mortality in this study is derived from an important observation of a single individual. Female-P108 was first captured as a young adult in 1987. In 1995 female-P108 was captured in an emaciated and distressed condition, months after a prior trapping and after the next night was found dead in a trap. This individual must have been more than eight years old, and was captured 17 times. This age exceeds the previous known longevity record for a wild potoroo of seven years (Guiler and Kitchener 1967). Four other individuals (two males and two females) had known life-spans of at least six years over the course of the study.

The intrinsic rate of natural population increase, r_m , in this study was found to be zero, since R_0 was 0.99, indicating stable population numbers.

Figure 2.9
Semilogarithmic survivorship plot based on cohort analysis of
potoroo recapture data.

Survivorship
($\ln(l_x * 1000)$)

Potoroo Survivorship Plot



2.2.14 Incidental Species Caught and Known from the Site.

In total 110 animals of eleven species other than the four reported above were captured (Table 2.9). The most numerically significant of these were Velvet Rats (*Rattus lutreolus velutinus*) and Black Rats (*R. rattus*). The 23 captures of Blotched-Bluetongue Lizards (*Tiliqua nigrolutea*) were restricted to the months of November to April.

Potentially significant predators are known from Porter Hill and its environs, but their numbers and impact on potoroos are unable to be quantified. These include tiger and copperhead snakes, *Notechis ater humphreysi* and *Austrelaps superbus* respectively, and birds such as the wedge-tailed eagle, *Aquila audax* and masked owl, *Tyto novaehollandiae*, for all of which predation pressure would be expected to predominantly fall on young individuals. Domestic dogs were often seen and heard on the study site, and although occasionally known to harass trapped animals, their impact on wild populations is unknown, although the survival of populations of potoroos, bettongs and bandicoots in near-urban Hobart indicates a measure of resilience to potential predation from this source.

Parasites regularly observed were fleas and ticks, the latter particularly around the margins of the ear and occasionally in body fur, and, on one occasion, in an empty pouch. No evidence of disease was encountered although some injuries were carried by individuals over periods of years, e.g. a resident male with an apparent eye cataract over a period of three years.

2.3 Discussion.

Marsupial studies involving the duration and number of individual recaptures of this study are uncommon in the literature, although Seebeck *et al* (1989) report unpublished data (of J. Seebeck) for a Victorian population of the potoroo on a comparable scale (in terms of recapture numbers) to that of this study. This study therefore affords an almost unique opportunity to examine the population biology of the potoroo in a longitudinal manner, and to a lesser extent of the bettong and brown bandicoot.

Table 2.9 Species and number of capture events other than for potoroos, bandicoots, bettongs and brushtail possums, over the course of the study.

| Common Name | Species Name | Captures |
|----------------------------|-----------------------------------|----------|
| Blotched Bluetongue Lizard | <i>Tiliqua nigrolutea</i> | 23 |
| Grey Shrike Thrush | <i>Colluricincla harmonica</i> | 16 |
| Blackbird | <i>Turdus merula</i> | 11 |
| Lewin's Rail | <i>Rallus pectoralis</i> | 1 |
| Echidna | <i>Tachyglossus aculeatus</i> | 1 |
| Eastern Quoll | <i>Dasyurus viverrinus</i> | 1 |
| Eastern Barred Bandicoot | <i>Perameles gunnii</i> | 1 |
| Ringtail Possum | <i>Pseudocheirus peregrinus</i> | 2 |
| Velvet Rat | <i>Rattus lutreolus velutinus</i> | 42 |
| Black Rat | <i>Rattus rattus</i> | 9 |
| Domestic Cat | <i>Felis cattus</i> | 3 |

2.3.1 Capture Numbers and Rates.

The temporal trends in gross capture rates, with the increase for both potoroos and bettongs, and the decline of the bandicoot gross capture rate, are open to a number of interpretations. Bandicoots seem vulnerable to the loss of pouch young through trapping (Clunie 1987), particularly when the young are intermittently free of the teat (i.e. greater than about 60mm crown rump length), and this could have affected their population over the early years of the study.

The carrying capacity of the habitat for each species may have altered over time (Chapter Five). There is insufficient knowledge of the behaviour of these species available to interpret the changes as due to inter-specific competition. Another possible explanation for capture rate trends is unintended changes in trap deployment. Experience indicates that the settled placement of traps so that no rocking of the trap is possible on an animal entering the cage may increase capture rates, but this potential effect was not quantified. The only conscious change in trap deployment was a technique developed during the course of the study of scarifying or gouging the earth at the entrance to a set cage, on the basis that soil-feeding omnivores may be attracted to disturbed soil as well as the bait used. Further, soil probings and excavations by the resident fungivore omnivores appeared to be clumped, although these are usually indistinguishable between species (e.g. Schlager 1981) and were not always evident in grassy areas on the Porter Hill study area. While this latter explanation may have had some effect, the differing directions of the capture rate changes for bandicoots and bettongs indicate either that the effect of

soil disturbance was species-specific or that it was insufficient to explain all of the changes in capture rates. The relative stability of individual capture rates, with the exception of bandicoots, is the strongest evidence that a combination of interference or deterrence effects (to bandicoots) and trapping techniques may explain the overall differences in capture rates. That is, individual potoroos and bettongs became more trappable due to a combination of habituation and enhanced skill in trap deployment.

Some burning of six to ten hectare patches in the study area occurred during the course of the study, and may have influenced the habitat, which was also undergoing concurrent changes such as progressive proliferation of she-oak, possibly following earlier fires (Joan Dorney, pers. communication), and invasion of the introduced boneseed. Such changes may have resulted in variability in habitat quality but are difficult to quantify.

The seasonal breeding of bandicoots found in this study falls within the usual Tasmanian season of July to February (Watts 1993), although Green (1973) reported year-round breeding. The female-bias in brown bandicoot trappability differs from the findings of Claridge, McNee, Tanton and Davey (1991), in southeastern NSW, and Heinsohn (1966) in northwestern Tasmania who, from fewer records, found a male bias in trappability. Studies in Victorian heathland populations (Stoddart and Braithwaite 1979; Lobert 1985) found no evidence for sex-ratio or sex based trappability bias. Although often hampered by sparse data, these results suggest ecological flexibility in such an r-selected species (Gordon and Hulbert 1991). Bandicoot populations may also be susceptible to population disturbance from human activity, including trapping programs (Claridge *et al* 1991; Heinsohn 1966).

2.3.2 Population Ecology of the Brown Bandicoot and Bettong.

The aseasonal breeding pattern of bettongs found in this study is consistent with other studies (Rose 1989). The maximum adult female longevity of 26 months for the bettong would allow a lifetime reproductive output of up to seven young. The observed male and female lifespans (to which must be added an initial age of at least ten months) are somewhat equivocal, since the low capture numbers and limited duration of bettong captures mean that longer lifespans may have been missed.

2.3.3 Seasonality of Breeding in the Potoroo.

Potoroos breed continuously. Guiler (1958) tentatively found a weak seasonal peak in breeding for potoroos, during winter to mid-spring and again in late summer, but later concluded that breeding occurred throughout the year (Guiler 1960b).

Subsequently Hughes (1962) concluded from a small-scale study that seasonal

periods of reduced breeding occurred. Bryant (1989) described seasonal breeding peaks from July to September and December to January, but a reexamination of those data (Bryant 1989; Figure 7) using chi-square analysis of monthly birth totals, yielded no significant departure from a random distribution across all months, i.e. a continuous breeding pattern, ($\chi^2_{11} = 17.91$; $P > 0.05$).

Potoroos therefore conform to the general potoroid pattern of continuous reproduction (Seebeck *et al* 1989), although in the long-footed potoroo (*Potorous longipes*) all recorded births have been in the second half of the year (Seebeck 1995a).

Other syntopic marsupials such as brown bandicoots and brushtail possums breeding in spring and summer at Porter Hill differ from potoroos and bettongs with respect to seasonal breeding. Food supply is usually invoked as the primary reason for seasonal breeding (Caughley and Sinclair 1994). Perhaps for the highly mycophagous potoroids food is a less limiting factor. This presumably reflects a long-term pattern of food availability, although it does not exclude the possibility that sporadic drought years may impose limits on potoroid fecundity (Chapter Five).

2.3.4 Maturation in Female Potoroos.

The female age at first breeding of approximately eight months is in contrast with previously accepted values of approximately twelve months (Bennett 1987; Lee and Cockburn 1985). Some of this variation between Victorian and Tasmanian potoroo populations may be attributable to natural variation but the difference may also be linked to the more rapid growth to a larger mean adult female body mass in potoroos in southern Tasmania (850 g in Victoria (Bennett 1987) cf 1190 g in southern Tasmania, this study).

Breeding at eight to nine months of age has implications both in terms of life history phenomena (i.e. age at puberty contributes to realized fecundity and to R_0), and of primiparous female body mass relative to mean male body mass. A primiparous receptive female would be of about half the body mass of an adult male of mean body mass. The behavioural criteria leading to female acceptance of importunate males have not been well documented, but males in captivity are known to fight in the presence of receptive females. If body mass (and condition) increases breeding success in males, receptive primiparous females may be physically less able to resist importunate males than multiparous females, due to the exaggerated body mass difference.

2.3.5 Survivorship and Life-Table Analysis.

The vital statistics of a population (fecundity, birth rate, death rate and age structure) are important parameters in population dynamics. They dictate its potential rate of change, and are therefore important determinants of the ability of a population to recover from perturbations from extrinsic factors (e.g. catastrophic climatic events), in colonising newly available habitat, and in the long-term viability of a population, especially in changing environments.

The life table provided in this study indicates a high level (approximately 80 %) mortality of animals in the first year of life, higher than the approximate 60 % first year mortality found by Bennett (1987). This result underlines the importance of establishment of individuals in the population. At least for adult females, lifetime reproductive output was quantifiable in this study, i.e. older females were known to have produced at least ten offspring. Most females produced at most one pouch young, however. Establishment in the population by young adult females is therefore a key to a high level of female genetic fitness.

The ability of free-living potoroos to survive for seven or eight years (this study; Guiler and Kitchener 1967), and up to ten years in captivity (Ullmann and Brown 1983) is compensated for by high levels of sub-adult mortality in a population that is stable in overall numbers. Another outcome of high longevity potential is a high value of r_{\max} , the maximal rate of natural increase of a population when no resource is limiting, and indeed high rates of recovery of potoroo populations after fire have been reported, e.g. a 100-fold increase over six years (Seebeck 1995b), although contributions of immigration to the increase were not stated.

The contribution to the population at an individual animal level is also of interest, particularly in a population where relatively few females seem to produce most of the offspring. Young animals entering the population were, however, not generally distinguishable as offspring of resident or transient females, or as immigrant offspring of extra-limital animals. Genetic methods for determining relatedness would assist in the interpretation of individual fitness over generations in the local potoroo population.

Data on survivorship in comparable species is sparse and thus difficult to interpret (e.g. Lee and Ward 1989; Eisenberg 1981), especially for species producing litters comprised of a single young. For a common ringtail possum (*Pseudocheirus peregrinus*) population in a tea-tree (*Leptospermum laevigatum*) thicket, first year mortality rates were in excess of 60 %, from one or two annual litters of one to three

young and adult longevity of at least two years (How, Humphries, Bradley, Barnett, and Martin 1984). Bandicoots have r-selected demographic parameters (Gordon and Hulbert 1989) and although variation occurs over their wide geographic range, first year mortality rates of approximately 85 % have been reported by Stoddart and Braithwaite (1979) in brown bandicoots.

2.3.6 Conclusion.

The potoroo population at Porter Hill is demographically characterised by a male-biased adult sex-ratio, sexual dimorphism in greater male body mass, and low rates of recruitment with compensatory high longevity of resident animals. Breeding is aseasonal, and intrasexual behavioural avoidance is evident. These results will be analysed further, especially in relation to home-range, in later chapters.

The potoroo demographic data presented here amplify previous knowledge from smaller-scale studies and provide evidence of intraspecific variation. Juvenile and sub-adult potoroos experienced high mortality, of the order of 80 % in this study. Longevity of the order of six to eight years is shown here to represent a pattern of significantly enhanced survivorship for individual potoroos which become established in the population as young adults. Breeding has been shown to be aseasonal in this study, in contrast with prior suggestions of seasonal peaks within an underlying continuous breeding pattern. Poroos are less fecund on an annual basis than comparable species such as bandicoots, but population viability is enhanced by relatively high adult survivorship and continuous breeding. Body mass sexual dimorphism was significant in this study but not in that of Bennett (1987) in western Victoria, indicating significant intraspecific variation in the long-nosed potoroo.

Chapter Three.

Habitat and Microhabitat Characteristics at Porter Hill in Relation to Mammalian Utilisation.

The habitat of a plant or animal often encompasses a spectrum of environments, especially for adaptable species such as many mammals. Within a generalised habitat, a population may make differential use of environmental resources, especially food and shelter. Microhabitats are relatively homogeneous components of broad local habitats and are of particular interest where they may provide specific resource requirements of fauna.

Potoroo habitat is generally described as coastal heathland and dry and wet sclerophyll forest, with the presence of thick ground cover and annual rainfall in excess of 760 mm as major habitat requirements (Seebeck 1981; Johnston 1983). In Tasmania the edges of thick tea-tree swamps are utilised (Green 1973), while grassy areas are avoided (Johnson and Rose 1983).

Microhabitat is defined as the spatial and qualitative characteristics of a species environment at the organism-sized level. Floristic and structural features of vegetation are useful descriptors of habitat cues to which mammals may respond (Fox and Fox 1981). Spatially, microhabitat can be expected to be important in terms of cover, particularly as protection from avian predators, and in providing refugia at ground level. Structural attributes of the microhabitat may also dictate access to some elements present (e.g. for soil-foraging species substrate friability may also be important in allowing cost-effective foraging). Food resources are usually an important aspect of microhabitat. In this study microhabitats within the various local generalised gradients of substrate, and floristic and structural vegetation are examined so that usage patterns by potoroos in particular, but also by bandicoots and the bettong, may be determined.

Porter Hill (E 147°23' S 52°54') is located five km southeast of Hobart and includes typical elements of residual bushland habitats of southeastern Tasmania. The site is

of significance for previous potoroo studies (e.g. Guiler 1958, Kitchener 1973, Johnson 1988), and includes a range of physical and biotic environments.

The principle aim of this chapter is to investigate patterns of potoroo utilisation, based on capture rates, of microhabitat components at Porter Hill. A general description of the habitat at Porter Hill and an analysis of detailed structural and floristic microhabitat characteristics are provided. Mammal capture rate patterns are analysed in relation to vegetation structure and floristic microhabitat characteristics.

3.1 Methods.

3.1.1 Microhabitat Definition.

Although a snapshot of the floristic and structural components of vascular plant distribution at Porter Hill (surveyed early in 1994) rather than an ongoing botanical survey, many individuals of the larger species existed throughout this study and reflect environmental gradients. Non-vascular plants have not been included in this survey because of unavoidable site disturbance and taxonomic uncertainties in surveying the hypogeal macrofungi which predominate in the diet of *Potorous tridactylus* (Claridge, Tanton and McNee 1993), and *Bettongia gaimardii* (Taylor 1988). At least in the case of ectomycorrhizal macrofungi, host-tree specificity is usual, in this context presumably predominantly with *Eucalyptus* and *Allocasuarina* species.

Determination of floristic microhabitats was based on vascular plant presence or absence at trapsites. Vascular plant species growing within or projecting into 4X4 metre quadrats (centered on the trapsite and oriented randomly) were recorded. An agglomerative classification program (PATN, FUSE procedure, CSIRO Wildlife Research) was used to cluster those sites having similar floristic composition, based on the presence or absence of each species at each site.

Structural attributes of sites were assessed following the methods of Bennett (1993), with the following modifications. Two-metre square quadrats of random orientation were centred on trapsites. A narrow three metre pole divided into 20 cm intervals was used to sample vertical vegetation density at ten points at each site. One sample

was taken at each corner and three at random, non-overlapping points along each two metre line across the centre of the quadrat. The presence or absence of plant material touching the pole within each 20 cm interval was recorded. A within-stratum comparative index of density was obtained by summing all contacts at each level at each site, and for each site total vegetation density (≤ 3.0 m) was obtained by summing all contacts at that site. An index of vertical diversity was calculated using the Shannon-Weiner formula :

$H = (-S (p_i \ln p_i))$, where p_i is equal to the proportion of contacts within stratum i.)

Structural microhabitat groups were determined using the agglomerative classification program (PATN, FUSE procedure, CSIRO Wildlife Research) to cluster those sites having similar structural composition, based on the sum of contacts within each stratum for each site.

3.1.2 Mammalian Utilisation Pattern.

Utilisation patterns of potoroos and other mammals were analysed using analysis of variance techniques with Tukey multiple comparison tests for site-specific capture rates of each species within floristic and structural groups of sites.

3.1.3 Seasonal Variation in Capture Rates Between Floristic Groups.

Seasons were defined as seasons from January-April, May-August and September-December in order to minimise the disaggregation of the data and broadly reflect local seasonal patterns. One-way analysis of variance was used to determine whether significant between-season variation in capture rate occurred.

3.2 Results.

3.2.1 Physical and General Habitat Description.

Geologically, Porter Hill includes Permian mudstone sedimentary substrates, with associated poor soils, and Jurassic dolerite with nutrient-rich, but poorly-structured, soils (Leaman 1972; Kirkpatrick, Gilfedder and Fensham 1988). Topographically it varies from gentle to often steep slopes. The vegetation is characterised by typical native species for such conditions but also includes vigorous invasive exotics reflecting, at least in parts, a frequent fire regime. Aspect strongly influences soil

moisture so that easterly and northerly slopes have different vegetation types to those on the southern side. Northern and eastern slopes tend to be dominated by dry sclerophyll elements such as white peppermint, *Eucalyptus pulchella* / white gum (*E. viminalis*) woodland with a shrubby or grassy / heathy understorey. Drooping sheoak (*Allocasuarina stricta*) may be present and where frequent fires have occurred it may form monospecific stands.

The southern and western slopes at Porter Hill are dominated by more mesic sclerophyll elements such as Tasmanian bluegum (*E. globulus*) open forest with a scrubby understorey. Drooping sheoak is commonly present with small trees such as sweet bursaria (*Bursaria spinosa*), hop bush (*Dodonea viscosa*) and blackwood (*Acacia melanoxylon*). At ground level fewer plants are present than on northern and eastern slopes, but sagg (*Lomandra longifolia*) and occasional tussocks (*Poa* spp.) provide thickets, as do fallen branches.

3.2.2 Floristics.

Ten floristic groups resulted from the agglomerative classification of the 200 site (Table 3.1). Several species were well represented within almost all groups. These were *Allocasuarina verticillata*, *Astroloma humifusum*, *Bossia prostrata*, *Lomandra longifolia*, and *Poa* spp., and unless noted are present in each group.

Group 1 These were all situated on the drier northern slopes of Porter Hill, predominantly on mudstone soils. Dominant trees included *Allocasuarina verticillata* and *Eucalyptus viminalis*, with a prominent shrub layer comprising *Dodonea viscosa* and the introduced *Chrysanthemoides moniliferum*. The field layer was comprised chiefly of sedges, heaths, grasses and herbs, mainly *Lomandra* sp., *Lepidosperma laterale*, *Themeda triandra*, *Dianella revoluta*, *Pimelea humilis*, *Gonocarpus* sp. and *Wahlenbergia* sp. Other trees present less commonly were *Allocasuarina littoralis* and *Eucalyptus pulchella*.

Figure 3.1
Floristic groups at Porter Hill in relation to trapsites.

Floristic Groups at Porter Hill

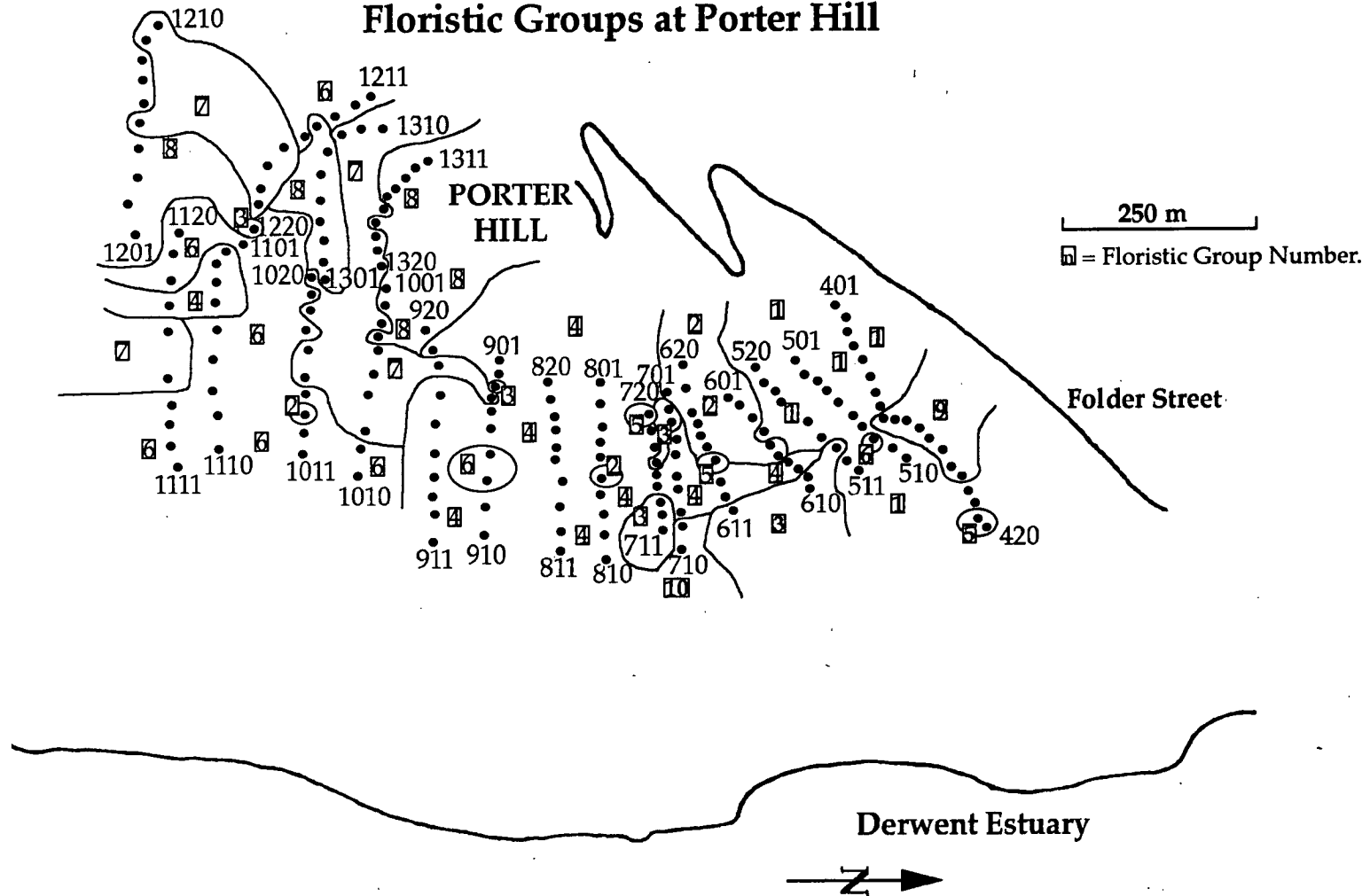


Table 3.1 Frequency of occurrence (%) of plant species within floristic groups at Porter Hill.

