

**The winter ecology of the feral cat, *Felis catus* (Linnaeus 1758), at
Wedge Island, Tasmania**

by

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CHAPTER 1

General Introduction

The domestic or house cat *Felis catus* (Carnivora: Felidae) is usually believed to be derived from the African or Arabian wildcat *Felis sylvestris lybica* (Randi and Ragni 1991, Bradshaw 1992). Circumstantial evidence suggests that domestication began about 8000 BP in the eastern Mediterranean (Zeuner 1958, le Brun *et al.* 1987) and continued until 4000 BP in the Middle East and perhaps also in the valley of the Indus (Baldwin 1975, Ahmad *et al.* 1980). Paintings and sculptures of cats from the Eighteenth Dynasty confirm that cats were fully domesticated and living in close association with humans in Egypt by 3600 BP (Clutton-Brock 1981, Serpell 1988). Domestic cats spread slowly from Egypt, but occupied much of Europe prior to the spread of the Roman Empire (Waldren *et al.* 1984, Kitchener 1991). In the last 2000 years domestic cats have been transported actively on sailing vessels to most parts of the world (Lumpkin 1993), either for food, their ability to control ship-borne rodents or as pets (Dickman 1995).

In the Pacific region, transport of cats has taken place relatively recently. Domestic cats were brought by the first European settlers to eastern Australia and New Zealand in the late eighteenth century (Dieffenbach 1843, Rolls 1969) and were introduced to islands of the subantarctic slightly later, in the early 1800s (Debenham 1945). Several Polynesian islands, including Tonga and the islands of Hawaii, also received cats in the late eighteenth or early nineteenth centuries (Baldwin 1980). Domestic cats were probably introduced to several islands in Micronesia by Spanish sailing ships as early as the sixteenth century, and could have been introduced to north-western Australia and New Guinea still earlier by Indonesian trading vessels (Baldwin 1980). Cats have also been introduced to several smaller islands of the Pacific region this century (Kirkpatrick 1966), especially to islands off the coast of Australia and New Zealand (Fitzpatrick and Veitch 1985, Dickman 1992).

Although initially confined to settled areas, cats in many parts of the Pacific region have established feral populations that persist in remote or little disturbed localities. In contrast to domestic cats which obtain most or all of the resources they need to survive and reproduce from humans, feral cats have little or no interaction with humans and maintain self-perpetuating populations. In Australia, populations of feral cats were augmented in the nineteenth century by the planned release of thousands of cats outside of settled areas (Rolls 1969). Releases were made to control numbers of mice at gold digs in south-eastern and western Australia (Howitt 1855) and also in an attempt to control plagues of rabbits (Rolls 1969) and native rats (Bennett 1879) (Dickman 1995).

Until European colonisation of the Pacific region, Australia, New Zealand, Antarctica and the many Pacific islands contained no species of felids, and were relatively depauperate in medium sized species of carnivorous mammals (Flannery 1994). Hence the arrival of *Felis catus* probably represented an important ecological event. Recent studies of domestic cats in Australia and New Zealand have shown that many species of native vertebrates are killed by cats each year, and suggest that the impact of cats in settled areas is substantial (Fitzgerald 1988, Paton 1991). The impact of feral cats on native fauna has not been critically investigated, but numerous historical and circumstantial accounts suggest that cats can have large deleterious effects (Dickman 1993).

Predatory impact: evidence from islands

Because of their physical isolation, many islands off the coast of Australia and elsewhere in the Pacific region have been subject to little disturbance from human activities. Islands that have been isolated for long periods (i.e. pre-Pleistocene) often have taxa that are endemic to them, while many islands isolated by sea level rises at the end of the Pleistocene retain biota that disappeared from the adjacent mainland after the onset of European settlement. However, some islands have also suffered limited disturbance, such as the introduction of cats. Feral cats occur on at least 40 islands off the coast of Australia (Dickman 1992), seven off the coast of New Zealand (Veitch 1985) and several dozen elsewhere in the Pacific (King 1973, 1984). While

they are usually not the only agent of disturbance that has been introduced, cats may be the most obvious or important agent that can be identified. Changes in island faunas after the introduction of cats can provide compelling evidence of the impact of the latter (Dickman 1995).