Floristic groups were compiled using an agglomerative classification program (PATN; Fuse procedure). Species that occur at a frequency of at least 50% within a group are shown in bold type.

| Species | Floristic Group | | | | | | | | | |
|-------------------------------------|-----------------|------------|-----------|-----------|------------|------------|------------|------------|------------|------------|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| <i>Acacia dealbata</i> | 10 | 57 | 42 | 23 | 50 | 9 | 0 | 5 | 63 | 0 |
| <i>Acacia melanoxylon</i> | 0 | 7 | 25 | 23 | 0 | 34 | 42 | 62 | 25 | 0 |
| <i>Acacia verticillata</i> | 0 | 0 | 0 | 0 | 0 | 6 | 0 | 100 | 0 | 0 |
| <i>Acrotriche serrulata</i> | 3 | 7 | 0 | 4 | 0 | 0 | 0 | 0 | 75 | 0 |
| <i>Allocasuarina littoralis</i> | 24 | 0 | 0 | 4 | 0 | 6 | 0 | 0 | 100 | 0 |
| <i>Allocasuarina verticillata</i> | 97 | 100 | 92 | 98 | 100 | 97 | 100 | 100 | 25 | 100 |
| <i>Astroloma humifusum</i> | 97 | 86 | 83 | 98 | 50 | 100 | 100 | 81 | 25 | 100 |
| <i>Bedfordia linearis</i> | 7 | 0 | 0 | 4 | 0 | 0 | 4 | 100 | 0 | 100 |
| <i>Beyeria viscosa</i> | 10 | 0 | 0 | 2 | 0 | 0 | 0 | 33 | 0 | 0 |
| <i>Bossia prostrata</i> | 97 | 14 | 83 | 98 | 100 | 91 | 92 | 81 | 50 | 0 |
| <i>Bursaria spinosa</i> | 24 | 0 | 58 | 0 | 0 | 19 | 77 | 67 | 38 | 0 |
| <i>Cassinia aculeata</i> | 3 | 14 | 0 | 0 | 50 | 9 | 12 | 0 | 0 | 0 |
| <i>Cassyltha pubescens</i> | 3 | 14 | 92 | 21 | 0 | 13 | 19 | 24 | 0 | 0 |
| <i>Centaurium australe</i> | 3 | 29 | 0 | 6 | 0 | 13 | 8 | 0 | 13 | 0 |
| <i>Chrysanthemoides monoliferum</i> | 83 | 50 | 92 | 65 | 75 | 34 | 23 | 0 | 100 | 0 |
| <i>Daviesia ulicina</i> | 0 | 7 | 0 | 12 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Dianella revoluta</i> | 66 | 14 | 33 | 54 | 25 | 6 | 19 | 5 | 100 | 0 |
| <i>Dodonea viscosa</i> | 97 | 93 | 92 | 31 | 25 | 34 | 73 | 52 | 38 | 0 |
| <i>Epacris impressa</i> | 3 | 0 | 42 | 67 | 0 | 44 | 12 | 48 | 0 | 0 |
| <i>Eucalyptus amygdalina</i> | 34 | 0 | 75 | 69 | 0 | 94 | 73 | 95 | 100 | 0 |
| <i>Eucalyptus globulus</i> | 0 | 7 | 33 | 19 | 0 | 50 | 38 | 29 | 0 | 50 |
| <i>Eucalyptus viminalis</i> | 83 | 93 | 83 | 77 | 0 | 22 | 4 | 5 | 13 | 50 |
| <i>Exocarpus cupressiformis</i> | 34 | 50 | 67 | 42 | 0 | 16 | 35 | 48 | 50 | 0 |
| <i>Gonocarpus</i> sp. | 90 | 36 | 50 | 79 | 50 | 88 | 12 | 29 | 100 | 0 |
| <i>Goodenia lanata</i> | 34 | 7 | 50 | 6 | 0 | 22 | 42 | 10 | 0 | 0 |
| <i>Goodenia ovata</i> | 3 | 0 | 8 | 10 | 0 | 28 | 8 | 52 | 0 | 0 |
| <i>Lepidosperma laterale</i> | 76 | 21 | 8 | 19 | 0 | 91 | 38 | 10 | 38 | 50 |
| <i>Leptospermum scoparium</i> | 0 | 0 | 0 | 2 | 0 | 25 | 0 | 24 | 0 | 0 |
| <i>Lissanthe strigosa</i> | 0 | 0 | 17 | 8 | 0 | 0 | 0 | 0 | 25 | 0 |
| <i>Lomandra</i> sp. | 62 | 79 | 92 | 96 | 0 | 100 | 96 | 100 | 63 | 100 |
| <i>Microseris scapigerum</i> | 3 | 14 | 0 | 0 | 0 | 44 | 35 | 19 | 0 | 0 |
| <i>Olearia ramulosa</i> | 3 | 0 | 8 | 2 | 0 | 16 | 4 | 5 | 0 | 0 |
| <i>Oxalis corniculata</i> | 31 | 0 | 8 | 0 | 0 | 19 | 15 | 10 | 0 | 0 |
| <i>Pelargonium australe</i> | 0 | 0 | 0 | 0 | 0 | 28 | 15 | 0 | 0 | 0 |
| <i>Pimelea humilis</i> | 62 | 0 | 8 | 8 | 0 | 6 | 8 | 10 | 25 | 0 |
| <i>Poa</i> spp. | 100 | 100 | 50 | 81 | 75 | 97 | 96 | 100 | 100 | 0 |
| <i>Pultenea daphnoides</i> | 3 | 0 | 25 | 27 | 0 | 13 | 4 | 14 | 0 | 100 |
| <i>Pultenea juniperina</i> | 0 | 0 | 33 | 2 | 0 | 6 | 0 | 5 | 0 | 0 |
| <i>Pultenea stricta</i> | 28 | 0 | 0 | 6 | 0 | 31 | 19 | 5 | 25 | 0 |
| <i>Stipa</i> sp. | 45 | 43 | 17 | 56 | 25 | 72 | 42 | 24 | 0 | 0 |
| <i>Stylidium graminifolium</i> | 0 | 0 | 0 | 12 | 0 | 19 | 15 | 10 | 0 | 0 |
| <i>Themeda triandra</i> | 48 | 57 | 50 | 62 | 25 | 66 | 42 | 19 | 0 | 0 |
| <i>Wahlenbergia gracilentia</i> | 66 | 79 | 75 | 75 | 0 | 44 | 27 | 0 | 0 | 0 |
| Number of Sites in Group | 29 | 14 | 12 | 52 | 4 | 32 | 26 | 21 | 8 | 2 |

Group 2 Group two was comprised of 14 sites situated on mudstone substrates on the eastern slopes of Porter Hill. Dominant trees included *Acacia dealbata*, *Allocasuarina verticillata* and *E.viminalis*, but in contrast with group 1, *E.pulchella* and *Allocasuarina littoralis* were absent. A prominent shrub layer comprising *Dodonea viscosa*, *Acacia dealbata*, *Chrysanthemoides moniliferum* and *Exocarpus cupressiformis* was present. The field layer was again of sedges, heaths, grasses and herbs, differing from group one in having a lower frequency of occurrence of *Lepidosperma laterale*, *Dianella revoluta*, *Pimelea humilis* and *Bossia prostrata*.

Group 3 Group three included twelve sites situated on mudstone substrates on easterly slopes. Dominant trees and shrubs were similar to group two except for *Eucalyptus pulchella* often being present. The field layer was also similar to that of group two, but with *Goodenia lanata* often present.

Group 4 With 52 sites, group two was the largest floristic group identified, again mostly situated on mudstone substrates on the eastern and south eastern slopes of Porter Hill. Dominant trees included *Allocasuarina verticillata* with *E.viminalis* and / or *E. pulchella*. The shrub layer was less prominent comprising *Chrysanthemoides moniliferum* and less frequently *Exocarpus cupressiformis* and *Pultenaea daphnoides* were present. The field layer differed from groups one to three in often including *Epacris impressa* and, as with group 1, *Dianella revoluta* was often present.

Group 5 Group five was comprised of only four sites of relatively dense and vertically diverse vegetation, but with low floristic richness. The dominant tree was *Allocasuarina verticillata* alone, with a grassy field layer.

Group 6 Most of the 32 sites of group six were underlain by dolerite substrates on the southern slopes of Porter Hill. Dominant trees are *Allocasuarina verticillata* with *Eucalyptus pulchella* and / or *E. globulus*. The variable shrub layer included *Acacia melanoxylon*, *Chrysanthemoides moniliferum* and *Dodonea viscosa*. The field layer differed from prior groups in often including *Epacris impressa* and, as with group 1, *Lepidosperma laterale*.

Group 7 Group 7 had 26 sites on dolerite substrates on southern slopes. Dominant trees were *Allocasuarina verticillata* with *Eucalyptus pulchella* and/or *E. globulus*. The shrub layer commonly included *Bursaria spinosa* and *Dodonea viscosa*, together with *Acacia melanoxylon* and *Exocarpus cupressiformis*. In contrast with group 6, *Epacris impressa* was uncommon in the field layer and *Lepidosperma laterale* less often present; *Goodenia lanata* was relatively more common.

Group 8 Twenty-one sites on dolerite substrates on southern and south western slopes, dominant trees were *Allocasuarina verticillata* with *Eucalyptus pulchella* and less often *E. globulus*. The shrub layer predominantly included *Bedfordia salicina*, a distinctive feature of this group. Other shrubs were similar to those of group 7, as were plants in the field layer.

Group 9 This group includes eight sites on mudstone substrates on dry, exposed northern slopes. Dominant trees were *E. pulchella*, *Acacia dealbata* and *Allocasuarina littoralis*. The shrub layer was intermittent and chiefly comprised of young *Acacia* and *Allocasuarina* regrowth after fire. The field layer was dominated by *Dianella revoluta*, *Acrotriche serrulata*, *Gonocarpus* sp.; *Wahlenbergia* sp. was absent.

Group 10 Group 10 was comprised of only 2 floristically depauperate sites. The dominant tree was *Allocasuarina verticillata*, with *Pultenaea daphnoides* and *Bedfordia salicina* in the shrub layer, and a non-grassy field layer with sedges present.

Sites common to floristic groups tended to be contiguous. A map of the floristic groups of the study area, with subjective interpolation, is presented in Figure 3.1.

3.2.3 Structural Vegetation Characteristics.

Structural characteristics of the floristic groups are presented in Table 3.2, and significant between-group differences in structural attributes in Table 3.3. Floristic groups one, two and three on mudstone soils were structurally similar, with both density at heights less than three metres above ground and vertical diversity moderate

compared to other groups. Floristic group four on mudstone soils was structurally less dense and diverse than the former groups. Group five had the highest total density and moderate structural diversity, but with little floristic richness. Groups nine and ten were of sparse vegetation (low density) over mudstone soils, with group ten having relatively high vertical diversity.

Groups six, seven and eight were all over dolerite soil, with groups six and seven characterised by low density with group seven having higher vertical diversity. In group eight sites, both density at heights less than 3m and vertical diversity were high in comparison with other groups.

Strata close to ground level (1-60 cm) all displayed significant between group differences in vegetation density. The main contributing factor to this was the presence of tussock grasses (*Themeda triandra* and *Poa* spp.) and sedges (*Lomandra* spp.). The grasses tend to be ephemeral, with considerable year to year variation in luxuriance, while the sedges are perennial and may provide cover and nesting sites for potoroos and bandicoots (Johnson 1988).

3.2.4 Mammal Capture Rate Patterns in Relation to Floristic Groups.

Of the mammal species studied at Porter Hill, potoroos and brushtail possums exhibited significant ($P < 0.05$) separate preferences for floristic groups, while no significant differences in association with floristic groups were found for bettongs or brown bandicoots (Table 3.4).

Potorous tridactylus

The floristically depauperate Group Ten, comprised of only two sites, featured in all significant between-group differences for potoroo capture rates by floristic group, with group ten sites having significantly higher capture rates than groups four, six, seven, eight and nine. The most distinctive contrast between group ten and the groups for which capture rates significantly differ is the absence of eucalypts and grasses in group ten.

Table 3.2. Mean values of structural attributes and floristic richness of floristic groups at Porter Hill.

Structural attributes are explained in the text.

| Structural attribute | Floristic Group | | | | | | | | | | F | Sig. |
|------------------------|-----------------|------|------|------|------|------|------|------|-------|------|------|------|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | | |
| Vegetation Height (cm) | | | | | | | | | | | | |
| 1-20 | 6.6 | 8.4 | 7.3 | 8.8 | 9.3 | 9.5 | 6.0 | 7.0 | 6.7 | 3.5 | 6.34 | *** |
| 21-40 | 4.8 | 6.4 | 5.6 | 7.6 | 7.7 | 8.1 | 4.7 | 5.0 | 4.1 | 1.5 | 6.68 | *** |
| 41-60 | 3.2 | 4.6 | 4.0 | 5.5 | 5.7 | 6.0 | 3.8 | 4.0 | 2.6 | 1.0 | 4.53 | *** |
| 61-80 | 2.8 | 3.8 | 2.0 | 3.4 | 4.2 | 3.4 | 2.7 | 3.5 | 1.8 | 1.5 | 1.47 | n.s. |
| 81-100 | 2.5 | 2.3 | 1.7 | 1.8 | 4.7 | 1.8 | 2.1 | 2.8 | 1.4 | 3.5 | 1.85 | n.s. |
| 101-120 | 2.7 | 2.3 | 2.8 | 1.9 | 4.2 | 1.3 | 2.0 | 2.5 | 1.1 | 3.5 | 2.40 | n.s. |
| 121-140 | 2.9 | 2.0 | 3.4 | 1.9 | 2.0 | 1.3 | 2.1 | 2.6 | 1.0 | 2.0 | 2.52 | ** |
| 141-160 | 2.8 | 2.1 | 2.9 | 1.5 | 2.0 | 1.0 | 2.1 | 2.8 | 1.1 | 3.0 | 3.17 | ** |
| 161-180 | 2.5 | 2.0 | 2.4 | 1.2 | 2.0 | 1.0 | 2.1 | 2.5 | 1.0 | 3.5 | 3.16 | ** |
| 181-200 | 2.2 | 1.7 | 2.2 | 0.8 | 1.3 | 1.0 | 1.7 | 1.9 | 0.8 | 2.5 | 3.02 | ** |
| 201-220 | 1.8 | 1.5 | 1.6 | 0.7 | 1.5 | 1.0 | 1.8 | 2.1 | 0.6 | 2.0 | 2.76 | ** |
| 221-240 | 1.6 | 1.4 | 1.5 | 0.7 | 1.5 | 1.0 | 2.0 | 2.5 | 0.9 | 3.0 | 3.56 | *** |
| 241-260 | 1.4 | 1.4 | 1.1 | 0.7 | 1.3 | 0.7 | 1.7 | 2.1 | 1.3 | 3.0 | 2.97 | ** |
| 261-280 | 1.2 | 1.4 | 1.0 | 0.5 | 1.5 | 0.6 | 1.0 | 1.6 | 0.8 | 1.5 | 2.08 | n.s. |
| 281-300 | 1.2 | 1.3 | 0.8 | 0.4 | 1.5 | 0.5 | 0.8 | 1.1 | 0.8 | 1.0 | 1.61 | n.s. |
| Tot 0-3m. | 40.2 | 42.6 | 40.3 | 37.4 | 50.4 | 38.2 | 36.6 | 44.0 | 26.0 | 36.0 | 2.15 | n.s. |
| Mean Vert. Div<3m | 2.14 | 2.09 | 2.05 | 1.94 | 2.34 | 1.91 | 2.33 | 2.4 | 1.85 | 2.56 | 4.21 | *** |
| Floristic richness | 14.7 | 10.9 | 15.7 | 13.7 | 6.5 | 15.3 | 12.7 | 14 | 11.88 | 7 | 9.59 | *** |
| Number of sites | 29 | 14 | 12 | 52 | 4 | 32 | 26 | 21 | 8 | 2 | | |

*** $P < 0.001$;** $P < 0.01$;

n.s., not significant.

Table 3.3 Multiple comparison (Tukey) of structural differences between groups. The first of paired groups was of higher density.

| | | | | | | | | | |
|---|-----|-----|-----|-----|-----|-----|-----|-----|------|
| Vegetation density (cm) | | | | | | | | | |
| 1-20 | 4-1 | 6-1 | 4-7 | | | 6-7 | 6-8 | | 6-10 |
| 21-40 | 4-1 | 6-1 | 4-7 | 4-8 | 4-9 | 6-7 | 6-8 | 6-9 | 6-10 |
| 41-60 | 4-1 | 6-1 | | | | 6-7 | | 6-9 | |
| 61-80 | | | | | | | | | |
| 81-100 | | | | | | | | | |
| 101-120 | | | | | | | | | |
| 121-140 | | 6-1 | 3-6 | | | | | | |
| 141-160 | | 6-1 | | | | | 6-8 | | |
| 161-180 | 4-1 | 6-1 | | | | | | | |
| 181-200 | 4-1 | | | | | | | | |
| 201-220 | | | 4-7 | 8-4 | | | | | |
| 221-240 | | | 4-7 | 8-4 | | | 8-6 | | |
| 241-260 | | | | 8-4 | | | 8-6 | | |
| 261-280 | | | | | | | | | |
| 281-300 | | | | | | | | | |
| Tot 0-3m | | | | | | | | | |
| Note : Between-group differences indicated are significant (P < 0.05). | | | | | | | | | |

Structurally, group 10 was significantly less dense at the lowest levels (1-40 cm) than group six and was of low density at all heights of less than 80 cm. It was also the most vertically diverse floristic group (Table 3.2).

Trichosurus vulpecula

Capture rates for Brushtail Possums were consistently higher in floristic groups seven and six than in group four. This represents a consistent preference for vegetation on dolerite soils over drier vegetation types on mudstone soils at Porter Hill. Structural characteristics of floristic groups preferred by brushtail possum did not exhibit clear trends and included significant differences in vertical diversity within preferred groups (Tables 3.2; 3.3).

Table 3.4 Capture rates (captures per 100 trapnights) by floristic group for mammal species at Porter Hill.

F values are based on one-way analysis of variance. Significant ($P < 0.05$) between-group differences were determined by Tukey comparisons. Groups with significantly higher capture rates are indicated by {n}, where n are groups with lower capture rates.

| | Floristic Group | Potoroo | Bandicoot | Bettong | Brushtail Possum |
|--------------|-----------------|---------------------|-----------|---------|------------------|
| — | 1 | 27.8 | 7.75 | 3.81 | 1.97 |
| — | 2 | 29.0 | 7.21 | 0.69 | 5.02 |
| | 3 | 29.9 | 5.91 | 0.82 | 3.76 |
| | 4 | 23.0 | 4.87 | 1.56 | 2.44 |
| | 5 | 34.5 | 7.38 | 0.83 | 2.46 |
| | 6 | 20.8 | 3.45 | 1.14 | 7.02{4} |
| | 7 | 20.7 | 1.75 | 0.46 | 7.75{4} |
| | 8 | 19.7 | 1.44 | 0.19 | 6.47 |
| | 9 | 18.0 | 8.48 | 2.23 | 3.12 |
| | 10 | 51.6{9, 8, 7, 6, 4} | 7.81 | 0 | 3.12 |
| F Value | | 4.07 | 1.76 | 1.78 | 2.62 |
| Significance | | *** | n.s. | n.s. | *** |

n.s. : not significant.
*** : significant ($P < 0.01$).

3.2.5 Variation in Capture Rates Between Floristic Groups.

Potoroo capture rates by floristic group are presented in table 3.4. Capture rate was generally homogeneous between floristic groups, with only one of the ten groups, group one, exhibiting significant seasonal variation (table 3.4).

3.3 Discussion.

3.3.1 Microhabitat Studies of Marsupials.

Many studies describe broad habitat characteristics of mammals, but only some, e.g. Barnett, How, and Humphries (1978), Fox and Fox (1981), and Bennett (1993) examine possible relationships with microhabitat. Often the findings have not indicated preferences for floristic or structural microhabitat, and have been interpreted as indicating a preference or requirement for a diverse vegetation mosaic (e.g. Bennett 1993).

3.3.2 Microhabitat Implications for Potoroids and Bandicoots.

Potoroos are primarily mycophagous omnivores (Guiler 1971; Bennett and Baxter 1989). Of the sympatric mammals at Porter Hill comparable in trophic niche and body mass, the brown bandicoot is a generalised omnivore (Heinsohn 1966), with mycophagy of dietary significance in at least some populations (Claridge and May 1994), while the bettong is predominantly mycophagous (Taylor 1992b). Omnivory in both the potoroo and bettong extends to dietary items including plant leaf and stem tissue, tubers, seeds and fruit, gum, and invertebrates (Kitchener 1967; Guiler 1971; Seebeck *et al* 1989; Taylor 1992b; Claridge, Tanton and Cunningham 1993). All of the dietary studies above were based on faecal analysis of traceable components of ingesta, and therefore susceptible to difficulties arising from differential digestion and excretion of ingested items. Observations at Porter Hill of extensive digging around the base of Tasman flax lily (*Dianella revoluta*) which possesses starchy rhizomes (Henderson 1987), of excavation of vanilla lily (*Arthropodium milleflorum*) tubers (not noted as a component of floristic groups, possibly due to its ephemeral occurrence), and the presence of other tuberous species such as the yam daisy (*Microseris scapigera*) indicates that foods with nutritional value, but which may easily be underrepresented in faecal sampling, are sought by omnivorous soil-foraging marsupials.

In view of the distribution of known food plants and the probable association of hypogeal fungi with some trees, floristic microhabitat differentiation is of interest in determining niche partitioning between omnivorous species. Caution in interpretation of capture data in this context is necessary, however, as behaviour leading to capture may not reflect general feeding activity, particularly for such a mobile species as the eastern bettong which can move up to 1.5 km per night (Taylor 1988).

3.3.3 Potoroo Capture Rates in Relation to Microhabitat.

Potoroo capture rates were significantly higher in a small group of sites characterised by depauperate vegetation and a lack of eucalypts. Hypogeal sporocarp productivity has been linked to proximity to *Eucalyptus tenuiramis* basal trunks (Johnson 1994c),

and in association with eucalypts more generally (Claridge and May 1994). An alternative explanation to a feeding association with floristic group 10 found in this study is that, since group ten sites had the least dense vegetation at 0-80 cm above ground level (Table 3.2), the result may indicate exploratory behaviour in more open areas.

The presence of dense heath or scrubby vegetation has often been cited as a general habitat requirement of *Potorous tridactylus*, e.g. Green (1973); Seebeck *et al* (1989). For the bettong, Taylor (1988) found that habitats with dense understorey did not support bettongs, implying mutually exclusive habitats for these potoroids. Although more suitable bettong habitat of open, grassy *Eucalyptus viminalis* / *E. pulchella* woodland occurs nearby on dolerite slopes on the eastern slopes of Mount Nelson, and to a lesser extent at Porter Hill, such inferences cannot be drawn on a fine scale from these data. Potoroos, brown bandicoots and bettongs at Porter Hill utilise a complex mosaic of dense and more open vegetation, which afford shelter from both predators and the elements and an available food supply, as was found by Bennett (1993) for the long-nosed potoroo.

Detail of dietary differences among the sympatric fungivore-omnivores discussed here remains intriguing. Marsupial communities in which potoroos, bettongs and brown bandicoots occur together are almost unreported, and occasionally the barred bandicoot occurs together with the above three omnivores (Hird 1994; Owen Wilkins, pers. communication). Studies of marsupial fungivory have been hampered by a lack of knowledge of the fungal taxa since potoroos excrete spores of up to 50 species, many of which may be undescribed (Claridge, Tanton and Cunningham 1993), or unrecorded locally. Perhaps chemical biomarkers, which utilise any unique fungal metabolites which persist through the digestive process may prove useful as either qualitative or quantitative indicators of fungal dietary intake.

An interesting corollary is the presumed reliance of hypogeal fungi on vertebrate fungivores as spore vectors (Taylor 1992b). The successful introduction of bettongs to Maria Island in eastern Tasmania (Rounsevell 1989), however, indicates that such an obligate relationship does not extend to all fungus / fungivore combinations.

Potoroos are indigenous to Maria Island, so bettongs must either overlap in their diet with potoroos on Maria Island or exploit fungi which are not used by potoroos and, since they were presumably originally present, lack an obligate reliance on a potoroid as a spore vector. Other offshore islands in Tasmania appear to include suitable potoroid or peramelid habitat but not fungivore / omnivore populations, e.g. Schouten Island (Hird 1993); fungi presumed to be reliant on vertebrate spore vectors should be absent from such locations.

3.3.4 Bettong and Bandicoot Capture Rates in Relation to Microhabitat.

Neither bettongs nor bandicoots exhibited significant association with floristic groups in this study, although for both species F-values were close to significant levels ($0.1 > P > 0.05$).

Bettong capture rates were highest in vegetation groups characterised by open physical structure on drier slopes. While such vegetation types are within the range of general habitats described for bettongs (Taylor 1988), potoroos and bettongs have usually been regarded as locally allopatric species (e.g. Johnson and Rose 1983). Bettongs had not previously been recorded at Porter Hill (Johnson 1988). This, together with the fact that bettong captures only occurred over the second half of the study, indicates that as well as being mobile species on a nightly basis (with movements of up to 1.5 km (Taylor 1993)), bettongs are locally able at least temporarily to exploit habitats previously unoccupied. A complicating factor is that land clearance in more typical bettong habitat further north on Mt Nelson during the course of the study may have displaced bettongs toward Porter Hill, possibly for shelter as much as feeding sites in view of their previous absence.

Bandicoots are often suggested to be ecologically flexible species, both in terms of diet and population parameters (e.g. Gordon and Hulbert 1991) and also to utilise vegetational mosaics. Their significantly higher capture rates in heathy woodland rather than open forest vegetation in this study is consistent with the the ecological flexibility of a generalist species and the findings of Bennett (1993).

3.3.5 Brushtail Possum Capture Rates in Relation to Microhabitat

For brushtail possums, the presence of larger trees on preferred sites (apparent but not quantified in this study), and thus den-sites, may be a factor influencing the distribution of this species over and above that of floristic composition of microhabitat.

3.3.6 Seasonal Variation in Potoroo Capture Rates Between Floristic Group.

Although seasonal variation in capture rate was found to be significant in one floristic group, no general trend was apparent. Group 1, in which the significant result was detected, is the most northerly (and thus most insolated) of the floristic groups in this study and may have been more subject to seasonal extremes.

In contrast with the findings of this study, significant seasonal variation in capture rates between floristic groups was reported by Bennett (1993). Unlike Porter Hill, however, the study site of Bennett (1993) in western Victoria was subject to seasonal inundation and the waterlogged soil at some times of the year may have then deterred potoroos from foraging in that microhabitat. Potoroos have also been reported as using the edges of tea-tree swamp habitats in Tasmania (Green 1973). The most extreme seasonal variation at Porter Hill is likely to be late summer drought with below-average rainfall for several months. Although lack of soil moisture may have a deleterious effect on hypogeal sporocarp productivity (Claridge and May 1994), long-term mean rainfall in Hobart is evenly distributed between all months and drought years are likely to be at most a minor contributing factor to any long-term seasonal variation in potoroo activity.

3.3.7 Conclusions.

Although floristic classification techniques produced plausible vegetation associations, the relation of marsupial capture rates with such groups seems tenuous. Although some significantly different capture rates were observed between floristic groups, for the potoroo they were difficult to explain in terms of known and presumed dietary requirements. Rather, the lack of clear vegetation association of potoroos is interpreted as reflecting utilisation of several, if not most, components of the local floristic and structural vegetational mosaic.

The floristic and ecological associations of hypogeal fungi in relation to their distribution and productivity is a fundamental but poorly known aspect of the biology of potoroids and bandicoots (and possibly other animals) as spore vectors and consumers of sporocarps. While such investigations have commenced (e.g. Bennett and Baxter 1989; Johnson 1994a,b,c), it is clear that hypogeal fungi are diverse in both taxonomy and productivity patterns.

Chapter Four.

Home-Range of Resident Potoroos.

4.1 Introduction.

The use of space by individual animals plays a central role in ecological studies. Spatial use may vary with factors such as resource availability, population density, reproductive activities and other social activities (Pianka 1994), and is therefore an important part of the biology of a species. Areas used by an animal may be distinguished as foraging area, nest sites (if used) or defended territory, which, when regarded together, can be called an individual home-range. Mammalian home-range is defined as "that area traversed by the individual in its normal activities of food gathering, mating and caring for young" (Burt 1943). Studies of home-range are therefore fundamental to understanding the ecology and behavioural biology of a species.

Home-ranges may be delineated from locational data derived from direct observations, trap-site records or radio-tracking (or other remote-sensing information). Intraspecific home-ranges may vary both between individuals and between populations in differing microhabitats (Pianka 1994). Similarly, within the lifetime of an individual, home-range may vary with factors such as maturation, availability of otherwise unoccupied habitat, and seasonal factors such as changes in food supply and reproductive cycles.

Home-range in potoroos has been studied by Kitchener (1973) and Johnson (1988) from the present study site, Heinsohn (1968) in north-western Tasmania, and Bennett (1987) and Seebeck (1995b) in western Victoria. Estimates of home-range size have varied widely (from 0.9 ha (females; Johnson 1988) to 19.4 ha (males; Kitchener 1967)), although often based on small sample sizes and methods which may not be strictly comparable. The population studied by Seebeck (1995b; female home-range 1.5 ha, male 2.0 ha) had an unusually high level of diurnal activity and tolerance of humans while that of Kitchener (1973; female home-range 5.2 ha, male 19.6 ha) was comprised of higher body-mass individuals, a factor which may have affected home-range.

Seebeck (1995b) regarded potoroo home-ranges as overlapping, but without reference to any sex-specific pattern. Potoroos in captivity are known to share nests, although adult males in the presence of oestrous females fight (Hughes 1962; Ullmann and Brown 1983). Sharing of nests has been reported in the field (Johnson 1988), although its extent and the wider social implications for individuals sharing

nests are unknown. On the other hand, defence of food resources has not been reported in captive potoroos. Home-range in wild populations of potoroos is therefore important in the biology of *Potorous tridactylus*, but has not previously been adequately quantified.

The principal aims of this study were to estimate male and female home-ranges using an objective, rigorous technique, to determine any significant sex differences in home-range, and, where feasible, to examine any seasonal, year to year or individual lifetime variation in home-range. Home-range in *Potorous tridactylus* is compared with other potoroids and comparable marsupials.

4.2 Methods.

4.2.1 Data Collection.

Individual fixes (mapped points of individual location) used in this study were trap sites at which potoroo captures were made. Cartesian coordinates were calculated for all trap sites (figure 2.2) and digitised to allow spatial analysis of individual capture patterns. Individual sets of fixes (including repeated captures at single sites) were retrieved from the database for further spatial analysis.

Techniques for interpreting an individual's mapped fixes as a home-range area have developed considerably with the advent of both remote sensing techniques and modern computers. Sampling of fixes involves an important assumption; that the fixes recorded are independent of each other. This particularly applies to radio tracking where sequential sampling points may be temporally very close. In a review of home-range studies, Harris, Cresswell, Forde, Trehwella, Woollard and Wray (1990) found that the majority of published papers gave insufficient attention to accurate and sufficient data collection and appropriate and sophisticated analytical techniques.

4.2.2 Home-Range Calculation.

The earliest and simplest techniques used to quantify home-range were polygons enclosing point locations on a plane. Of these, the minimum convex polygon (MCP), (Mohr 1947), is objective and commonly used. Variations include MCPs supplemented by "boundary strips" with a width usually representing half the average inter-locational distance, and "peeled polygons" for which a proportion of outermost points are successively discarded (Harris *et al* 1990). MCP estimates tend to suffer from a high degree of correlation between estimated home-range and sample size, and from the fact that the area mapped by the MCP may include areas rarely or never used by an individual animal (Worton 1987).

The probability density function (PDF) based on a sample of independent point-locations as an individual's "utilisation distribution" (Jennrich and Turner 1969), has been used as in recent studies. Probabilistic methods have the common feature of attempting to assess the probability of occurrence of the subject animal at each point in space, the "utilisation distribution", and can be divided into two classes. The first of these techniques is based on measurement around a parametric "centre of activity" (Hayne 1949), frequently a geometric or harmonic mean. Such techniques produce probabilistic circles or ellipses as home-ranges or internal structural boundaries, but have disadvantages in that the measure of centrality may be unduly affected by outlying fixes and in that the boundaries are constrained by the distribution adopted. A second class of probabilistic methods involves adoption of a non-parametric statistical interpretation of capture or observation points to constitute an estimated home-range. The latter techniques do not make an *a priori* assumption as to location of a "centre of activity" or the shape of the home-range boundary, and are less affected by outlying fixes than parametric PDFs.

PDF methods have been developed with a variety of techniques available to determine isopleths representing different probability-level boundaries.

Non-parametric PDF methods include the kernel method proposed by Worton (1989) and adopted here.

Consensus as to the most reliable or appropriate method for calculating home-range (as defined) is lacking. Some popular methods, e.g. the Harmonic Mean Method of Dixon and Chapman (1980) and the probability density function of Forde and Krumme (1979), have been criticised as unreliable in not providing robust probability distribution functions (Worton 1987). Despite the recent availability of a range of methodologies for home-range determination, with differing underlying assumptions and ensuing results, many studies and reviews (e.g. Seebeck, Bennett and Scotts 1989) have provided estimates or comparisons of home-range based on unstated or potentially incompatible methodologies.

4.2.3 Adequacy of Datasets for Home-Range Calculation.

Adequacy of a database can be assessed by examining the relationship between the number of fixes and the stable or asymptotic home-range estimate (Kenward 1990). Repeated random samples of various sizes are drawn from data for individuals having many available fixes, and mean home-range is calculated for each such sample. When plotted, the sample size at which the mean home-range value consistently approaches the maximal home-range estimate for each individual was considered to be a sufficient threshold value to use with real data.

For each of the seven individuals for which 40 or more fixes were held, ten random samples of each of five, ten, 15, 20, 30 and 40 fixes were taken from all fixes for that individual. Home-range kernel estimates of 90 percent PDFs (Worton 1990) were calculated using Ranges IV software (Kenward 1990). Home-ranges were also calculated as Minimum Convex Polygons (MCPs) (Kenward 1990) for comparison with kernel estimates. The mean proportions of each individual's home-range (calculated over all fixes) was then plotted against sample size.

This analysis indicated that 20 captures was a reasonable value for which sampled points gave a result asymptotic to the full home-range value (see results). Home-ranges (90 percent PDFs) for the 24 individuals with at least 20 capture records were subsequently calculated.

An important assumption of PDF calculation is that fixes are independent of each other. In this study capture or recapture events were only possible, at most, twice on sequential nights within a transect (Chapter Two). Therefore, capture trappings of individuals used as fixes in this study are considered independent.

4.2.4 Home-Range Overlap and Individual Variation.

A t-test was used to test for sex difference in home-range size. Individual isopleth boundaries (based on 90 percent PDFs) obtained from Ranges IV (Kenward 1990) were plotted and compared for their degree of range overlap. Mean overlap of individual home-ranges by sex was examined using a t-test comparing proportional overlap of each individual with overlapping neighbours of either sex.

4.2.5 Home-Range Variation Within Individual Lifespans.

Analysis of potential seasonal and intra-lifespan variation in home-range was undertaken on those individuals with sufficient capture records. Home-range size and position was examined for potential seasonal variation using both a t-test and plotted PDF boundaries. Home-ranges were also examined for variation between the first and second half of individual known lifespans.

4.3 Results.

4.3.1 Number of Fixes Required to Estimate Home-Range.

Figure 4.1 shows a range of sample-sizes plotted against home-range size for each of the seven individuals for which 40 or more fixes were obtained. Small samples (ten fixes) predicted total home-range relatively poorly (mean = 81.4 % of total; s.d. = 14.8%). Samples of 20 fixes yielded mean home-ranges closer to those based on 40 fixes for each individual (mean = 93.8 % of total; s.d. = 9.0 %). A

minimum of 20 capture points was therefore selected for further analysis of home-ranges.

4.3.2 Characteristics of Individuals in Home-Range Analysis.

A total of 24 potoroos, eight females and 16 males, had 20 or more available fixes for home-range analysis. These individuals represented 25 and 20 per cent respectively of the total individual males and females identified in the study. In general, individuals captured 20 or more times were long-lived compared to individuals trapped less often, although life-span was not significantly correlated with number of captures for these 24 individuals ($r = 0.28 : P > 0.1$).

4.3.3 Sex Differences in Home-Range.

There was a significant difference in mean home-range between sexes (Table 4.1.) This is evident on the basis of both home-range calculation methodologies, with males occupying larger areas. A considerable range of home-range area is also evident both within and between sexes. Of the two methods used for calculating home-range, only the 90% PDF yielded a significant difference between male and female areas (Table 4.1).

Table 4.1. Sex differences in long-nosed potoroo home-range, in the 24 individuals with at least 20 capture records. Methodologies are 90% PDF (Probability Distribution Function) and MCP (Minimum Convex Polygon); see text for definition.

| | N | Area (ha) | | | |
|--------------|----|-----------|------|------|------|
| | | Method | | | |
| | | 90 % PDF | | MCP | |
| | | Mean | s.d. | Mean | s.d. |
| Females | 8 | 5.7 | 2.1 | 6.2 | 1.9 |
| Males | 16 | 10.8 | 6.8 | 9.2 | 6.3 |
| Significance | | * | | n.s. | |

n.s. : non-significant ($P>0.5$).
* : significant ($0.05>P>0.01$).

4.3.4 Differences in Home-Range Over Individual Lifespans.

The results of a paired t-test to determine potential temporal shifts in home-range size between the 90% isopleth home-ranges over the first and second halves of lifespans are presented in table 4.2. No difference in home-range within lifespans is evident, either within sex or for pooled results.

Boundaries for 90% isopleth PDFs for individuals analysed for intra-lifespan home-range analysis are presented in figure 4.2. Inspection of PDF overlap between

halves of known lifespan indicates considerable range overlap, and only slight shifts in location of home-range between halves of known lifespans.

4.3.5 Seasonal Variation in Individual Home-Range.

Seasons were defined as January-April, May-August and September-December in order to minimise the disaggregation of the data and broadly reflect local seasonal patterns. The sample size (N) for some cells is nonetheless well below the preferred threshold (of 20 captures per individual) for home-range analysis. Seasonal 90% PDF home-ranges for those individuals with at least 40 fixes are presented in Table 4.3. No difference in home-range between season (as defined) is evident, either within sex or for pooled results (Figure 4.3).

Table 4.2. Temporal shifts in home-range during individual lifespans. Home-range values are based on first and second halves of all capture locations each individual having at least 40 captures are compared. Differences are not significant (ITl = 0.92; P > 0.35).

| Individual | N (total) | Home-range area (Ha) | | Difference |
|------------|-----------|----------------------|--------|------------|
| | | Half of lifespan | | |
| | | First | Second | |
| P113 | 59 | 11.7 | 4.9 | 6.7 |
| P136 | 92 | 18.5 | 18.5 | 0 |
| P137 | 47 | 6.9 | 7.4 | -0.4 |
| P138 | 44 | 7.7 | 4.2 | 3.5 |
| P145 | 55 | 16.8 | 5.9 | 10.9 |
| P152 | 40 | 4.2 | 11.1 | -6.9 |
| P155 | 53 | 4.0 | 3.8 | 0.2 |

4.3.6 Individual Home-Range Overlap.

Boundaries for 90% isopleth PDFs for all individuals with at least 20 captures are presented in figure 4.4 a, b, c, d, e. Overlays of individual home-ranges are presented on the basis of substantial overlap, and on apparent contrasts between different sets of individual home-ranges.

From inspection of PDF overlap, considerable range overlap both between individuals and within and between sexes is evident. It is presumed that some delineated home-ranges partly extend beyond the trapping grid, although on several sides of the grid natural habitat extended only a short distance.

Figure 4.1

Plots of sample-size of fixes against sample mean home-range size as a percentage of mean 40-fix home-ranges, for each of the seven individuals for which 40 or more fixes were known.

Sample Size Determination for Home-Range Analysis

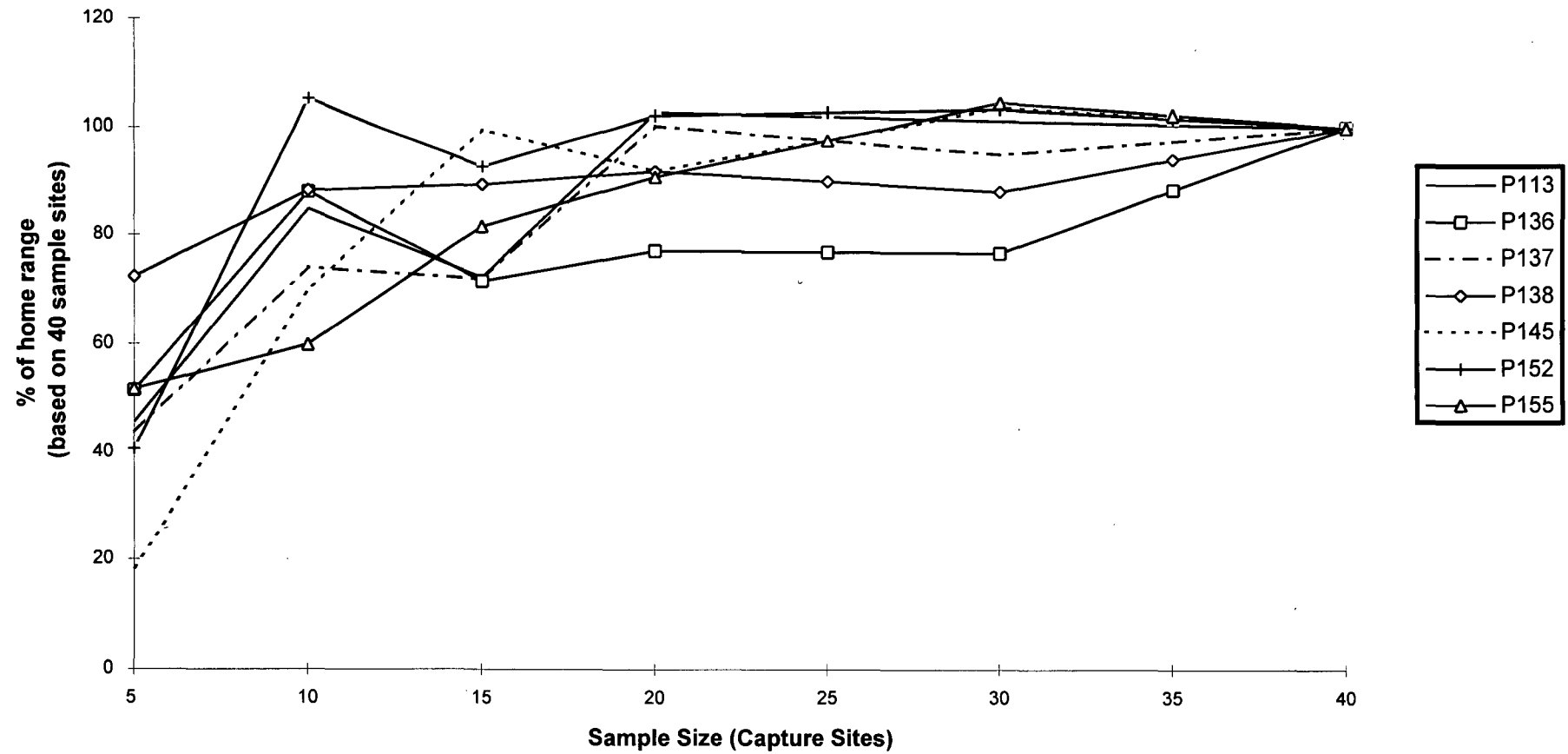


Figure 4.2a, b, c, d, e, f, g.

Intra-lifespan home-range boundaries for 90% isopleth PDFs for the 7 individuals analysed for intra-lifespan home-range variation. Each individual's boundaries are based on first and second halves of captures for that individual.

Outer boundary is 90% isopleth PDF for all sites.

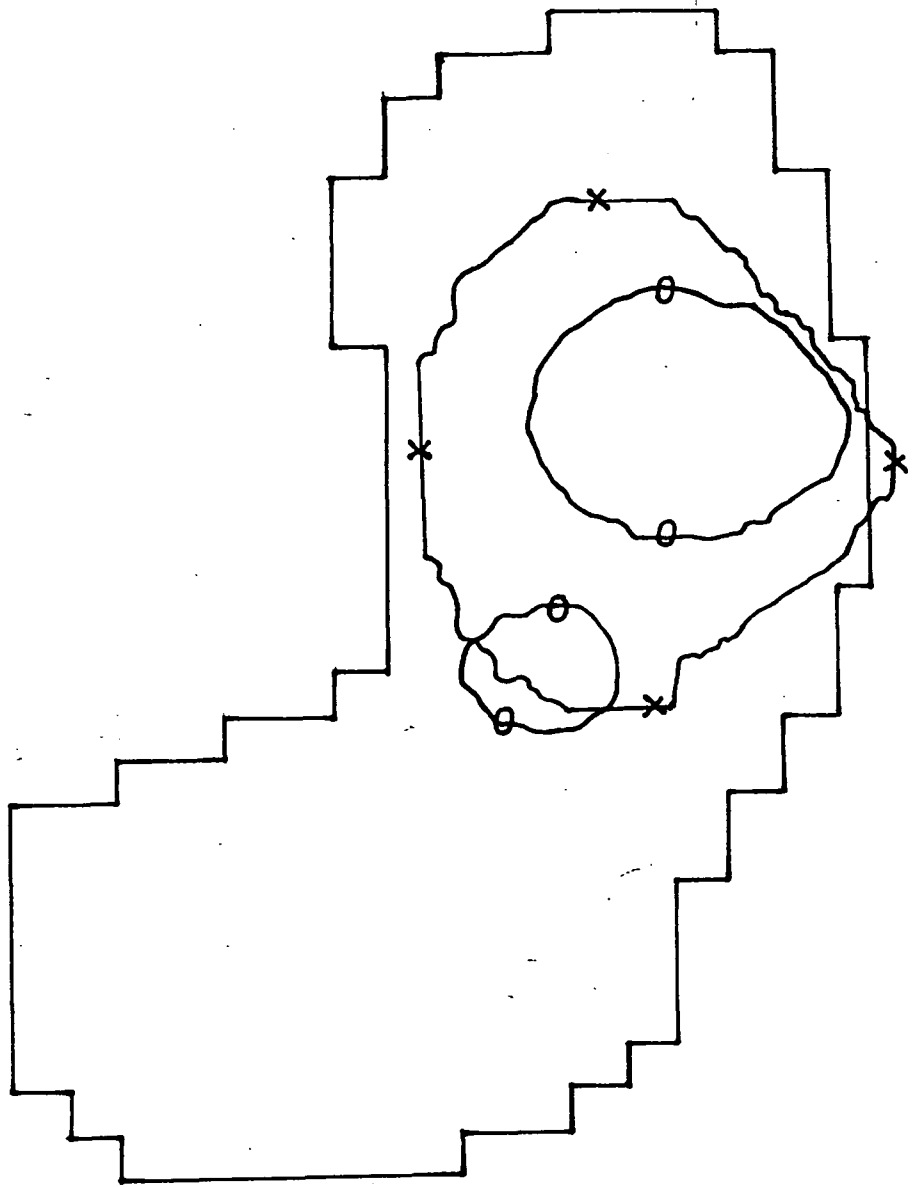
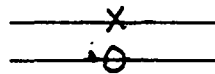


Figure 4.2a.
P113 female

First 50% of Captures
Second 50% of Captures



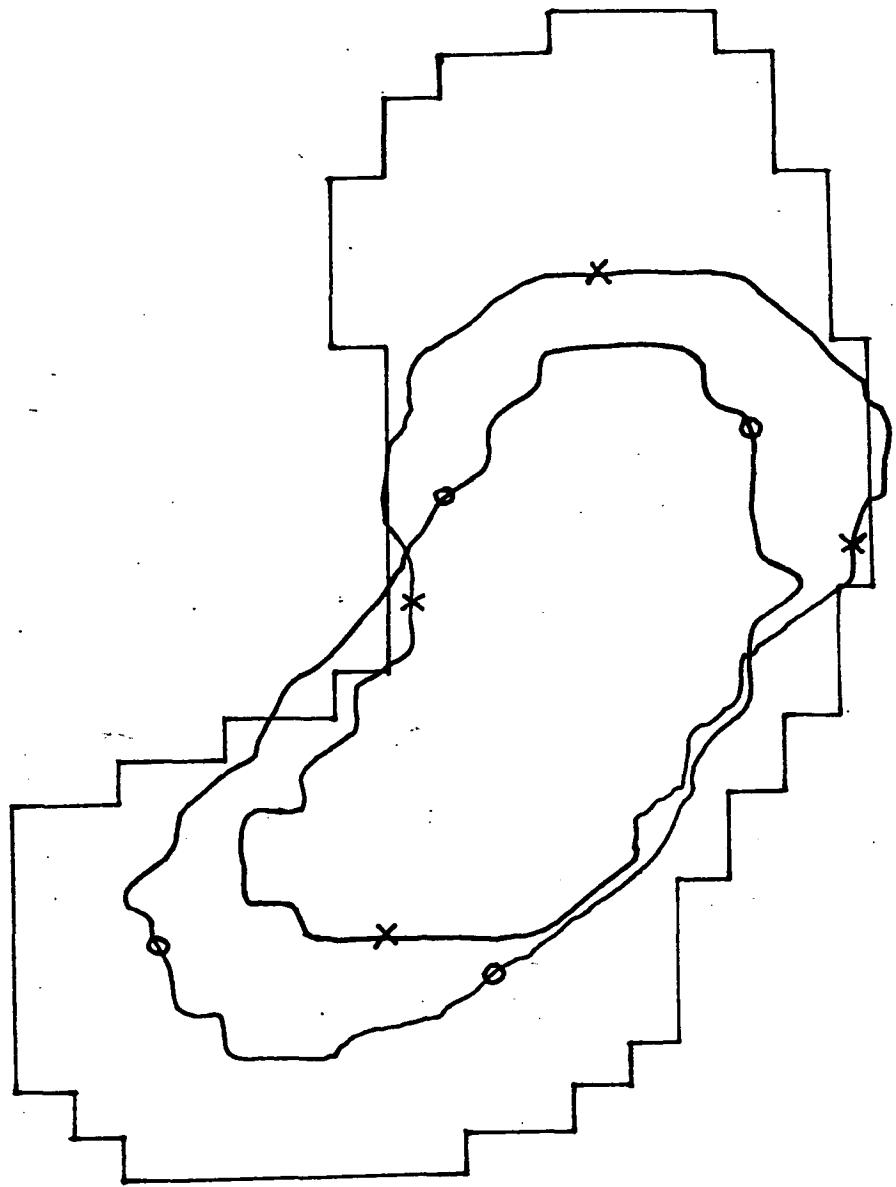
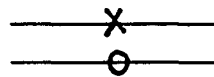


Figure 4.2b.
P136 male

First 50% of Captures
Second 50% of Captures



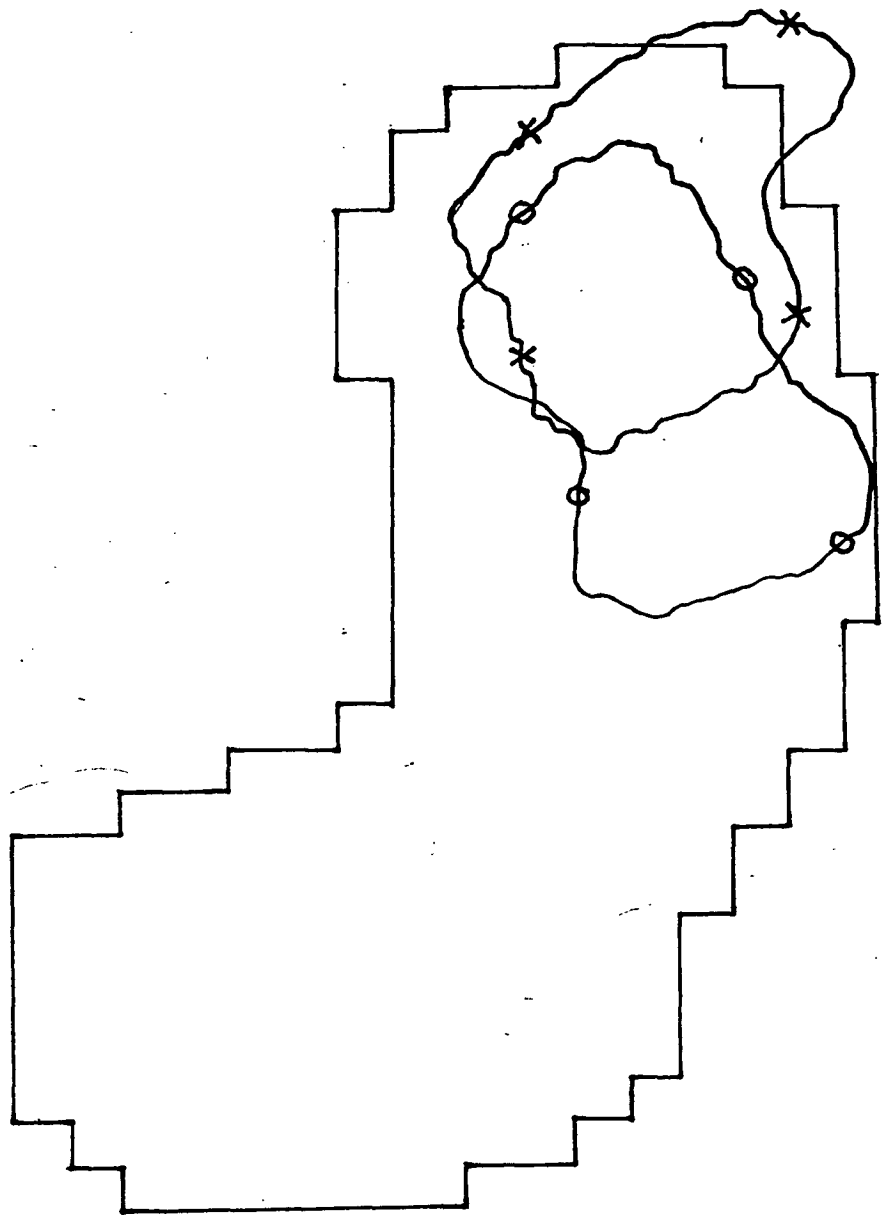
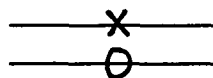


Figure 4.2c.
P137 male

First 50% of Captures
Second 50% of Captures



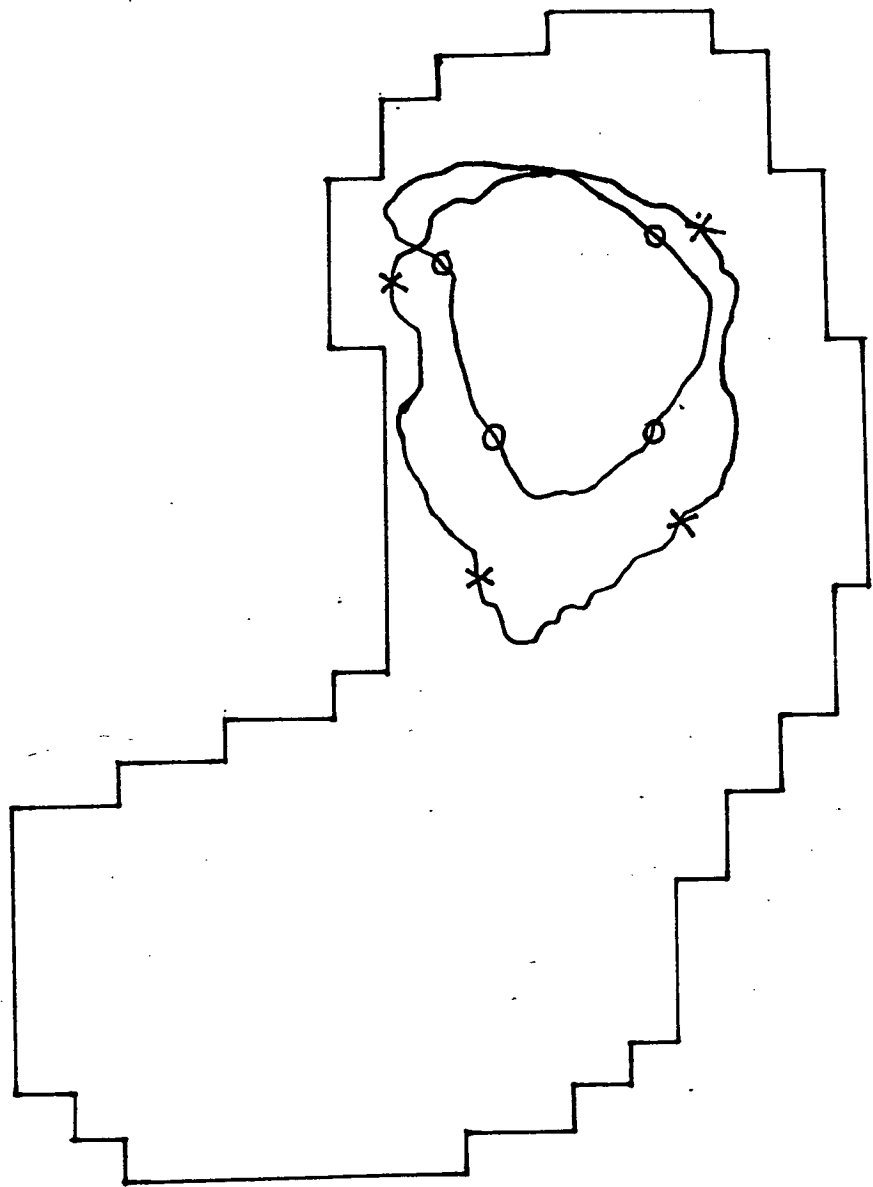
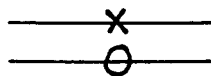


Figure 4.2d.
P138 female

First 50% of Captures
Second 50% of Captures



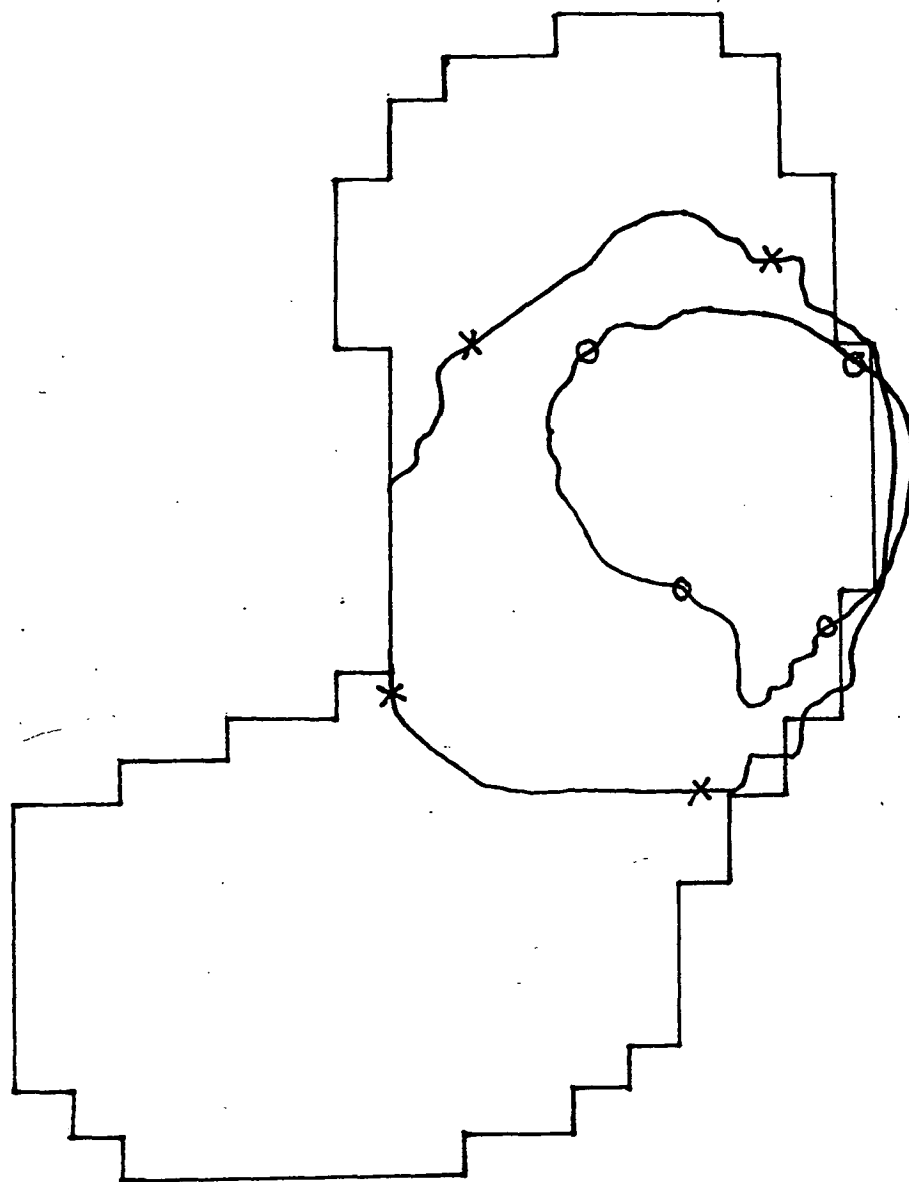
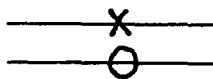


Figure 4.2e.
P145 male

First 50% of Captures
Second 50% of Captures



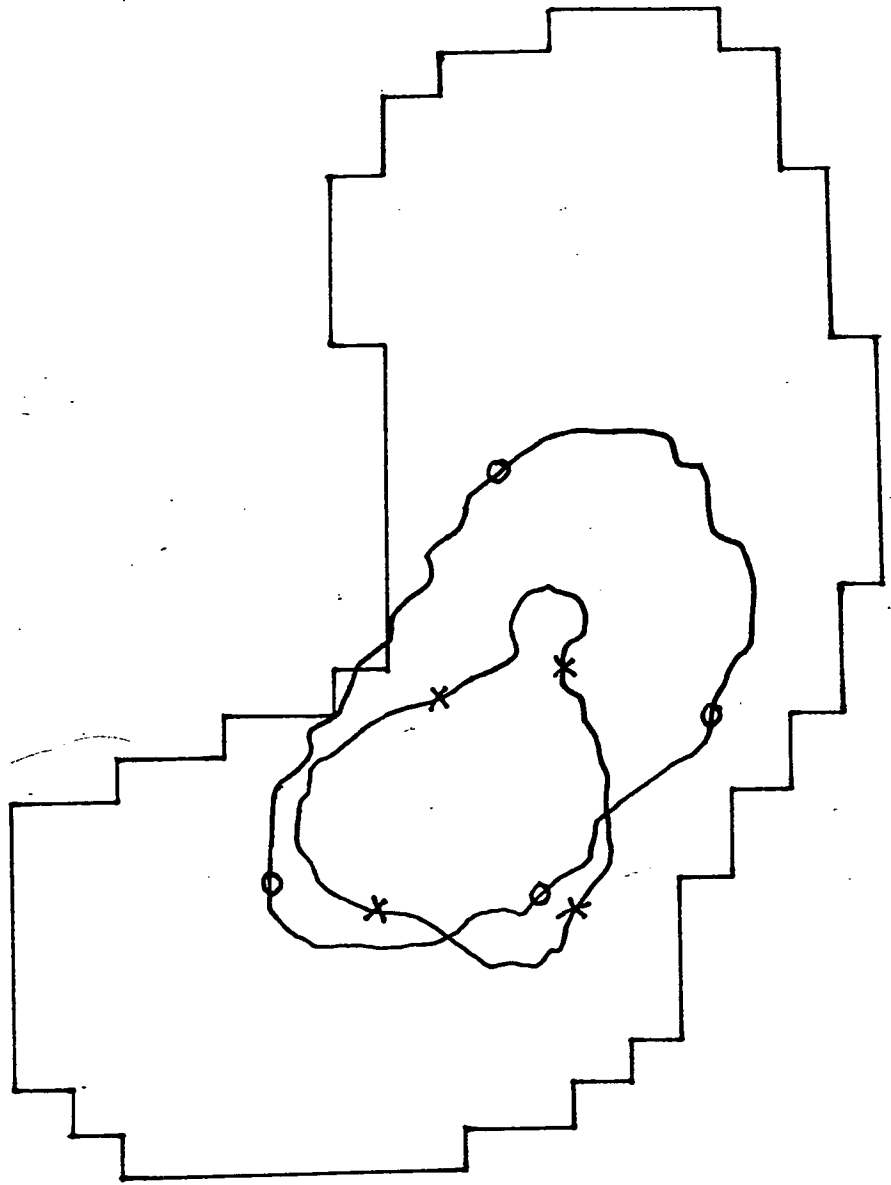
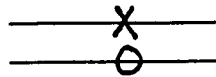


Figure 4.2f.
P152 female

First 50% of Captures
Second 50% of Captures



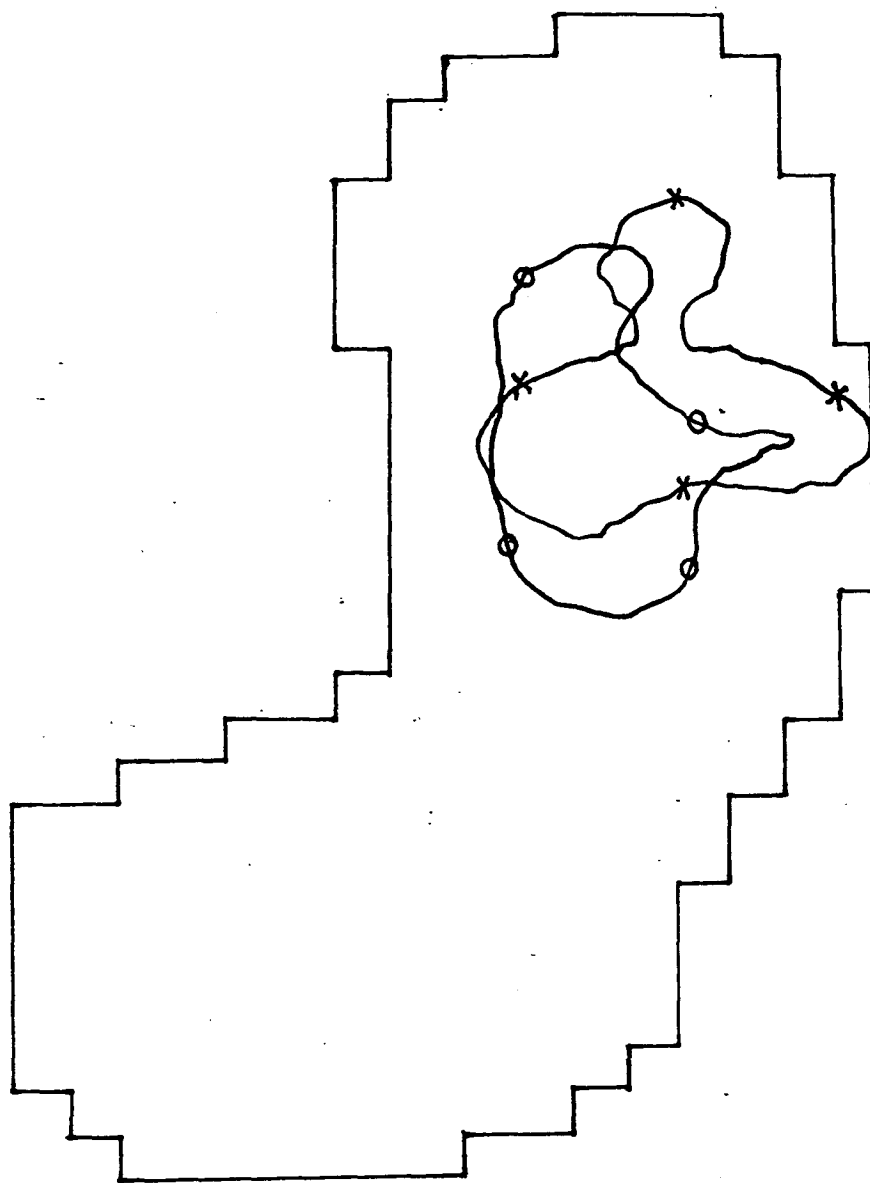


Figure 4.2g.
P155 female

First 50% of Captures
Second 50% of Captures

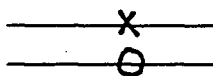


Figure 4.3 a, b, c, d, e, f, g.

Boundaries are for 90% isopleth PDFs for the seven individuals analysed for intra-lifespan home-range variation.

Seasons are of four months, see text for explanation.

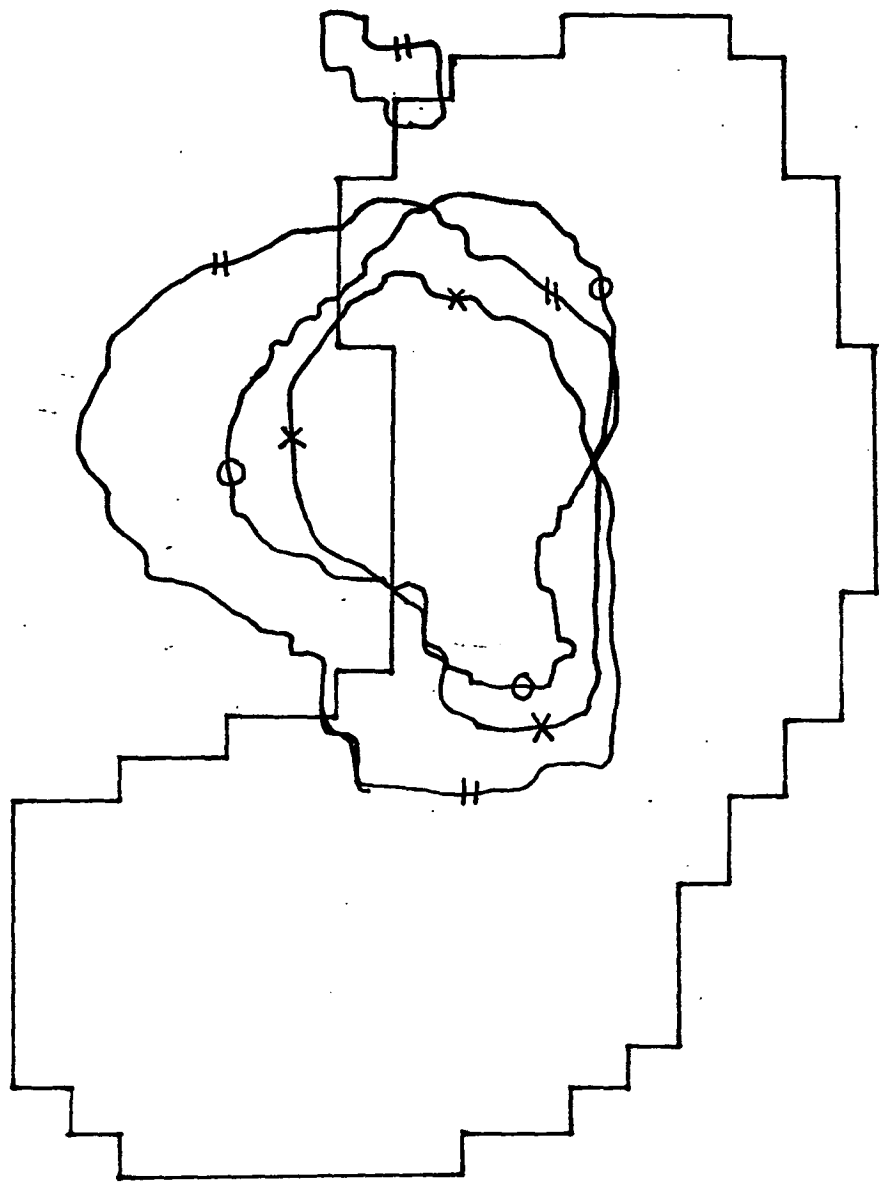
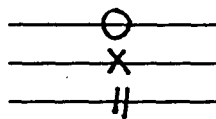


Figure 4.3a
P113 female

January - April
May - August
September - December



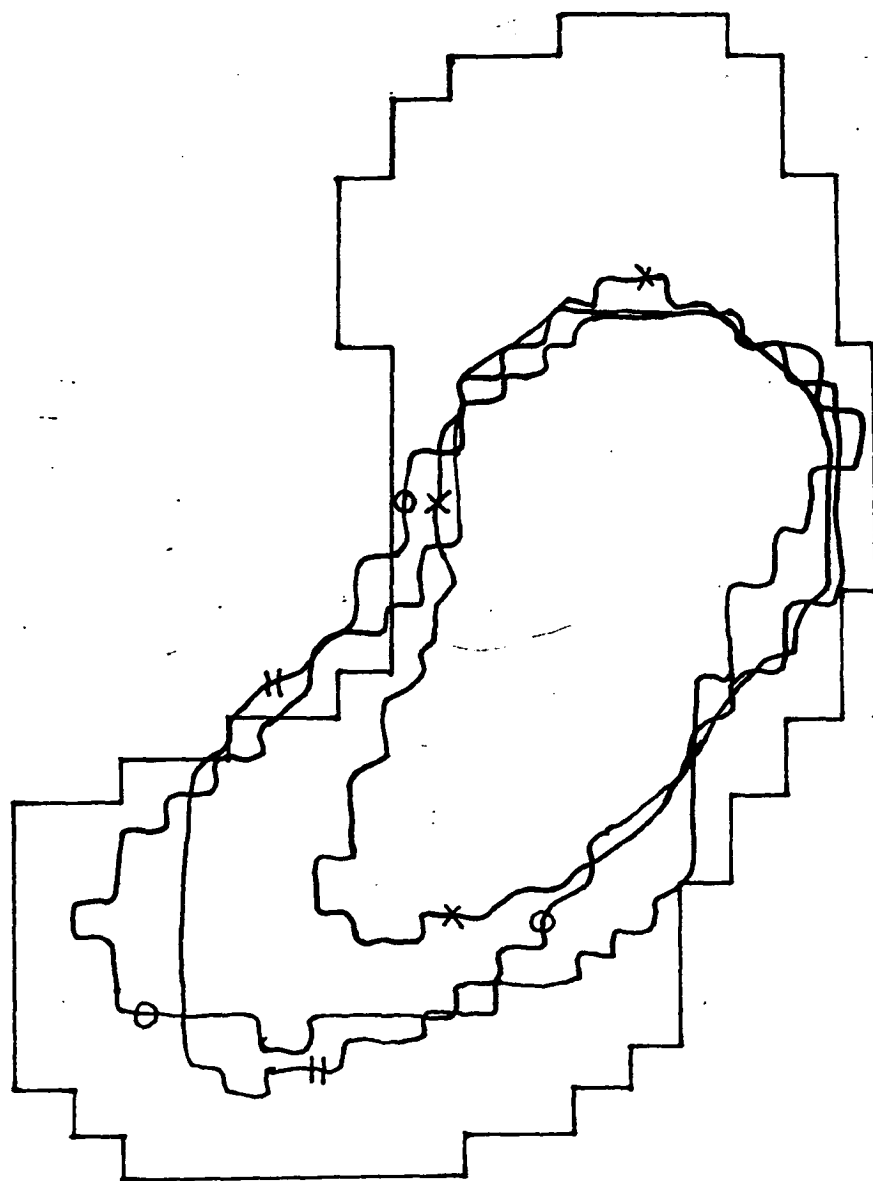
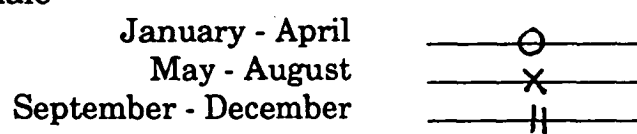


Figure 4.3b
P136 male



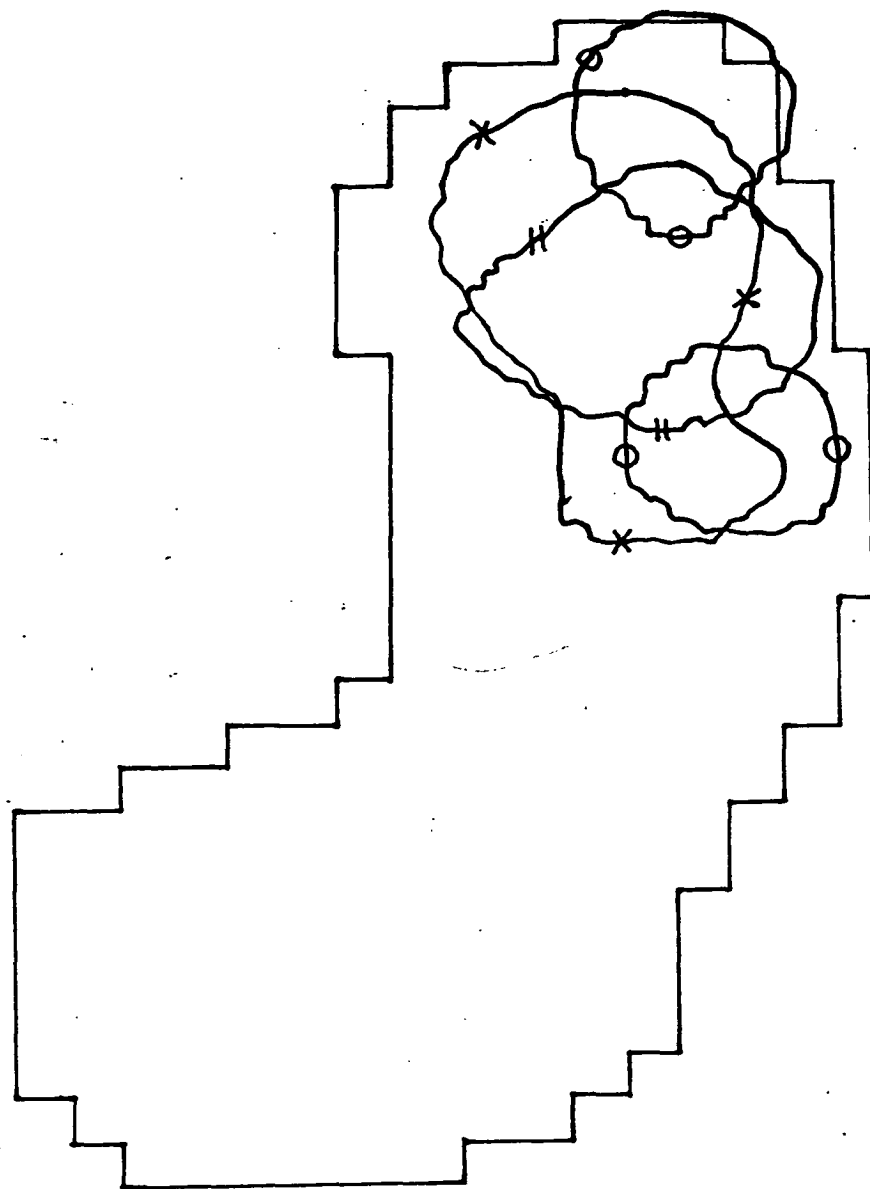
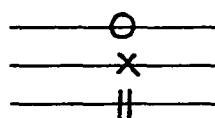


Figure 4.3c
P137 male

January - April
May - August
September - December



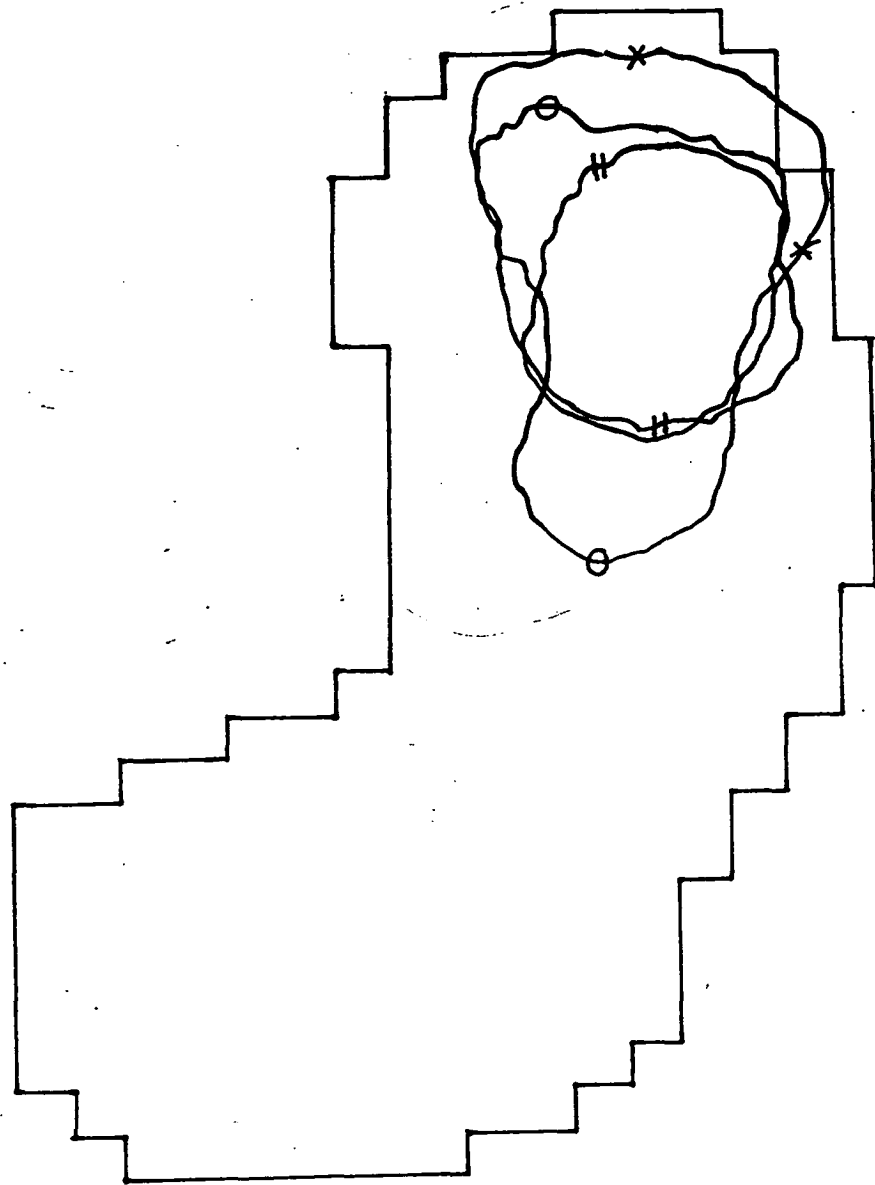
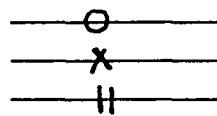


Figure 4.3d
P138 female

January - April
May - August
September - December



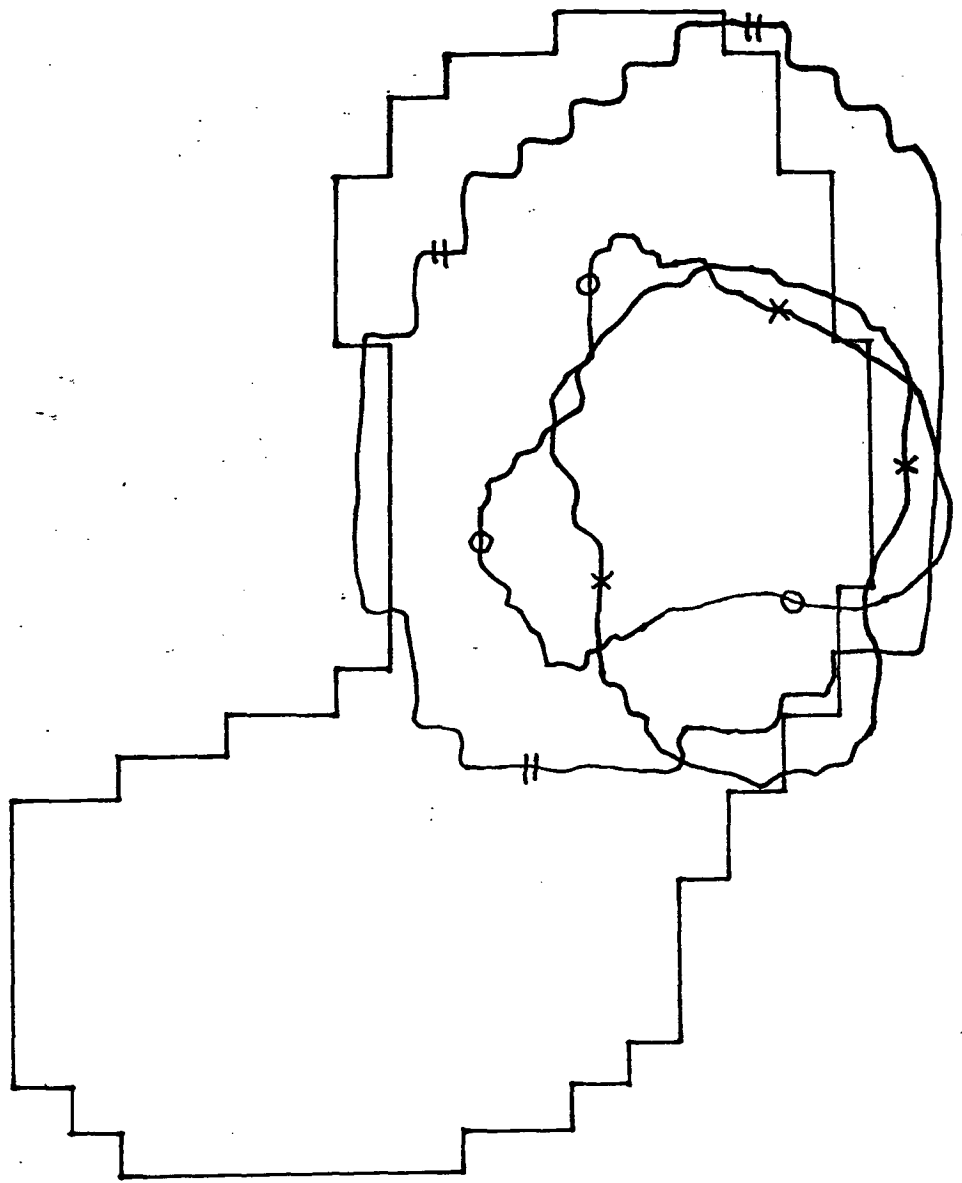
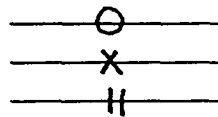


Figure 4.3e
P145 male

January - April
May - August
September - December



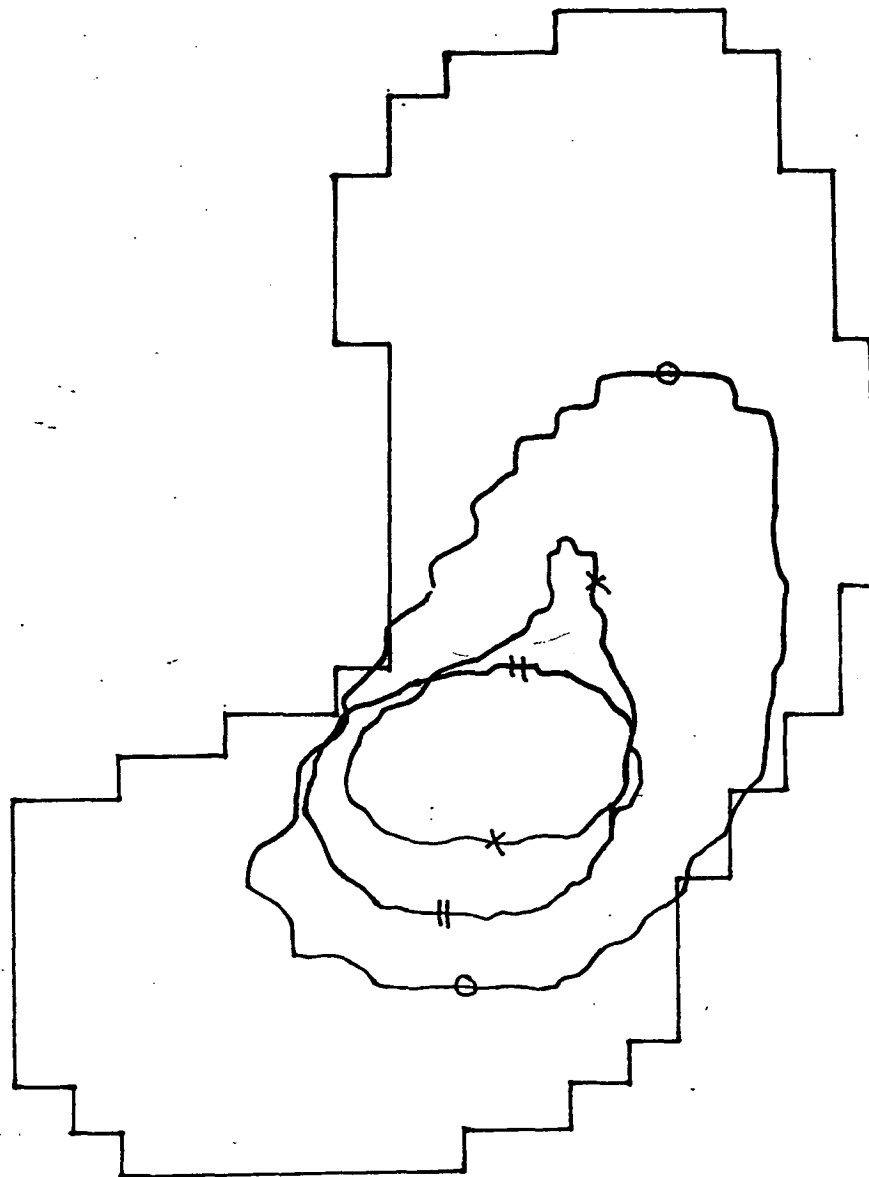


Figure 4.3f
P152 female

| | |
|----------------------|------|
| January - April | —○— |
| May - August | —x— |
| September - December | —//— |

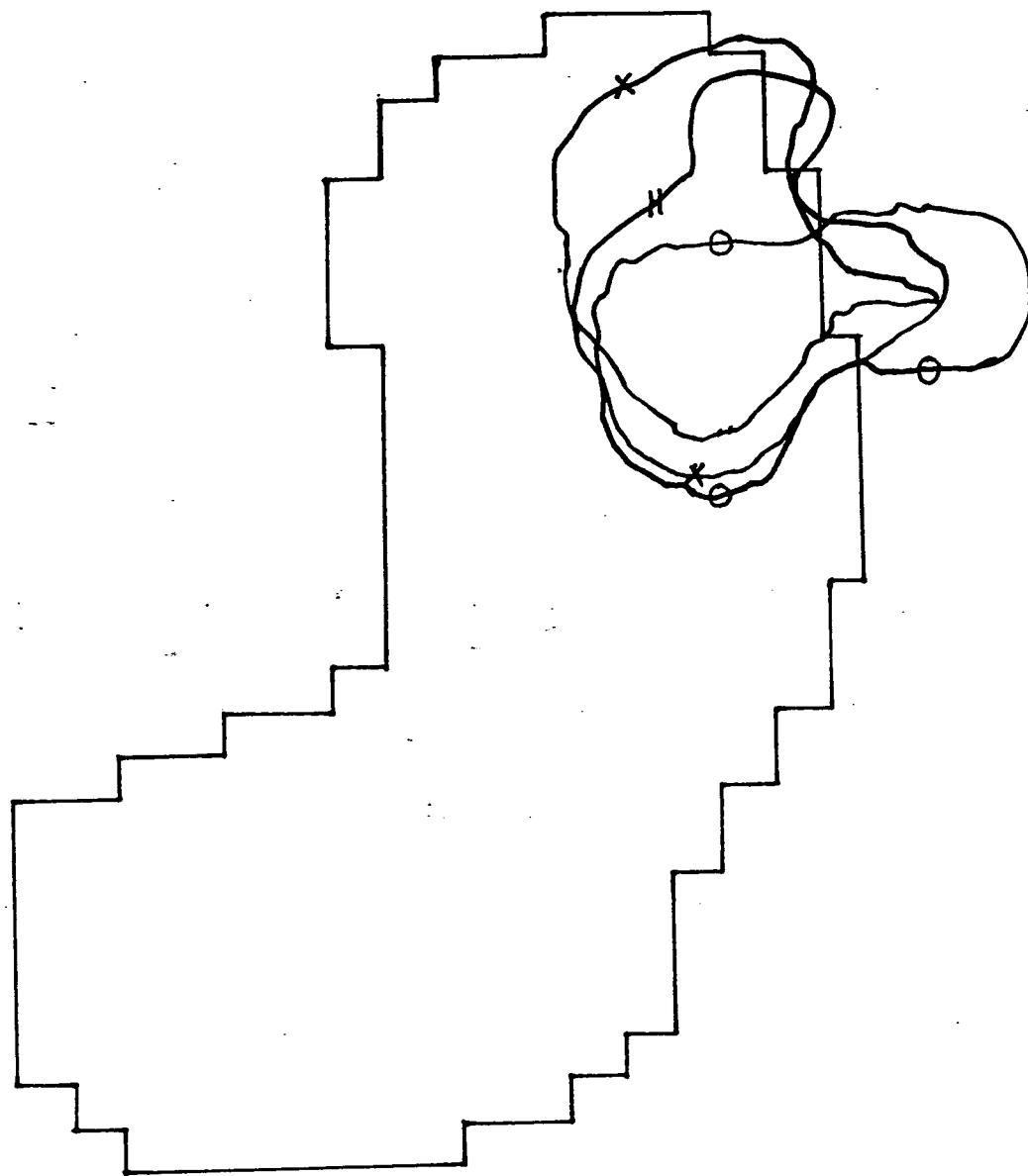


Figure 4.3g
P155 female

| | |
|----------------------|---|
| January - April | o |
| May - August | x |
| September - December | |

Table 4.3. Seasonal analysis of home-range area.

| Individual | Sex | Season | | | | | |
|------------|--------|---------|------|---------|------|---------|------|
| | | Jan-Apr | | May-Aug | | Sep-Dec | |
| | | N | Area | N | Area | N | Area |
| P113 | Female | 19 | 8.0 | 24 | 6.2 | 16 | 17.4 |
| P136 | Male | 36 | 21.8 | 32 | 13.3 | 24 | 20.3 |
| P137 | Male | 9 | 5.15 | 23 | 6.9 | 15 | 5.0 |
| P138 | Female | 9 | 5.2 | 20 | 5.4 | 15 | 3.2 |
| P145 | Male | 14 | 7.4 | 22 | 8.6 | 18 | 29.8 |
| P152 | Female | 18 | 14.1 | 10 | 2.9 | 12 | 3.8 |
| P155 | Female | 16 | 3.8 | 21 | 5.1 | 16 | 3.2 |

Of the individual home-ranges plotted, that of male P136 appears particularly significant in that this individual had many (92) captures and the largest recorded home-range. This individual was present over most of the study area and duration (Figure 4.5), and exhibited home-range overlap with many individuals, both male and female.

Some temporally non-overlapping known lifespans for individuals with strongly overlapping home-range areas are also apparent, e.g. individuals P118m and P123m were replaced by P152f and P1175m at around half way through the study period (Figures 4.4d, 4.5), and individuals P111m and P113f were similarly replaced by P188m (Figures 4.4b, 4.5), although other possible replacement effects are not clear from the limited data available.

4.3.7 Home-Range Overlap Within and Between Sexes.

Overlap data for individuals was produced using the Ranges IV software package (Kenward 1990). Table 4.4 presents a matrix of home-range overlap for all individuals with at least 20 capture records. A chi-square test indicated no significant difference in substantial (50% or greater) individual home-range overlap with other individuals of either sex ($P > 0.5$).

4.3.8 Home-Range in Relation to Body Mass.

To test for a relationship between individual home-range and body mass, correlation coefficients for these variables were calculated for the 24 individuals with at least 20 capture records, both within sexes and for all individuals. Body mass was tested on both mean values over all recorded captures and on the maximum body mass recorded for each individual. Results are presented in Table 4.6. No correlations were significant, either within sex or for all individuals tested.

Figure 4.4 a, b, c, d, e.

Boundaries for 90% isopleth PDFs for all individuals with at least 20 captures.

Overlays of selected groups of individual home-ranges are presented on the basis of substantial overlap and on apparent contrasts between different sets of individual home-ranges.

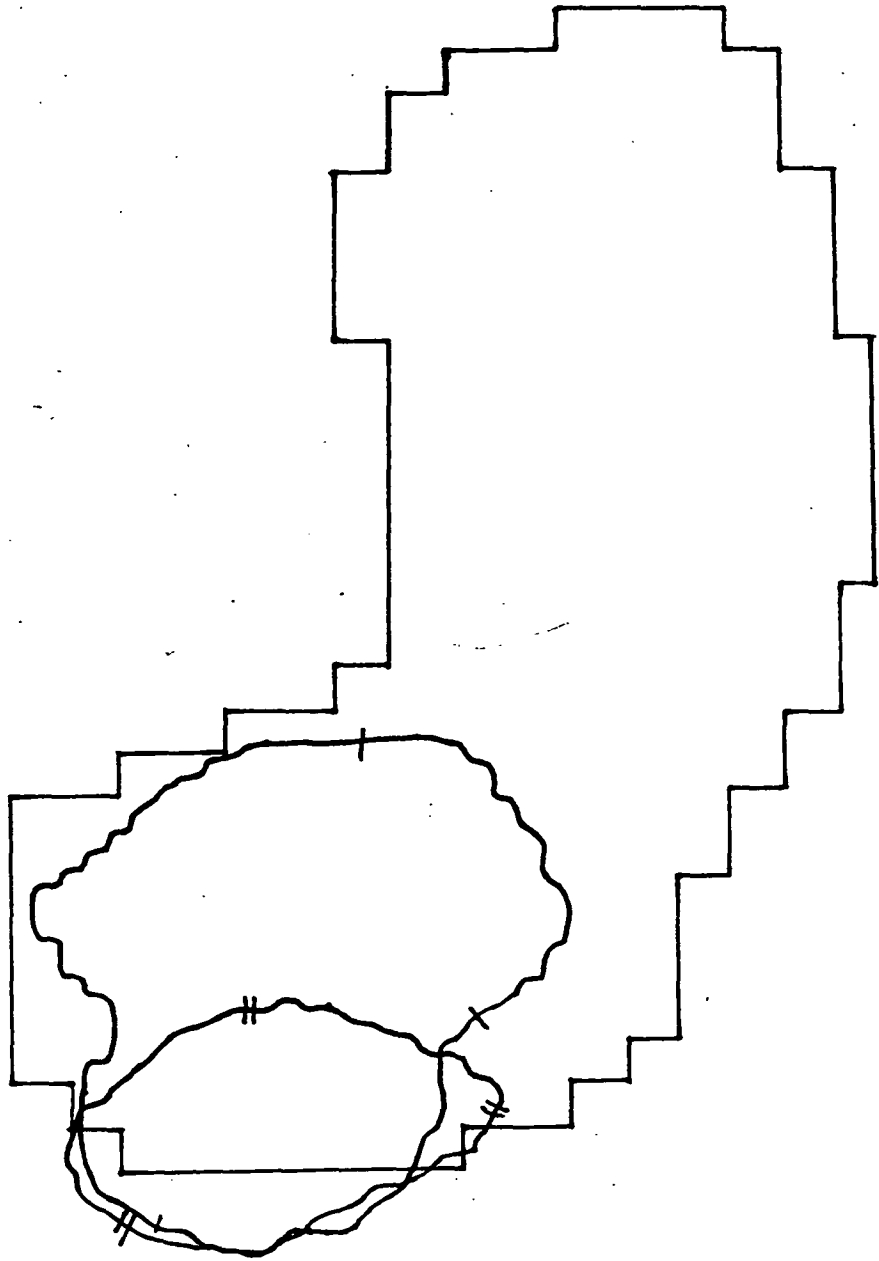
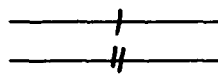


Figure 4.4a.

P107 male
P131 female



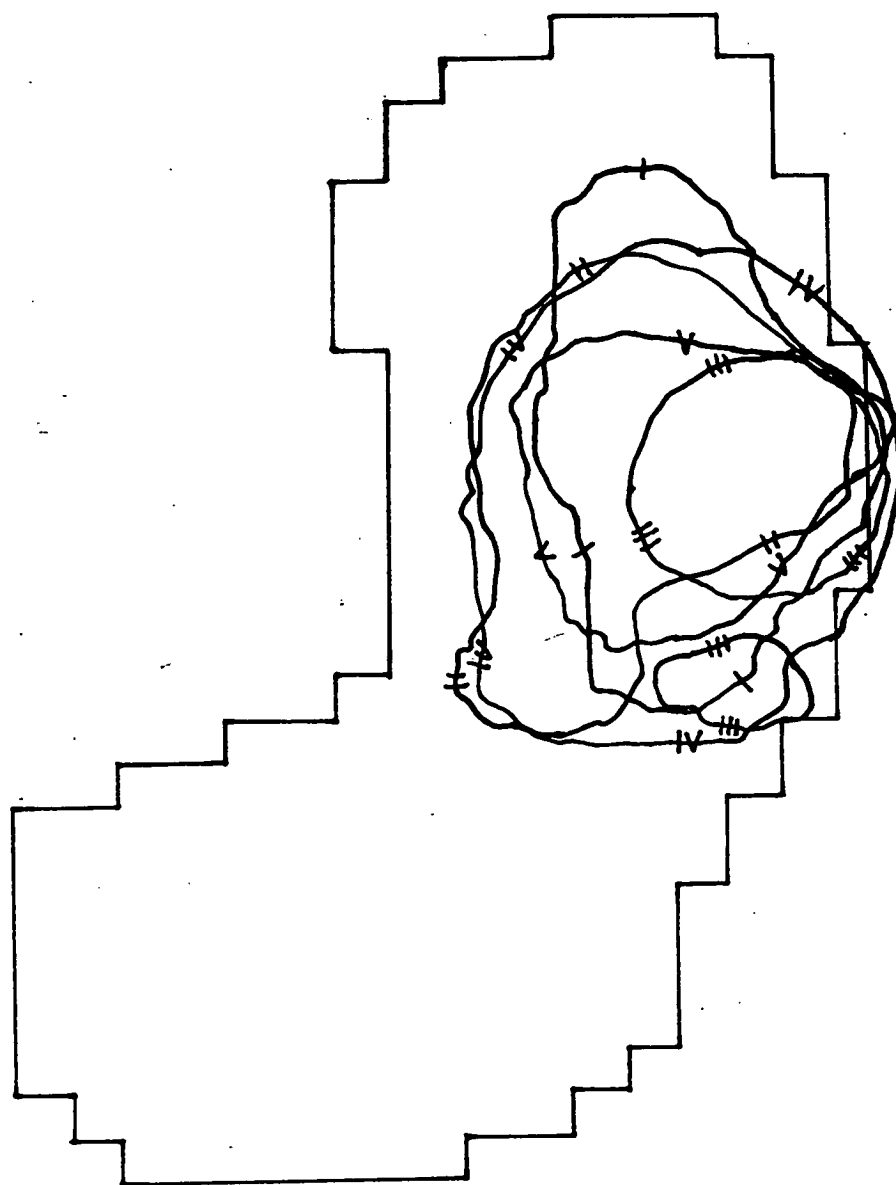
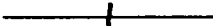






Figure 4.4b.

| | | |
|------|--------|---|
| P111 | male |  |
| P113 | female |  |
| P127 | female |  |
| P145 | male |  |
| P188 | male |  |

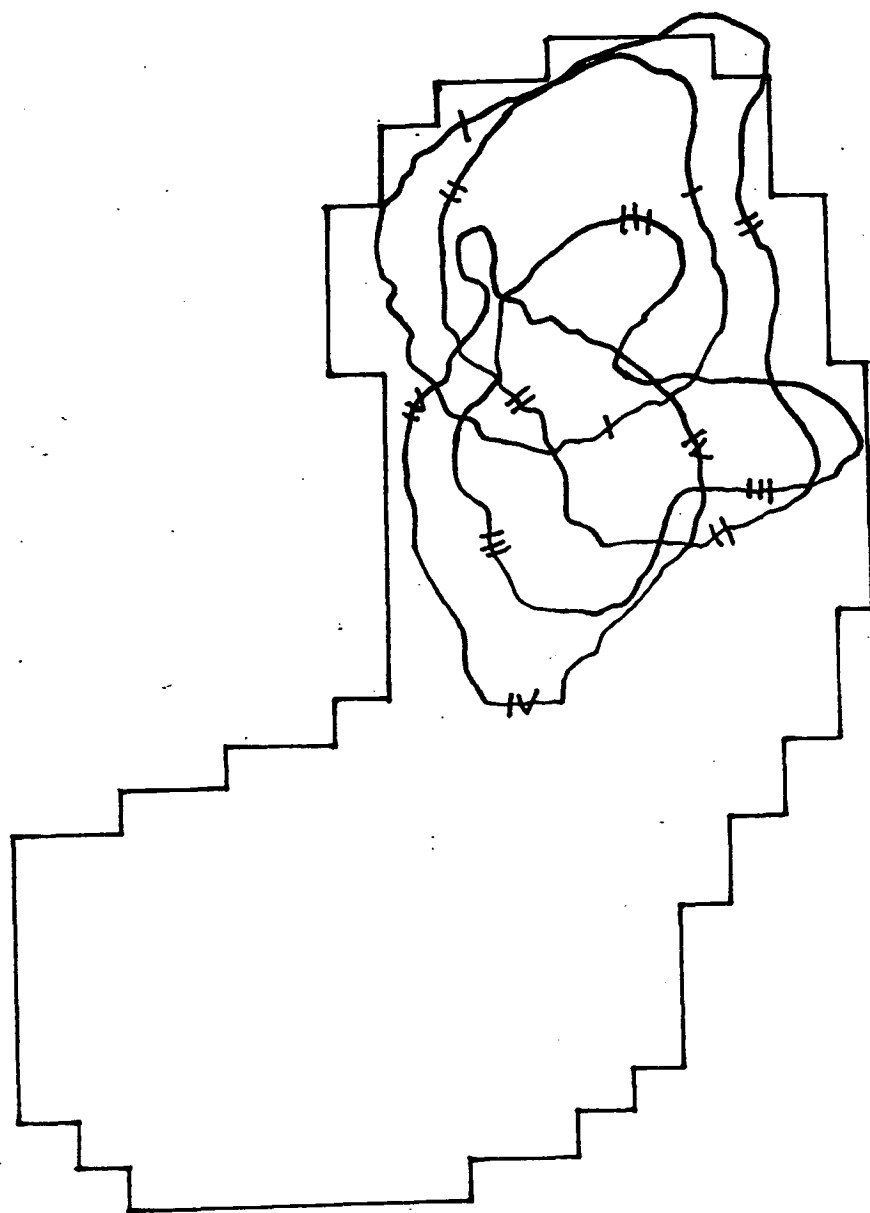
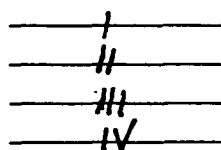


Figure 4.4c.

P114 male
P137 male
P155 female
P158 female



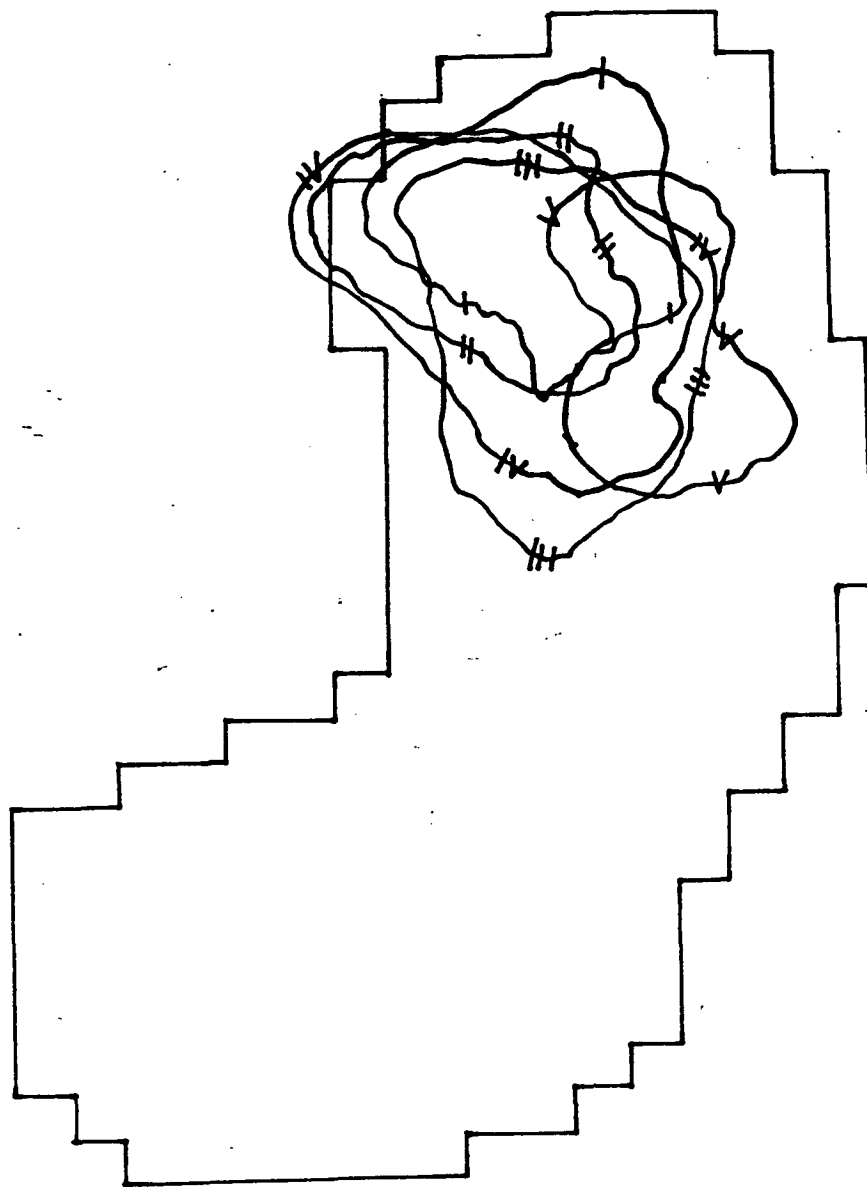


Figure 4.4d.

| | | |
|------|--------|---|
| P115 | male | |
| P128 | female | |
| P138 | female | |
| P156 | male | |
| P180 | male | ✓ |

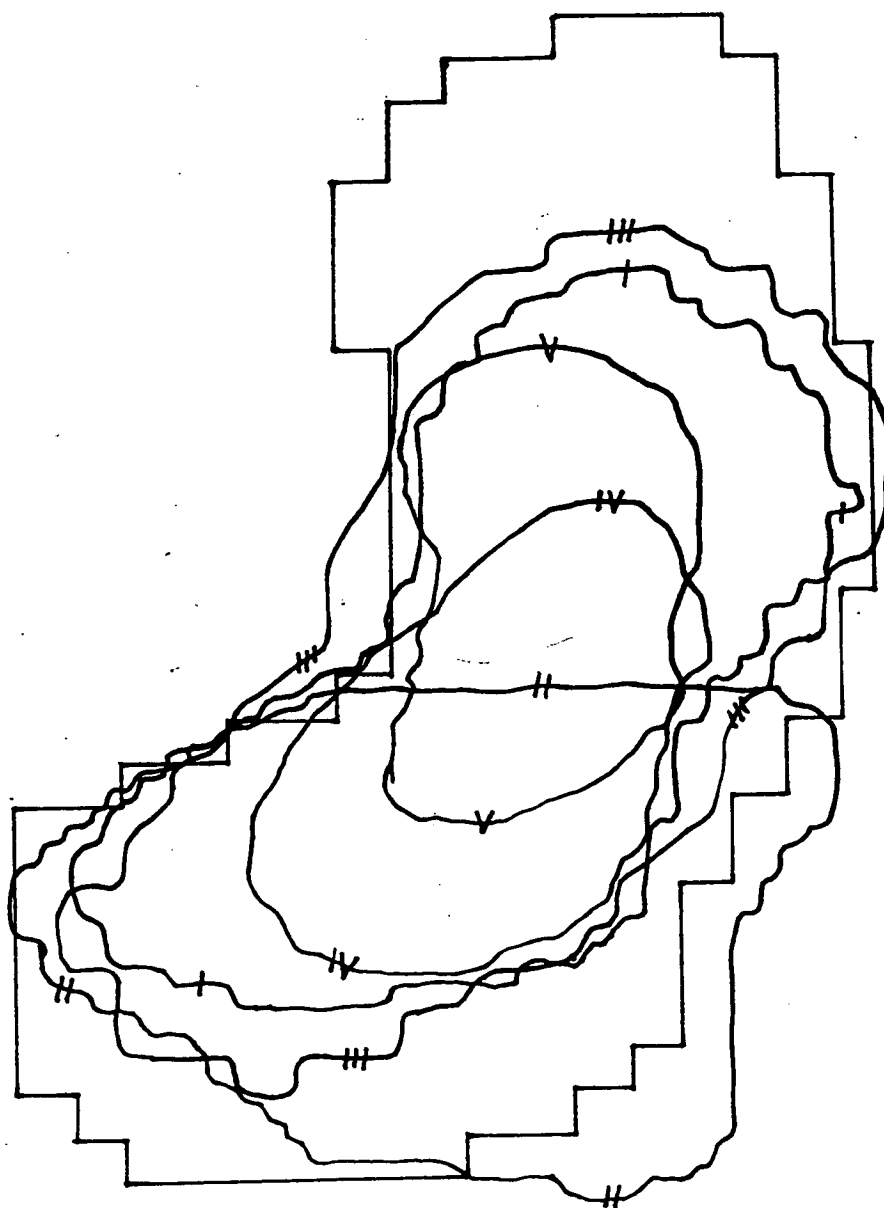


Figure 4.4e.

| | | |
|------|--------|-----|
| P118 | male | I |
| P123 | male | II |
| P136 | male | III |
| P152 | female | IV |
| P175 | male | V |

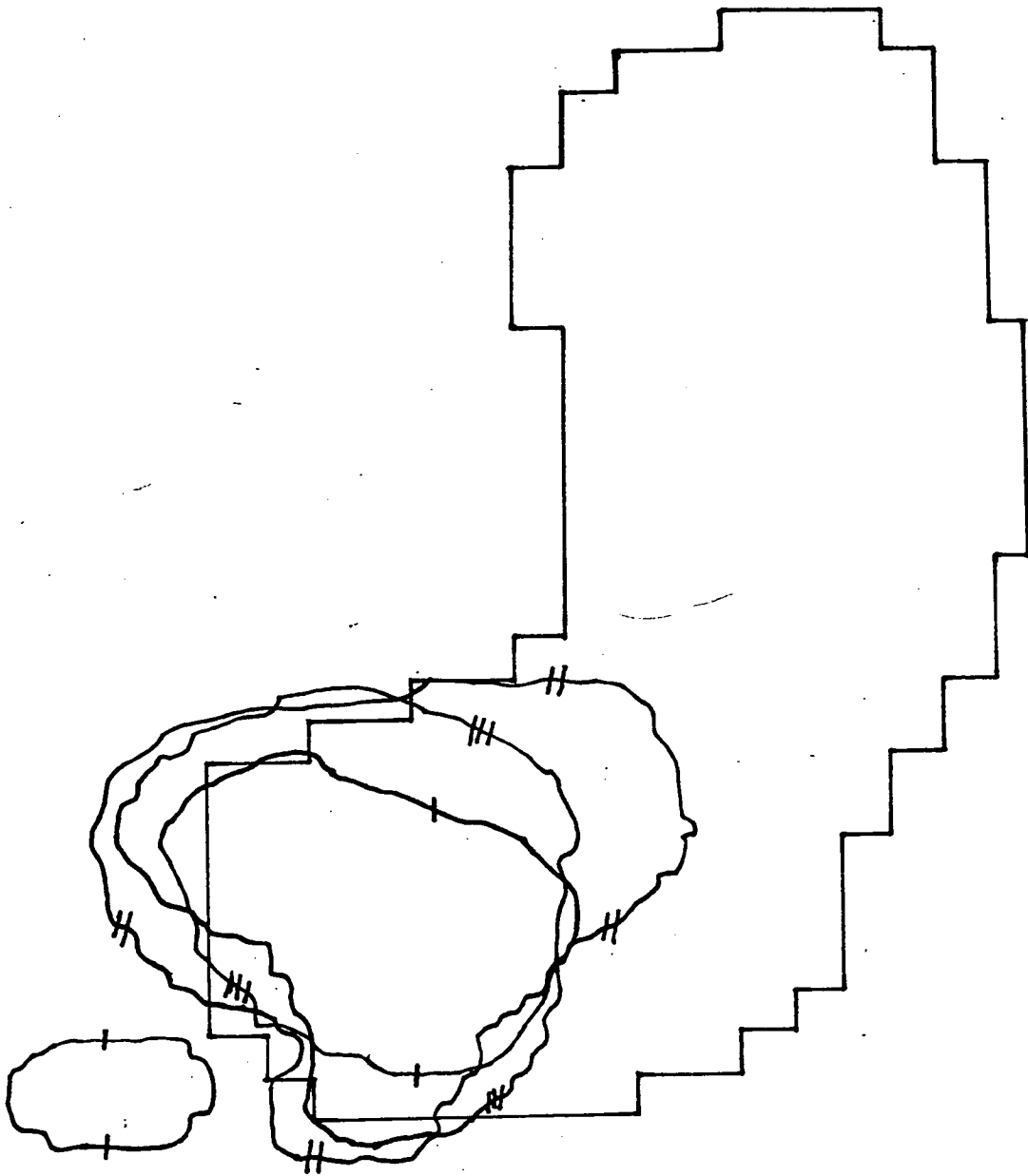


Figure 4.4f.


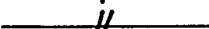

| | | |
|------|------|---|
| P121 | male |  |
| P130 | male |  |
| P172 | male |  |

Figure 4.5.
Duration of known life-span for individuals examined for overlap
of 90% PDF home-ranges.

Lifespan Range of Potoroos with at least 20 Captures

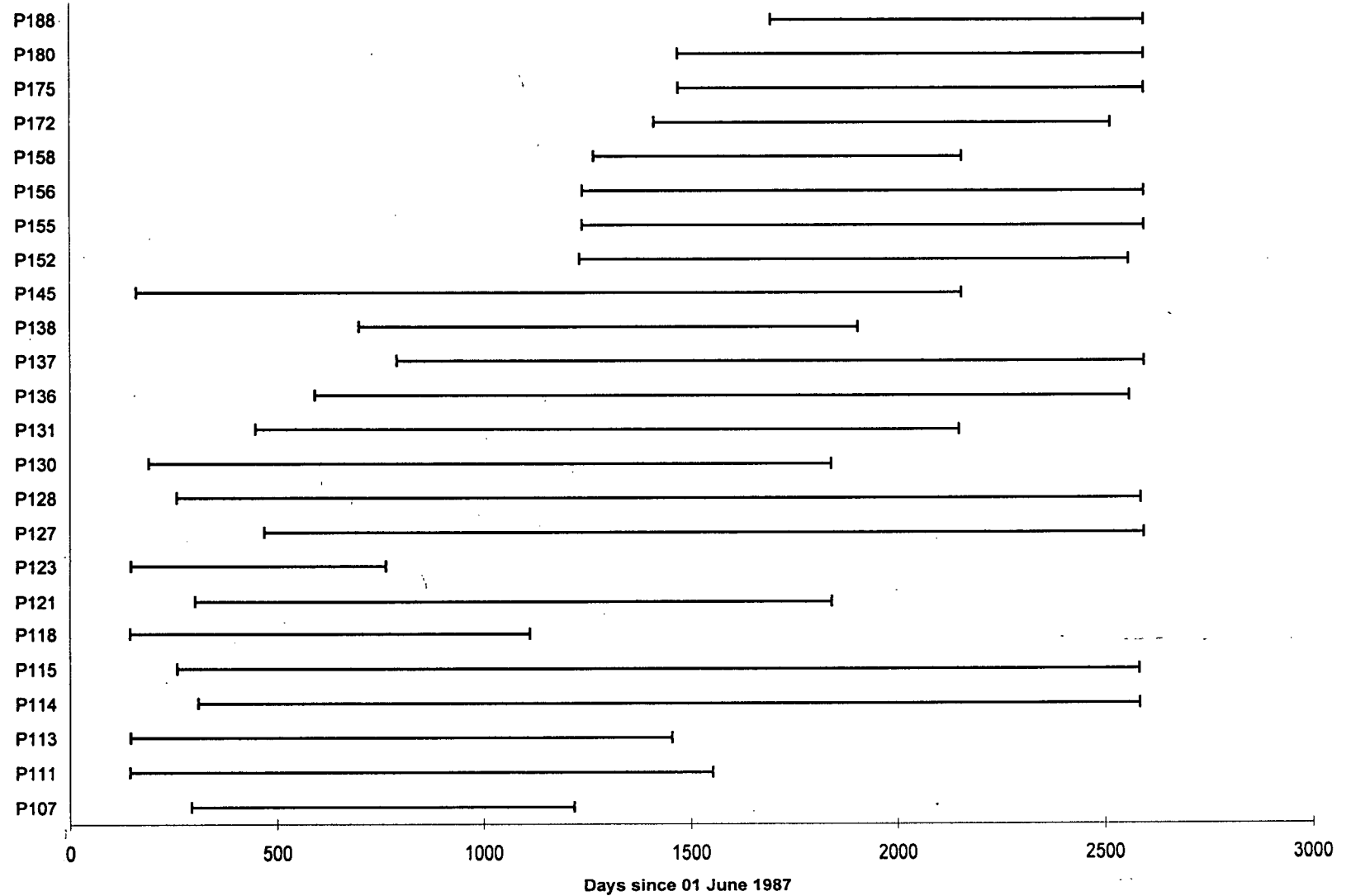


Table 4.4 Matrix of home-range overlap for all individuals with at least 20 capture records.

A chi-square test indicated no significant difference in substantial (50% or greater) individual home-range overlap with other individuals of either sex ($P > 0.5$; Table 4.5). Cells are percentage overlap by individual in column.

| | 107m | 111m | 113f | 114m | 115m | 118m | 121m | 123m | 127f | 128f | 130m | 131f | 136m | 137m | 138f | 145m | 152f | 155f | 156m | 158f | 172m | 175m | 180m | 188m |
|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|
| 107m | * | 0 | 0 | 0 | 0 | 52.5 | 43.3 | 77.7 | 0 | 0 | 74.0 | 34.0 | 65.7 | 0 | 0 | 0 | 29.2 | 0 | 0 | 0 | 61.7 | 3.7 | 0 | 0 |
| 111m | 0 | * | 67.9 | 28.3 | 16.8 | 74.9 | 0 | 2.3 | 42.7 | 10.1 | 0 | 0 | 91.5 | 57.2 | 34.7 | 89.7 | 16.2 | 47.4 | 27.8 | 26.1 | 0 | 31.3 | 42.6 | 61.1 |
| 113f | 0 | 70.3 | * | 23.4 | 11.4 | 92.5 | 0 | 5.0 | 30.8 | 11.6 | 0 | 0 | 100 | 49.4 | 42.6 | 96.4 | 30.5 | 58.2 | 31.8 | 50.1 | 0 | 56.1 | 33.1 | 59.4 |
| 114m | 0 | 36.1 | 29.4 | * | 62.1 | 29.2 | 0 | 0 | 0 | 49.4 | 0 | 0 | 43.8 | 80.9 | 61.5 | 28.9 | 0 | 32.7 | 66.4 | 24.7 | 0 | 11.5 | 30.1 | 10.9 |
| 115m | 0 | 33.3 | 22.5 | 98.0 | * | 21.1 | 0 | 0 | 0 | 66.2 | 0 | 0 | 35.6 | 85.7 | 65.3 | 21.2 | 0 | 33.1 | 75.1 | 17.3 | 0 | 2.9 | 26.7 | 4.0 |
| 118m | 32.1 | 30.9 | 36.1 | 9.3 | 4.3 | * | 15.2 | 50.6 | 14.6 | 5.2 | 34.0 | 0 | 97.5 | 18.5 | 17.8 | 43.0 | 45.9 | 22.4 | 13.0 | 25.0 | 23.1 | 37.5 | 11.9 | 24.9 |
| 121m | 65.9 | 0 | 0 | 0 | 0 | 37.4 | * | 63.9 | 0 | 0 | 81.0 | 17.1 | 53.8 | 0 | 0 | 0 | 8.0 | 0 | 0 | 0 | 78.1 | 0 | 0 | 0 |
| 123m | 48.1 | 0.8 | 1.8 | 0 | 0 | 51.3 | 25.7 | * | 1.5 | 0 | 44.1 | 10.5 | 59.0 | 0 | 0 | 4.9 | 31.6 | 0 | 0 | 0 | 34.8 | 9.8 | 0 | 0 |
| 127f | 0 | 87.1 | 61.3 | 0 | 0 | 73.0 | 0 | 8.1 | * | 0 | 0 | 0 | 91.8 | 37.6 | 6.3 | 97.4 | 5.0 | 35.7 | 2.9 | 13.0 | 0 | 15.2 | 27.3 | 70.5 |
| 128f | 0 | 21.6 | 24.2 | 83.7 | 70.9 | 27.0 | 0 | 0 | 0 | * | 0 | 0 | 40.2 | 64.0 | 68.9 | 20.7 | 0 | 31.8 | 98.0 | 27.8 | 0 | 8.0 | 14.4 | 7.7 |
| 130m | 68.4 | 0 | 0 | 0 | 0 | 51.4 | 48.8 | 65.8 | 0 | 0 | * | 16.9 | 59.6 | 0 | 0 | 0 | 26.6 | 0 | 0 | 0 | 70.9 | 4.8 | 0 | 0 |
| 131f | 90.2 | 0 | 0 | 0 | 0 | 0 | 29.5 | 45.0 | 0 | 0 | 47.8 | * | 15.5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 52.1 | 0 | 0 | 0 |
| 136m | 31.9 | 30.2 | 31.8 | 11.0 | 5.7 | 78.7 | 17.2 | 46.7 | 15.0 | 6.1 | 31.7 | 3.2 | * | 18.6 | 17.6 | 41.2 | 36.8 | 20.4 | 13.8 | 21.0 | 22.9 | 30.2 | 11.6 | 21.5 |
| 137m | 0 | 53.8 | 45.3 | 59.6 | 39.9 | 43.1 | 0 | 0 | 17.4 | 28.1 | 0 | 0 | 54.2 | * | 45.9 | 46.5 | 1.3 | 41.6 | 42.0 | 25.2 | 0 | 15.2 | 39.8 | 31.3 |
| 138f | 0 | 50.4 | 60.2 | 69.4 | 46.9 | 63.6 | 0 | 0 | 4.6 | 46.0 | 0 | 0 | 78.2 | 70.3 | * | 59.2 | 5.6 | 64.5 | 80 | 57.7 | 0 | 42.0 | 38.6 | 32.3 |
| 145m | 0 | 64.5 | 67.1 | 16.3 | 7.5 | 75.6 | 0 | 8.9 | 34.1 | 7.0 | 0 | 0 | 90.7 | 35.5 | 29.2 | * | 25.9 | 39.5 | 20.9 | 34.8 | 0 | 43.0 | 23.9 | 47.7 |
| 152f | 38.5 | 14.8 | 25.9 | 0 | 0 | 99.9 | 7.3 | 68.1 | 2.2 | 0 | 38.7 | 0 | 100 | 1.2 | 3.5 | 31.6 | * | 8.2 | 0.3 | 17.4 | 16.3 | 50.6 | 0 | 12.5 |
| 155f | 0 | 73.2 | 87.3 | 39.5 | 25.7 | 85.8 | 0 | 0 | 27.1 | 23.1 | 0 | 0 | 96.7 | 68.3 | 69.1 | 85.1 | 14.2 | * | 52.7 | 62.9 | 0 | 51.6 | 47.4 | 61.7 |
| 156m | 0 | 37.9 | 42.0 | 70.8 | 51.1 | 44.4 | 0 | 0 | 1.9 | 62.1 | 0 | 0 | 57.5 | 61.3 | 76.1 | 39.8 | 0.6 | 46.3 | * | 40.5 | 0 | 26.3 | 29.3 | 21.9 |
| 158f | 0 | 39.7 | 73.6 | 29.2 | 12.8 | 93.2 | 0 | 0 | 9.8 | 19.5 | 0 | 0 | 97.1 | 40.4 | 60.3 | 73.5 | 30.3 | 61.3 | 44.7 | * | 0 | 82.0 | 19.5 | 44.2 |
| 172m | 75.9 | 0 | 0 | 0 | 0 | 46.2 | 62.9 | 69.9 | 0 | 0 | 94.3 | 24.5 | 58.2 | 0 | 0 | 0 | 15.2 | 0 | 0 | 0 | * | 0 | 0 | 0 |
| 175m | 6.4 | 34.2 | 58.1 | 9.5 | 1.3 | 98.3 | 0 | 26.4 | 8.0 | 3.8 | 8.4 | 0 | 100 | 17.1 | 30.6 | 63.6 | 61.1 | 35.3 | 20.5 | 58.1 | 0 | * | 11.0 | 33.3 |
| 180m | 0 | 99.3 | 75.9 | 55.3 | 31.2 | 68.9 | 0 | 0 | 30.7 | 15.7 | 0 | 0 | 83.6 | 100 | 62.2 | 77.6 | 0 | 72.3 | 50.2 | 29.8 | 0 | 23.8 | * | 55.2 |
| 188m | 0 | 93.4 | 86.9 | 12.5 | 2.8 | 91.9 | 0 | 0 | 52.2 | 5.5 | 0 | 0 | 99.8 | 50.2 | 33.6 | 100 | 21.3 | 60.5 | 24.1 | 43.9 | 0 | 47.1 | 35.5 | * |

Table 4.5 Sex based home-range overlap.

Observed cell values are of a 2X2 contingency table for overlap of home-range of at least 50%. The higher number of male overlap events reflects the sex ratio in the population.

Chi-square analysis provides no evidence ($\chi^2_1 = 0.31$; $P > 0.5$) that home-range overlap is sex biased.

| | | Overlapping Sex | | Total |
|----------------|----------|-----------------|------|-------|
| | | Female | Male | |
| Overlapped Sex | | | | |
| Female | Observed | 13 | 40 | 53 |
| | Expected | 11.7 | 41.3 | |
| Male | Observed | 16 | 62 | 78 |
| | Expected | 17.3 | 60.7 | |
| Total | Observed | 29 | 102 | 131 |

Table 4.6. Correlation of home-range with body mass.

Pearson Correlation Coefficient r is presented, with associated P value for correlation of home-range with each of mean and maximum individual body mass. No correlations were significant.

| | Mean Body Mass | | Maximum Body Mass | |
|---------|----------------|--------------|-------------------|--------------|
| | r | Significance | r | Significance |
| Females | .04 | $P > 0.9$ | .03 | $P > 0.9$ |
| Males | -0.11 | $P > 0.6$ | -0.30 | $P > 0.25$ |
| Total | .20 | $P > 0.3$ | .04 | $P > 0.8$ |

4.4 Discussion.

Home-range, in terms of size, location and stability is central to the viability of individuals in a population. Despite this, individual potoroo home-ranges, sex differences in mean home-range area, and the extent and nature of overlap of home-ranges have not previously been quantified. Spatial distribution of individual potoroos in this study involves individual use of areas which overlap considerably both within and between sexes. Further, males occupy larger average home-range areas than females (based on 90% isopleth PDFs).

While some of the home-ranges calculated and plotted in this study may underestimate total home-ranges which overlap with surrounding untrapped habitat, many are within the study area and exhibit definite boundaries. Further, because this effect is unlikely to be sex-specific, the demonstrated significant sex difference in home-range is likely to reflect a real difference in the population.

4.4.1 Home-Range Calculation Methods and Their Comparability.

Capture / recapture based estimates of mammalian home-range are open to interpretation, particularly in relation to whether behaviour which leads to a capture is representative of the "that area traversed by the individual in its normal activities of food gathering, mating and caring for young" (Burt 1943). Other methods are available, with radio-tracking the most popular alternative. Methodological differences between capture / recapture and radio-tracking based estimates were investigated by Lobert (1979) in a population of brown bandicoots. With concurrent use of the two techniques, capture / recapture estimates led to underestimated home-range areas compared with those based on radio-tracking. The differences found by Lobert (1979) appear to relate to animals being detected by radio-tracking beyond the limits of the trapping grid. Home ranges determined by radio-tracking and trapping were also determined for sugar gliders (*Petaurus breviceps*) by Quin, Smith, Green and Hines (1992), who concluded that range sizes obtained from either method were comparable provided that sufficient numbers of independent fixes were available. The demonstration in this study that increasing numbers of fixes reach asymptotic values indicates that individuals utilise restricted areas, but some individuals' ranges probably did extend beyond the study area. It is nonetheless likely that the demonstrated significant difference between male and female home-ranges is valid, although mean home-range values for males and females may somewhat underestimate true values.

4.4.2 Other Home-Range Studies on *Potorous* spp.

Mainland Australian long-nosed potoroo populations are geographically widespread and they extend from Victoria to southern Queensland, principally in coastal regions. Distribution is also patchy, with the disappearance of potoroos in some regions such as the Sydney basin in European times (Schlager 1981). Parameters such as home-range may be expected to vary over the geographic range of the species, as do body mass and some morphometric cranial parameters (Johnston and Sharman 1976).

Table 4.7 provides a summary of statistics on long-nosed potoroo home-range studies

Table 4.7. Long-nosed Potoroo Home-Range Estimates in This and Prior Studies.

MCP : Minimum Convex Polygon

MCP + b.s. : Minimum Convex Polygon with supplementary boundary strips.

kernel : kernel probability distribution function.

n.a. : not available.

n.s. : non significant ($P > 0.5$).* : significant ($0.5 > P > 0.01$).

| Study Reference | Location | Individuals | | Mean Fixes | | Method | Area (ha) | | |
|------------------|----------|-------------|--------|------------|--------|------------|-----------|--------|--------------|
| | | Male | Female | Male | Female | | Male | Female | Significance |
| Kitchener (1973) | SE Tas. | 5 | 5 | 15.2 | 16.2 | MCP | 19.4 | 5.2 | * |
| Bennett (1987) | Victoria | 6 | 6 | 14.7 | 15.2 | MCP + b.s. | 2.0 | 1.5 | n.s. |
| Johnson (1988) | SE Tas. | 10 | 1 | 8.3 | 4 | MCP | 4.4 | 0.9 | n.a. |
| Seebeck (1995b) | Victoria | n.a. | n.a. | n.a. | n.a. | unstated | 2 | 1.4 | n.a. |
| This Study | SE Tas. | 16 | 8 | 35.5 | 40.9 | kernel | 10.8 | 5.7 | * |

and methods. Study populations were located in SE Tasmania (Kitchener (1973), Johnson (1988) and this study at Porter Hill), and at Naringal in western Victoria (Bennett (1987), Seebeck *et al* (1989) and Seebeck (1995b)). All home-ranges were based on capture / recapture studies.

The largest home-ranges areas of long-nosed potoroo were reported by Kitchener (1973). Although based on a mean of 16 recaptures, the study was of short duration (an eight month recapture study) and the MCP method was used to calculate home-range area. This, together with the three to five-fold variation in individual home-range areas within each sex casts doubt on the reliability of the results, although the finding that male home-ranges were significantly greater than those of females ($0.05 > p > 0.02$) is consistent with the findings of this and other studies (Table 4.7).

Kitchener (1973) also concluded that considerable home-range overlap existed between adult potoroos, with a mean density of resident adults of 0.19 ha^{-1} (based on twelve residents occupying a 62 ha site), although specific sex-based individual distribution was not specified. In this study the resident adult density is estimated at 0.67 ha^{-1} (based on 35 residents occupying a 35 ha physical site which was multiplied by 50% to allow for individuals overlapping the study area and surrounding habitat). Johnson (1988) conducted an eight month recapture study but, because recapture numbers were low and only one female was recaptured, the results appear equivocal. In view of the lower numbers of recaptures used in previous studies at Porter Hill, in combination with the use of MCP rather than a PDF methodology, the home-range estimates of this study are likely to be more accurate than those of Kitchener (1973) and Johnson (1988).

Bennett (1987) collected recapture data for *Potorous tridactylus* over 24 months in relic habitat patches around Naringal in western Victoria. Male and female home-ranges were estimated to be around 2.0 and 1.5 ha respectively, but although mean male home range was consistently greater than that of females this result was not statistically significant. Bennett's inclusion of boundary strips supplementing MCPs would be expected to render relatively less conservative home-ranges compared to those of Kitchener (1973), thus increasing the disparity in home range area between the studies, although the body mass of Bennett's population (mean 0.8 kg) was less than that of long-nosed potoroos at Porter Hill (mean 1.4 kg; this study). Seebeck *et al* (1989) attribute this disparity in home-range estimates between Victorian and Tasmanian populations to probable differences in habitat quality, with the soil-type and climate at Naringal leading to conditions suitable for plant growth

throughout most of the year. Stability of individual home-ranges over time and considerable home-range overlap between individuals of both sexes were also reported by Bennett (1987).

Seebeck (1995b) reported mean male and female home-ranges of 2.0 and 1.4 ha respectively (also from the Naringal population; pers. communication), with a high degree of overlap between individuals but because the calculation method for home-ranges was unspecified direct comparison is difficult. The finding of considerable home-range overlap does, however, agree with this study.

Despite methodological differences between studies, home-range size differences between different populations of long-nosed potoroos are apparent. These differences may be partly explained by size differences between populations since inter-population body mass differences are greater than amongst individuals in this study, for which correlation with home-range area was not significant. Habitat quality is likely to be significant in this context. In Tasmania the Porter Hill population occurs on dolerite and mudstone substrates and in a regime of regular monthly rainfall on a long-term basis, but is nonetheless susceptible to late-summer drought. Dolerite substrates are generally more fertile than those of mudstone in south eastern Tasmania (Kirkpatrick, Gilfedder and Fensham 1988), although potoroos also live in habitats over Triassic sandstone (Hird and Hammer 1995) or coastal sandy (Heinsohn 1968) substrates which are less fertile than either dolerite or mudstone (Kirkpatrick *et al* 1988). Although the more fertile habitats have often been used for agricultural or other uses, the effects of habitat productivity based on soil fertility and favourable climate is worth further investigation.

Consistent features of the home-range usage of long-nosed potoroos are male home-range areas exceeding those of females, stability of home-ranges over time, especially given the longevity of the long-nosed potoroo of up to eight years, and considerable home-range overlap between individuals of both sexes. Findings of nest-sharing in captivity and the field, male fighting in the presence of females and the findings of this study in relation to intersexual intolerance (Chapter Two) and co-trapping (i.e. capturing more than one adult in a single cage) are also significant, and appear to be usual features of the biology of the species. These observations suggest that intimate knowledge of the home-range, including the social environment, is important for the species.

4.4.3 Home-Range Studies on *Potorous longipes*.

With the extinction of the broad-faced potoroo (*Potorous platyops*), the other extant

congeneric potoroid is the long-footed potoroo which has a distribution from central-eastern Victoria to south eastern New South Wales. The habitat of the long-footed potoroo is based on shelter sites in a floristic mosaic of gullies and drier forest foraging areas (Pascoe *et al* 1995; Seebeck 1995a). Long-footed potoroos occupy territorial home-ranges estimated at from three to six ha (Seebeck *et al* 1989) which are shared by monogamous adult pairs and subadult young, but not other adults (Seebeck 1995a). The species is rare, having been first described by Seebeck and Johnston (1980), and insufficient information is available to make meaningful and detailed comparisons with long-nosed potoroo home-ranges. In general, however, species with monogamous adult pairs occupying shared home ranges are often characterised as seasonally breeding and occupying habitats with reliable but dispersed food supplies (Pianka 1994).

4.4.4 Comparable Home-Range Studies of Potoroids Other Than *Potorous* sp.

The potoroid outside the genus *Potorous* with which the potoroo can most directly be compared ecologically with respect to home-range is the eastern (Tasmanian) bettong. Common elements in the biology of the potoroo and the bettong include similar body mass (fully-grown male and female bettongs weigh around 1.8kg (Taylor 1990)), with male and female potoroos weighing 1.2 and 1.4kg respectively in southern Tasmania (this study, Bryant (1989)) and 0.8 kg in southern Victoria (Bennett 1987), a highly mycophagous diet (Taylor 1992, Johnson 1994 for the bettong; Bennett and Baxter (1989) and Claridge, Cunningham and Tanton (1993) for the potoroo), broadly similar reproductive patterns (Rose 1989), and their sympatric geographic distribution (Seebeck *et al* 1989).

The distributions of the two species at European settlement were similar, but the extinction of the eastern bettong on mainland Australia has meant that such comparisons are now only possible in Tasmania, although the habitats occupied by bettongs in Victoria were probably similar to the dry woodland and open forest habitats occupied in Tasmania (Seebeck 1995c). Bettongs are confined to the eastern half of Tasmania, where the two species are generally sympatric, whereas the potoroo's distribution extends into wetter heathland, woodland and wet forest including rainforest in western Tasmania (Rounsevell *et al* 1991). In eastern Tasmania, both potoroos and bettongs may be syntopic (locally sympatric) in wet and drier forests and woodland; in situations where potoroos and bettongs occur syntopically potoroos tend to occupy microhabitats near drainage lines between drier ridges and slopes (Green 1973).

Bettong home-ranges have been investigated using radiotelemetry at a dry open forest site in Tasmania's northern midlands near Epping Forest (Taylor 1993a). Home-ranges were large (65 and 45 ha for males and females respectively) compared to those of the smaller potoroo (10.8 and 5.7 ha for males and females respectively, this study), and comparable to even those of much larger grazing macropods such as the eastern grey kangaroo, *Macropus giganteus* (Croft 1979). The habitat at the site near Epping Forest was in many respects typical of a range of dry sclerophyll woodland sites found to be utilised by bettongs by Taylor (1993b), including a local absence of potoroos.

The relatively large size of bettong home-ranges may result from bettongs utilising lower quality and more patchily dispersed food items than, for example, larger grazing macropodids such as the grey kangaroo (Taylor 1993a). That potoroos subsist on a broadly similar diet, are more closely related and are of similar size to bettongs, and yet have markedly differing home-range areas, suggests that factors other than carrying capacity of habitat may be important. This seems especially the case as potoroos and bettongs may be syntopic, or at least maintain close populations in Tasmania (this study, Johnson 1994d; Kershaw 1971; Owen Wilkins, pers. communication). Moreover, where detailed studies have examined faecal fungal spores (e.g. Taylor 1992; Johnson 1994; Bennett and Baxter 1989; and Claridge *et al* 1993), all of the known local fungal taxa have been found to be ingested, suggesting probable overlap in food items. No studies have examined this in detail, although in south-eastern New South Wales complete dietary overlap in hypogeal fungi was found in potoroos and long-nosed bandicoots (Claridge 1993).

Another potoroid marsupial of similar body mass, with significant dietary overlap, and of a similar reproductive pattern to the potoroo is the rufous bettong. Although unknown from Tasmania in European time, rufous bettongs are sympatric with potoroos in areas of New South Wales and southern Queensland (Schlager 1981). Nests constructed by rufous bettongs appear to be more elaborate than those of potoroos and important in predator-defence (Wallis, Jarman, Johnson and Liddle 1989). Feeding behaviour in rufous bettongs involves pairs of adults (Southgate 1989, quoted in Seebeck *et al* 1989), and since few such pairs were mothers with young-at-foot Wallis *et al* (1989) concluded that the species may be less solitary than other potoroids. Home-range in rufous bettongs has been estimated at about 20 ha with a smaller nightly feeding area of one to two ha (Southgate 1989, quoted in Bennett *et al* 1989), but methods of home-range derivation and the reliability of these estimates are unclear.

Home-range size of long-nosed potoroos therefore appears to be relatively small in comparison with other macropodoids, including other potoroids such as the eastern and rufous bettongs. Home-range size differences between the long-nosed potoroo and other potoroids appear to be best explained by differences in trophic strategy and concomitant adjustments to social and other behavioural attributes. While the details of the social organisation remain unclear, the long-nosed potoroo appears to be more gregarious and philopatric than the eastern bettong. The larger area utilised by bettongs appears to indicate exploitation of resources which are more sporadic in both space and time, possibly through greater exploratory prowess. Such a strategy, however, implies a relatively great mean distance between individuals, potentially less regular social contact, and consequent higher energetic demands.

4.4.5 Comparable Marsupial Home-Range Studies.

Another group of marsupials occupying a similar niche to the potoroo are bandicoots of the family Peramelidae. In Tasmania, brown and eastern barred bandicoots are syntopic with the long-nosed potoroo, while in Victoria the long-nosed bandicoot is also often syntopic with the long-nosed potoroo and with the long-footed potoroo. Bandicoots differ significantly in their reproductive patterns, typically with seasonal breeding involving multiple litters of several young and female reproductive potential of around 32 per lifetime (Lobert and Lee 1990). In southern Victoria radio-tracked brown bandicoots of both sexes had overlapping home-ranges of 0.8 to 3.0 ha, with densities of up to five individuals per hectare (Lobert 1990). Home-range details of eastern barred bandicoot populations in natural habitats are unknown. While some dietary overlap between bandicoots and potoroos is evident, the higher proportion of nutritionally-rich invertebrate food apparently taken by bandicoots (Quin 1988, Opie 1990) may allow higher population densities.

4.4.6 Home-Range Fidelity.

Resident long-nosed potoroos utilise a specific home-range area significantly smaller than that of bettongs, both across a resident adult potoroo's lifespan and between seasons. Some aspects of the population biology of the long-nosed potoroo also differ significantly from those of the bettong. Potoroo populations appear to be characterised by more intraspecific competition, with establishment in quality habitat being a primary determinant of lifetime success, whereas bettongs appear to be more vagile (moving up to two km from shelter to feeding areas per night (Taylor 1988)), and demonstrate less site fidelity. Adult bettongs thus presumably intermix with more individuals (although perhaps less often) than potoroos. The few data available on the behavioural repertoires of the species, such as duration of mating activity

(Rose 1989, Hughes 1962), and the small but marked sexual dimorphism of potoroos contrasting with the homomorphy of bettongs, tend to corroborate this trend in imputed sociality. Such differences may indeed be related to variation in the abundance and distribution of specific food resources, but not just because food availability is limiting, as suggested by Taylor (1992b).

Other differences in the population ecology of potoroos and bettongs may be explained by differences in site fidelity. The altitudinal limit of long-nosed potoroos is apparently approximately 700 m above sea level (asl) in Tasmania (pers. observation) and Victoria (Seebeck 1995a), whereas the bettong is found at altitudes of at least up to 1000 m asl (Driessen and Hocking 1980). Altitudes above 700 m are subject to regular winter snow cover (in Tasmania), and occasional other snowfalls which would disadvantage a species such as the potoroo with enduring site fidelity relative to an ecologically similar but more vagile species such as the bettong. In potoroos this effect may be amplified by the combination of a continuous breeding pattern, adverse sporadic altitudinal weather effects and site fidelity of individuals, an effect which may be avoidable by the vagility of bettongs.

The bettong is extinct on mainland Australia, having last been recorded early in the twentieth century (Johnson and Rose 1983). The potoroo has maintained a wide geographic range and locally common status at some sites. The relatively open vegetation utilised by bettongs may have placed them at a disadvantage due to predation pressure from the red fox on mainland Australia but not in Tasmania where the fox is absent. Site fidelity and associated close familiarity of potoroos with their home-range may be important in predator defence in this context. Tasmanian potoroo habitats have often been assumed to be restricted to densely vegetated habitat (e.g. Seebeck *et al* 1989) on the basis of intensive studies in such areas, e.g. Heinsohn (1966), but systematic survey evidence is lacking and some studies indicate that potoroos also utilise more open vegetation (Taylor *et al* 1985, Hird 1992, 1995).

Another manifestation of the potoroo's home-range fidelity may be its differential survival on Bass Strait islands when compared with that of the bettong (Hope 1974). Potoroo populations survive on several islands whereas none of the bettong have persisted in the 12 000 or so years since the last glaciation and the separation of Tasmania from mainland Australia (Hope 1974). This may indicate a smaller minimum viable population size for potoroos compared to bettongs.

4.4.7 Potoroo Behaviour in Relation to Home-Range.

Few data on potoroo behavioural repertoires are available. Observations on captive populations have indicated that individuals cohabit amicably, with the exception that adult males confined in the presence of an oestrous female fight (Hughes 1962, Ullmann and Brown 1983). Fights in captive potoroids have been described as rapid, direct and violent, with no sex differences in fighting ability apparent (Coulson 1979). Behaviours include kicking, cuffing and pawing opponents and the stylized method of delivering kicks (Buchmann in Coulson (1979)), for example, indicates that the fighting is more than an artefact of confinement.

Communal nesting behaviour in long-nosed potoroos has been occasionally reported from field studies (e.g. Johnson 1988, Othmar Buchmann, pers. communication), and in most observations on captive colonies (e.g. Ullmann and Brown 1983, Hughes 1962). Although the significance of such behaviour has not been quantified, its occurrence indicates obligate home-range overlap between individuals, and socialisation potentially extending beyond the nesting behaviour itself.

Evidence for defence of females by males is scant, consisting in this study of two captures of a male and a female (other than mother and young at foot) together in a trap. Both females were close to weaning offspring, and therefore close to oestrous. In potoroos, copulations occur over several nights around or following ovulation (Hughes 1962). The chance of two adults simultaneously entering a trap for feeding is small. Rather, it is likely that the male concerned in each case was closely following (and probably defending) the receptive female. A similar conclusion was drawn by How (1976) from co-trapping adult male and a female mountain brushtail possums, *Trichosurus caninus*.

4.4.8 Home-range in the Context of Population Biology of Potoroos.

Two processes are usually considered germane to patterns of the use of space by a population. First, and ultimately limiting (Eisenberg 1981), is the individual's need to have access to adequate resources, primarily food, within their domain of activity. Second, and especially in higher vertebrates, individuals seek to maximise long-term reproductive success through repertoires of social behaviour. Both processes are subject to selection pressures resulting in patterns of intra- and inter-specific variation in both spatial resource allocation and in mating systems (e.g. Eisenberg 1981, for home-range (chapter 16); Clutton-Brock 1989, for mating systems). Interacting with these fundamental physiological processes are body-size, mobility, demographic parameters, population density, and the physical and biotic

environment, especially climate and seasonality of food resources. Complex inter-relationships between all of these factors are to be expected.

An individual's knowledge of its home-range, particularly where vegetation is dense and visibility limited, may well be important especially for an animal such as the potoroo which is relatively long-lived for its size (Eisenberg 1981). One male in this study was regularly captured for three continuous years despite having one eye obscured by a cataract. Knowledge of home-range may extend to a range of individual resources including food sites, pathways, shelter sites and social information.

Individual potoroos exhibit persistent, non-random proximity to others over time, evidenced in this study by substantially overlapping home-ranges, which distinguishes *Potorous tridactylus* from species better classified as solitary.

Grouping behaviour nonetheless appears to be less significant than in larger macropodid marsupials like grey kangaroos, with the difference probably related to

- (i), habitat density, and thus difficulty in relying on visual cues,
- (ii), the patchiness of food resources, and
- (iii), related to (ii), an absence of herding (harem-forming) behaviour in females.

The little available evidence for sex-based grouping such as sex bias in sequential-night trapping, and co-trapping, indicates intermittent between-sex social grouping. Male potoroos may closely follow and defend females close to receptivity and, in that male success may be partly related to dominance hierarchies established in a more general population context, may be a behaviour similar to that of grey kangaroos. Potoroos, however, apparently do not display the "alpha male" syndrome of grey kangaroos (Croft 1989) in which males of relatively large body mass fight for apical behavioural dominance amongst local males (typically over a small proportion of their lifespan), and access to a harem of females.

Individual variation in home-range area was considerable and persisted over time (table 4.3), indicating that some individuals such as male P136 consistently occupied a relatively large area that overlapped that of several other males and females (figure 4.4e). This indicates that home-range is likely to be determined by behavioural as well as ecological factors. "Scramble competition" (Lott 1991) by males seeking receptive females is frequently observed amongst species with overlapping home-ranges, and may apply to long-nosed potoroos since, in comparison with grey kangaroos, visual cues are less effective and reliable.

Tasmanian potoroo populations exhibit sexual dimorphism, with males significantly larger, on average, than females (Bryant 1989; this study). Body mass dimorphism is not, however, as marked as it is in larger macropodids (Jarman 1989), nor does it extend to parameters such as a large difference in forearm length as in larger macropodids (Jarman 1989). While a significant but relatively small dimorphism in potoroo forearm length occurs (Bryant 1989), little difference is expected since potoroos utilise the forelimbs extensively for foraging. Ecological differences between sexes of a species, as well as sexual selection, can contribute to sexual dimorphism (Shine 1989).

Reviews of social systems in the Macropodoidea (e.g. Croft 1989) have suggested, on the basis of the little available evidence, that potoroos are comparatively solitary and asocial, except around breeding events. The continuous breeding season of potoroos in Tasmania, leading to their relatively high fecundity amongst the Macropodoidea, their significant body mass dimorphism, and the extent of home-range overlap demonstrated in this study indicate that *Potorous tridactylus* is less solitary than suggested by Croft (1989), but the behavioural details of potoroo sociality are worth further investigation.

Intrasexual rivalry, especially amongst males, and female choice are frequently involved in mating systems, although both male and female behavioural repertoires can vary widely within species (Clutton-Brock 1989). Polygynous mating systems are characterised by a prolonged association between a male and two or more females, and are distinguished from polygamous mating systems where multiple matings by at least one sex occur, but on an essentially random basis (Clutton-Brock 1989). The substantial overlap of relatively stable home-ranges over time in *Potorous tridactylus* demonstrated in this study indicates polygyny. Mating systems may be further subdivided on the basis of temporal and spatial dimensions of mating pattern (Lee and Cockburn 1986), and for potoroos successive female defence polygyny appears to best describe the mating system under these criteria..

Male behaviours are frequently related to a parental role (if any), defence of both feeding areas and females (temporarily or more permanently) and thus to female ranging behaviour. A male parental role in potoroos has not been generally reported, although Ullmann and Brown (1983) observed captive male potoroos assisting late-term pouch young to return to the pouch. Defence of feeding areas is also unknown and, extrapolating from captive situations where fighting has been reported only in other contexts, is probably of little ongoing significance. Further evidence for differential intrasexual tolerance is the significantly higher than random

probability of trapping individual potoroos of opposite sexes on sequential nights at the same trap site (Chapter Two). Urinary and possibly other pheromones may be residual on traps, at least on sequential nights, and indicate a more general role for such cues in the population. Some evidence of seasonal breeding has been imputed for potoroos (Bryant 1989); but none was detected in this study (Chapter Two). Potoroos are thus likely to have a mating system involving dominance amongst males, with continuous vigilance for sexually receptive females, and close following and defence of them, similar to the pattern exhibited in many larger macropodids.

4.4.9 Conclusion.

Male potoroos occupy home-ranges which are on average 90% larger than those of females. However, home-range sizes are variable and overlap of home-range between sex is considerable. This may have evolved as a balanced outcome of competition for food resources and the defendability of resources within the home-range. The mating system in potoroos may involve temporary bonds between behaviourally dominant males and sexually receptive females, with attentive importunate males fending off potential rivals. The mating system in male *Potorous tridactylus* is best described as successive female-defence polygyny. For females, facultative serial polyandry (or monogamy if an individual male maintains local dominance) best describes the mating system.

Chapter Five.

General Discussion and Conclusions.

Longitudinal population studies provide data which are unavailable or rarely obtained from shorter-term "snapshot" studies. This study has found a survivorship pattern involving high (greater than 70%) mortality of individuals up to the age of one year, with longevity of surviving adults typically of five to eight years. Potoroos use definite home-ranges throughout their reproductive life, with males occupying significantly larger ranges on average than females, and similar sexual dimorphism is evident in body mass. Individual home ranges of both sexes exhibit considerable overlap. Tolerance between individuals of each sex exceeds intra-sex tolerance, probably reflecting attention to mating opportunities in a continuously breeding population.

5.1 Habitat Requirements of the Long-nosed Potoroo.

Typical descriptive accounts of potoroo habitats cite sclerophyll forest and heathland, often emphasising a perceived requirement for thick ground cover through which runways are made (e.g. Seebeck 1981, Johnston 1983, Green 1993, Watts 1993). This presumption has been invoked to distinguish the habitat of potoroos from that of bettongs, e.g. on the basis of presence or otherwise of grassy habitat (Johnson and Rose 1983). Potoroos also utilise more open understorey components such as in rainforest (Taylor, Bryant, Pemberton and Norton 1987), grassy coastal forest, inland grassy forest (Hird 1992, 1995), and coastal scrub at Marion Bay (R. J. Taylor, pers. communication).

Unlike Victoria, which has had a relatively intensive terrestrial mammal survey program in residual habitat types in recent decades (e.g. Menkhorst 1995a), Tasmania has only a sporadic survey record for mammals (Rounsevell *et al* 1991). Differences are nonetheless apparent between Victorian and Tasmanian potoroo populations in habitat utilisation. In Tasmania thick ground cover is a frequent, but not invariable, characteristic of potoroo habitats.

Another feature of potoroo habitat is the frequent presence of a mosaic of local vegetation types (this study; Seebeck 1981; Bennett 1987). Such mosaics result from fire-succession vegetational stages, seral vegetational stages and ecotonal situations, or combinations of such stages. Preferred vegetation types within such mosaics are not obvious (this study; Bennett 1987), indicating that locally diverse vegetation may be of greater importance than the presence of specific patches of structural or floristic vegetation. Vegetational mosaics have been suggested to have evolved widely in

Australia as successive results of browsing and or grazing by now extinct megafauna up until around 30 000 years ago, and by aboriginal firestick burning since (Archer 1981; Archer, Hand and Godthelp 1991). These habitat changes are thought to have had an impact on the evolution of smaller faunal elements occupying them. While such microhabitat patterns are undoubtedly important in formulating conservation strategies, the appropriate management regime and indeed the characteristics of the mosaics themselves are not easy to determine.

This study included a range of microhabitats of differing structural complexity, some of which are both grassy and relatively open. Potoroos were not restricted to closed, non-grassy vegetation; rather they use a mosaic of vegetation types present in the study area. This supports the suggestion that potoroos utilise locally complex vegetation types (e.g. Seebeck *et Al* 1989). Whether such a mosaic is an actual habitat requirement would need to be tested across larger patches of more homogeneous habitat. The suggestion that potoroos are restricted to closed vegetation in Tasmania is overly proscriptive and based on a limited number of specific studies rather than thorough habitat investigation. Where habitats have been investigated more thoroughly (in Victoria, Menkhorst 1995a), the survival of potoroos appears to be linked to habitat characterised by dense vegetation. However, it is possible that the introduction of the red fox may have reduced the range of mainland potaroo habitats occupied at European settlement compared with Tasmanian habitats where foxes have not become established.

5.2 Food Distribution and Availability.

Early dietary studies on potoroos reported undigested spores in faecal samples (Kitchener 1967; Guiler 1971), indicating a heavy utilisation of fungal material. Other dietary items found in smaller quantities included fruit and seeds, invertebrate remains and plant cuticle. Mycophagy was confirmed by Bennett (1987) and Bennett and Baxter (1989), who also found a similar range of food items (invertebrate remains and remnants of vascular plant tissue) complementing those derived from sporocarps. Interpretation of diet based on faecal samples is difficult due to the possibility of differential digestion and thus identifiability and quantification of faecal material (Claridge 1993), especially where food items like starchy tubers could result in insignificant faecal residue. It is nonetheless clear that potoroos and bettongs may predominantly utilise hypogeal fungi, with significant use of this resource also by bandicoots, possums and rodents (Claridge and May 1994). Invertebrates also exploit fungal sporocarps (e.g. Lawrence 1989; Martin 1979), but

the extent to which they act as spore vectors and or as potential competitors with or prey of mammalian fungivore/omnivores is unknown.

5.3 Significance of Mycophagy to the Potoroidae.

The functional utility of mycophagy to small mammals, at least for hindgut-fermenting rodents, was questionable until recently. Cork and Kenagy (1989) concluded that fungal tissue could only supplement other high-nutrient sources such as seeds in a North American ground squirrel. While hindgut fermenters may benefit somewhat from selective retention of solutes and fine particles of digesta, and in some taxa from coprophagy, mycophagy alone is not known to provide an adequate diet for such species (Foley and Cork 1992).

Potoroids are, however, foregut fermenters (Hume 1982), a digestive strategy that allows slower but more effective digestion of some plant fibres and nitrogenous compounds via the passage of microbial products including high-quality protein from the forestomach to the gastric stomach. Subsequently Claridge and Cork (1994) have demonstrated the ability of potoroos to maintain body condition on a diet of hypogeal sporocarp material. Bandicoots are also partly mycophagous, but have a relatively simple digestive tract in comparison with that of potoroids. Mycophagy appears to be the predominant dietary strategy for potoroids, but is only supplementary in the diet of some other fungivorous mammals.

Production of hypogeal sporocarps is thought to be a spore dispersal strategy for soil dwelling fungi, which are often, but not always, in a symbiotic mycorrhizal association with a vascular plant (Claridge and May 1994). The fungus derives carbohydrates from the higher-plant host, enhances the plant's uptake of water and soil nutrients, and may help in protection from root pathogens (Claridge and Cork 1994). Not only is the mycophagist implicated in physical spore dispersal, the process of gut passage has been shown to enable or enhance the ability of spores to germinate on roots of a potential associate seedling (Claridge, Tanton, Seebeck, Cork and Cunningham 1992). The tripartite relationship (between fungus, fungal host and fungivore) appears to be particularly highly developed as an ecological strategy in temperate Australia (Claridge and May 1994). The fungal resource available to mycophagous animals is not known in detail for Porter Hill since Claridge and May (1994) note that the dietary studies at Porter Hill of Kitchener (1967) and Guiler (1971) report several taxa that are imprecise or erroneous, and that others are present but were unrecorded in prior studies (T. May; pers. communication).

The known mycophagist / food-taxa lists have been supplemented by estimates of productivity of the sporocarpic flora at some potoroo locations where a bandicoot

species (Claridge, Robinson, Tanton and Cunningham 1993) and, in Tasmania, also the bettong (Johnson 1994d) are syntopic. Annual yields were estimated at $21\text{--}181 \times 10^3$ sporocarps per hectare per month representing 1.8–8.3 kg per hectare per month (Claridge, Robinson, Tanton and Cunningham 1993) and at least 38×10^3 sporocarps per hectare per month representing at least 3.1 kg per hectare per month (Johnson 1994d). A wide diversity of fungal taxa was encountered at each site (26 and 23 species respectively), and at another site studied in taxonomic detail but not in terms of quantitative production (50 species; Bennett and Baxter 1989). The size of hypogaeal sporocarps and their dispersion in soil also varies considerably. Sporocarps have been reported to be closely associated with proximity to the base of trees (*Eucalyptus* spp.; Claridge *et al* 1993; Johnson 1994a,b,c), and predominant at depths of 0–15 cm.

Although a relationship between fungi, mycophagists and trees (as mycorrhizal fungal hosts) is clearly established, many details of this mutualism are unknown and others appear to be paradoxical. For example, some fungal species known to be significant to mycophagous potoroids produce sporocarps to depths of 50 cm (e.g. *Mesophelia* spp; May and Claridge 1994), a depth at which potoroids are not known to forage. This may indicate that the fungal strategy in producing attractive sporocarps has not evolved solely from coevolution with potoroids, but may reflect a range of potential vectors. A beetle, *Elaphastomus* sp. (Bolboceratinae) locates its oviposition burrows over hypogaeal sporocarps in sandy soils in Tasmania (Peter McQuillan, pers. communication), although whether it is a potential spore vector as well as consumer is unknown. If such species are spore vectors, their presence may explain why some hypogaeal sporocarps are found at depths beyond the digging range of potoroids and other vertebrate fungivores.

Resource partitioning between syntopic mycophagists is another somewhat paradoxical situation in view of the competitive exclusion principle. Claridge (1993) reported complete overlap of ingested spore taxa between potoroos and long-nosed bandicoots (*Perameles nasuta*) in Victoria. Johnson (1994d) reported syntopic potoroos and barred bandicoots in a larger study of the nutritional ecology of the bettong (Johnson 1994a), although the faecal spore overlap between the marsupial fungivores was not studied.

Enigmatic situations also arise in the case of some sporocarps which are reported to be regularly utilised by potoroos but for which attraction to mycophagists does not coincide with spore maturation (e.g. *Geastrum* spp.). This appears to indicate that fungivory may not always coincide with spore dispersal and thus that fungivores may

also effectively be predators on some fungi. The fact that another potoroid, the eastern bettong, and a bandicoot were syntopic with potoroos, at least over part of this study, indicates that the resource partitioning between such fungivores may be complex.

Fungal sporocarps fruit year-round in Tasmania (Johnson 1994c; Taylor 1992b), and in south-eastern Australia occasionally become superabundant (Claridge *et al* 1993). Their presence is not usually obvious, requiring pronounced olfactory ability at least in bettongs (Donaldson and Stoddart 1992). The variability of the sporocarp resource on a longer term basis and the effects of extreme seasons are little known. This, together with the unpredictable spatial dispersion of the sporocarps, means that foraging is an active process covering a large area. Unlike many grazers or arboreal foliovores for which food may be more concentrated, at least within localised patches, potoroo foraging must be an active and opportunistic process. This may have led to individual home range areas significantly greater than long-term minima required for sustenance (i.e. compared with the fungal production rates cited above), in order to minimise the probability of very localised stochastic food shortages and thus have led to substantial overlap in general use of space. Poroos nonetheless have smaller mean home-range areas and higher population densities than bettongs.

5.4 Body Mass and Home-Range Dimorphism in the Potoroo.

In this study, male potoroos were significantly heavier than females. This is in agreement with Johnston and Sharman (1976) and Bryant (1989), at least for potoroos in south-eastern Tasmania. It should also be noted that considerable variation occurred between individuals and within individual lifetimes. Johnston and Sharman (1976) examined body mass differences between sexes within seven separate populations of *Potorous tridactylus* from both mainland Australia and Tasmania, and found males significantly heavier on average in all but the western Victorian (Portland) population. More generally, Johnston and Sharman (1976), concluded that considerable geographical variation exists in parameters such as body-size and craniological features of potoroos.

In this study, male potoroos had both larger mean home-ranges and body mass than females, consistent with the conclusion of McNab (1963) that the bioenergetics of mammals of dimorphic body size is frequently reflected in home range size. An alternative interpretation is that home range dimorphism may reflect a reproductive constraint, such as a female requirement for nest sites (Morris 1984). In the absence of identifiable differences in habitat requirements between male and female potoroos, it is most likely that sexual selection is the best explanation for the dimorphism

found in this study. Males may move more to enhance their chance of encountering females and to monitor their reproductive status, while female movements are confined to finding adequate food. Nesting sites may also be important, although the simplicity of shelters or simple nests regularly used by potoroos may mean that they are usually less of a limiting factor than other habitat requirements.

5.5 Implications of Predation for Potoroo Populations.

Anthropogenic introductions of the domestic / feral cat and the red fox are implicated in recent mammalian extinctions and population declines in Australia (e.g. Kennedy 1989). Also of particular significance in the Tasmanian context are the absence of the dingo, *Canis familiaris*, in aboriginal time (despite its introduction to mainland Australia 3450 to 8000 years bp (Newsome and Coman 1989)), and of the red fox (introduced to mainland Australia in the 1860's (Rolls 1969)). The absence of the dingo in Tasmania is usually suggested as the reason for the survival of its two endemic marsupicarnivores, the Tasmanian devil (*Sarcophilus harrisii*) and the thylacine (*Thylacinus cynocephalus*). As these species are a slow, opportunistic carnivore / scavenger and an open-country pursuit carnivore respectively, little predation pressure on the potoroo is probable from these sources. Quolls; the spot-tailed quoll, *Dasyurus maculatus*, and the eastern quoll, *D. viverrinus*, were present in both Tasmania and mainland Australia at European settlement and while some predation from these sources was likely it would not have acted differentially across Bass Strait. Conversely, the red fox is implicated in the substantial demise of a range of mammals, especially those in the critical weight range (CWR) of 0.2 - 5 kg body mass, throughout mainland Australia (Johnson, Burbidge, and McKenzie 1989).

Potoroos have been less drastically affected than some other CWR marsupials, including some potoroids such as the bettong, but the patchy modern distribution of the potoroo in Victoria and their restriction there to dense vegetation (Seebeck 1981) may have resulted from introduction of the red fox. Declines in fox populations due to epizootic disease have led to population increases in prey species that were unforeseen prior to the fox epidemic (Lindstrom, Andren, Angelstam, Cederlund, Hornfeldt, Jaderberg, Lemnell, Martinsson, Skold and Swenson 1994), leading to the conclusion that the effects of predation may not be evident under an ongoing predation regime. Differential predation by the dingo, and possibly the red fox, may also have led to selection for body size differences between potoroo populations, including the body size differential across Bass Strait.

Some authors (e.g. Rose and Johnson 1983, Seebeck 1978) have suggested that causes other than fox predation may explain differential survival of potoroids in different regions, markedly across Bass Strait. Higher densities of the introduced rabbit on mainland Australia, and consequently more disturbance to grassland habitat, was considered by Rose and Johnson (1983) to help explain survival of bettongs in Tasmania compared with Victoria, although it is difficult to reconcile this explanation with the early and complete demise of eastern bettongs from their original wide geographic range in mainland Australia. The lack of potoroo remains in fox scats from a potoroo population in forest in western Victoria led Seebeck (1978) to conclude that foxes may not prey on local potoroo populations, but equally fox predation may have restricted potoroos to dense microhabitat within a previously more widely utilised range of habitat. Fox predation appears to be the most parsimonious single factor identified in differential survival of potoroids in south-eastern Australia including Tasmania.

Feral and domestic cats occur at Porter Hill, but the success of potoroos there and in other near-urban and more remote locations (e.g. Hird 1995) indicates these species may co-exist, at least over decades. Some cat predation of newly independent young, of body mass 200 to 700 g at Porter Hill, may nonetheless occur as cats are known to successfully prey on CWR mammals, including rabbits (Menkhorst 1995b).

Predation must be considered in the context of environmental changes, most significantly of habitat quality and availability. Not only has Australia's predation regime changed with the introduction of adaptable exotic mammalian predators, forest habitats have changed both in scale and quality since European settlement (Lunney 1993). The most significant effect on forest habitats has been the widespread reduction of native forest to islands which, through isolation and altered fire regimes, are typically of lower diversity and have CWR-mammal faunas which have been shown to be more susceptible to indigenous and recently introduced predators such as the dingo (Catling 1993). Predation thus has the potential to have an insidious ongoing effect in that forest patches may superficially appear to retain their natural integrity, but may have lost, or be susceptible to the loss of, components of their native faunas.

5.6 Reproduction in *Potorous tridactylus*.

Poroos exhibit the typical potoroid reproductive pattern of year-round breeding, in contrast with most macropodids which exhibit seasonal breeding. Hypogeal fungi may be a more seasonally-predictable food supply than that of grazing or browsing herbivores (Johnson 1994a). Some seasonal effects are to be expected, however,

since growth flushes in some subsidiary food plants are evident and because prolonged dry periods may limit the productivity of hypogaeal sporocarps (Claridge and May 1994). In this study most of the pouch young were borne by resident females rather than transients, which supports the notion that establishment in the resident population, and presumably detailed knowledge of a limited home-range, are important factors in individual lifetime success. Late-lactational physiological loads on females can often be amongst the most demanding periods of the life history of mammals (Lee and Cockburn 1985). The ability to cope with the combination of environmental stress and physiological load may at times (e.g. under sporadic prolonged-drought conditions) be profound for species breeding aseasonally.

Continuous breeding may also have resulted from the use of successional and fire-induced mosaic habitats, and an ability to colonise new areas of habitat rapidly, with dispersal primarily of juveniles and young adults. Catling (1992) suggested that potoroos are fire-susceptible on the basis of their requirement for dense shelter, while Seebeck (1995b) provided evidence for a rapid population recovery after fire, with a 100-fold increase in population size occurring within six years of a local fire. Fire is often an ecologically heterogeneous factor, with intensity and patch-size of the burn important factors in the response of the ecosystem. Fruiting of some species of hypogaeal fungi after fire and their utilisation by bettongs has been demonstrated (Taylor 1991), but the long term dependence of potoroids on fire has been challenged as equivocal (Claridge 1993). The principal issue in contention is the assumption of dependence of potoroids on fire, and its implication for management. While examples of post-fire fruiting of hypogaeal fungi and feeding responses of potoroids can be found (Taylor 1991), so can potoroo populations which occupy forests unburnt in more than 25 years, for example on Mt Wellington near Hobart (pers. observation).

5.7 Potential for Further Studies of Potoroos.

Further studies of potoroo behaviour will assist in complete interpretation of the results of this study. Radio-tracking, especially of individuals with overlapping home-ranges could be used to examine whether, for example, male potoroos more actively patrol their home-range than do females, indicating a social as well as trophic basis for relatively large home-ranges observed. Further, and especially for animals known to be resident and with overlapping home-ranges, knowledge of the spacing dynamics of individuals is of interest. For example, such cases could be used to test whether the co-trapping observed in this study represent a significant and

regular behavioural episode between apparently closely-attentive, solicitous male / female individuals, and whether males largely avoid each other.

Other aspects of the population ecology of the potoroo require further attention. Dispersal of young animals and their potential recruitment into the resident population in relation to their maternal home-range and residential status of their mother is of interest. Juvenile dispersal of potoroos was investigated by Bennett (1987) in a recapture study more conducive to obtaining such data, but in this study young juveniles were rarely captured, and especially recaptured, so that important parameters such as juvenile dispersal and recruitment could not be examined.

Parent-offspring relationships in mammals have been postulated to involve inherent conflict (Trivers 1974), but are probably more dynamic than simple models of mutually aggressive demands would indicate (Bateson 1994). Such dynamics may involve mutual monitoring of condition of mother and offspring, with, for example, responsive adjustment to the offspring's demands for food. Weaning was the peak time for conflict postulated by Trivers (1974), but aggression between mammalian mothers and offspring tends to occur at times other than weaning (Bateson 1994). In long-nosed potoroos maternal aggression is limited, with only occasional cuffing of offspring attempting pouch re-entry after permanent pouch vacation observed by Johnson (1988).

Philopatry, the affinity of newly independent juveniles for the natal home-range, is generally related to turnover of individuals in the population, with opportunistic philopatry occurring where home-ranges are vacated by dying individuals. Philopatry has been shown to be particularly prevalent in species utilising locally valuable resources, for example bannertailed woodrats, *Dipodomys spectabilis*, which cache seeds as food and maintain elaborate burrows, have high rates of "parental-consent" philopatry, although this is probably less common than opportunistic philopatry (Waser 1988). In the absence of evidence for aggression-mediated dispersal in potoroos (Johnson 1988), opportunistic or parental-consent philopatry is worth investigating, although relatively low rates of adult mortality (Chapter Two) are likely to mean that such opportunities are usually uncommon.

5.8 Conclusions.

The small proportion of individual *Potorous tridactylus* which establish residence in a population occupy limited, overlapping home-ranges and may exhibit significant longevity in comparison with minimal population maintenance requirements. Sexual

dimorphism in body mass and sexual differences in home-range area are likely to be significant in the social dynamics of the population. Microhabitat discrimination does not appear to be marked and it is possible that a floristic mosaic may be a general characteristic of potoroo habitats.

In comparison with other potoroids, and especially the syntopic bettong, potoroos are conservative in their use of space. This has social and ecological implications in that potoroos occur at higher population densities and may exhibit more social interaction than bettongs. Detailed resource partitioning between the four or more Tasmanian marsupials which include hypogeal fungi in their diets remain unclear.

Behavioural aspects of individual spacing over time are of particular interest in relation to the home-range overlap demonstrated in this study, but are not easy to investigate. The physical variability of potoroos, between both contiguous and disjunct populations, may be at least partly explained by differences in interspecific competition, e.g. across northern Tasmania where potoroos populations continue beyond the geographic western limit of bettong distribution (Rounsevell et al 1991). Resource partitioning, particularly dietary overlap with other syntopic fungivore / omnivores both generally and on a seasonal basis is unclear, and the implications of fungivory as a mutualistic process in disseminating fungal spores is of interest.

Poroos are well represented in Tasmania's reserve system, but loss of some specific habitat-types is of concern, and a more complete characterisation of habitats occupied by potoroos in Tasmania would be valuable. The islands around Tasmania are of interest in their implications for ecological plasticity of potoroo populations and environments (having been isolated for three to twelve thousand years (Hope 1974)), and are of conservation significance (Rounsevell 1989). Such islands also provide examples of woodland habitats which on the nearby Tasmanian mainland would appear suitable for marsupial fungivores, but lack such populations, and therefore potential fungivore spore vectors (Hird 1993). The fungal flora of such islands is of interest in view of the imputed dependence of some fungi and trees on marsupial fungivores.

Potoroo populations in Tasmania have survived to a greater extent than those of mainland Australia, both in terms of the range of habitat types occupied since European occupation and apparently in numbers of individuals. This is probably due to the absence of the red fox in Tasmania and is often manifested by survival of potoroo populations in more open vegetation and in near-urban habitats in Tasmania

compared to mainland habitats. This means that relic mainland populations of CWR mammals require appropriate management, both of foxes directly and of habitat, and that utmost care be exercised to exclude the red fox from Tasmania.

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