Australian offshore islands

In the Australian region feral cats have caused or contributed to population declines and extinctions on many offshore islands (Appendix 1). Among the best documented case studies are the loss of brush tailed bettongs from St. Francis Island, South Australia and the losses of several small and medium sized mammals from Dirk Hartog Island, Western Australia. In addition to these well documented studies, feral cats have been implicated strongly in losses of mammals and birds from Hermite Island in the Monte Bello group (Burbridge 1971) and probably also in the loss of the greater stick-nest rat *Leporillus conditor* from Reevesby Island in the Sir Joseph Banks group (Robinson 1989). Some species of birds and seabirds seem to have fared better than mammals on Australian offshore islands, although the white faced storm petrel *Pelagodroma marina* has declined markedly on three islands (Appendix 1). The exposed burrows, nocturnal activity and clumsy movements of this species on land perhaps increase its proneness to predation from feral cats.

Taken together, the studies summarised in Appendix 1 and 2 demonstrate that feral cats can decimate insular island populations of native mammals and birds. However it is more surprising that stable coexistence may apparently be possible between certain species and feral cats. For example, the golden bandicoot *Isoodon auratus* disappeared from Hermite Island after the introduction of cats, but the ecologically similar southern brown bandicoot *Isoodon obesulus* persisted with feral cats on St. Francis Island (Robinson and Smyth 1976) and occurs commonly with cats on Kangaroo Island (Inns *et al.* 1979). Detailed ecological studies on insular species with stable populations are sparse but suggest that some native species can coexist with feral cats if refuges are available.

The general stability of seabird populations on Australian offshore islands (Appendix 1) perhaps best reflects the effect of certain features of community type and structure. Different community types and structures could very well be the determining factor which shape the extent of feral cat predation and its corresponding impact on island populations. For example, seabird populations may be able to sustain relatively high levels of predation on islands, providing that immigration rates equal or exceed losses (Saunders and Rebeira 1985, 1986). Other modifying factors such as behavioural aspects, foraging and breeding patterns or even habitat preferences could either neutralise or enhance predation impacts by feral cats. Conversely, the population dynamics of local island fauna could represent limiting parameters governing feral cat ecology.

Aims of the study

This study examines the winter ecology of the feral cat *Felis catus* on Wedge Island in the south-eastern region of Tasmania. The general aims of the project were to:

1. quantify the diet of the feral cat population over the winter months;
2. relate the quantified diet to prey availability and abundance during winter;
3. relate prey availability and abundance to reproductive condition of feral cats throughout the winter months; and
4. determine the home ranges and spatial organisation of individuals in the feral cat population.

CHAPTER 2

Study site

Wedge Island (43° 09'S, 147° 33'E) is located 1.25 kilometres off the Tasman Peninsula in the south-eastern region of Tasmania (Fig 2.1). The length of the island is approximately 1.3 kilometres from north to south, with a maximum width of 0.55 kilometres, at mid-island. The area of the island is approximately 50 hectares (Fig. 2.2). Wedge Island is characterised by steep dolerite cliffs (igneous rock formations) framing the western border while large irregular boulder platforms/cliffs and rocky outcrops forming the north and southern ends of the island. The eastern shoreline consists of a level rocky shore, beginning at the northern extremity which extends to the cliffs at the south end. A ridge line runs in a north-south direction, with a peak of 96 metres above sea-level (Figure 2.2). Wedge Island possesses a temperate climate and experiences a wide range of weather conditions, with an average annual temperature range of 8.1 C to 14.7 C (Palmer's Lookout Weather Station, Bureau of Meteorology) and a recorded rainfall of 797 mm in 149 raindays (Port Arthur Weather Station, Bureau of Meteorology).

Wedge Island is an important island rookery for nesting seabirds during the breeding season. These seabirds include little penguins (*Eudyptula minor*) and two species of petrels: short-tailed shearwaters (*Puffinus tenuirostris*) and fairy prions (*Pachyptila turtur*). The island has two major rookeries, the North and South Rookery, which are situated at opposite ends of the island (Fig. 2.3). The total area of the North Rookery is approximately 0.02 square kilometres, whereas the total area of the more extensive South Rookery is approximately 0.17 square kilometres. Both rookeries are utilised by petrels, fairy penguins and native hens; the North Rookery is almost exclusively used by penguins (Fig. 2.3). Juvenile muttonbirds are commercially harvested within a limited period on the island during the breeding season between 27th March and 30th April (Schodde 1986).

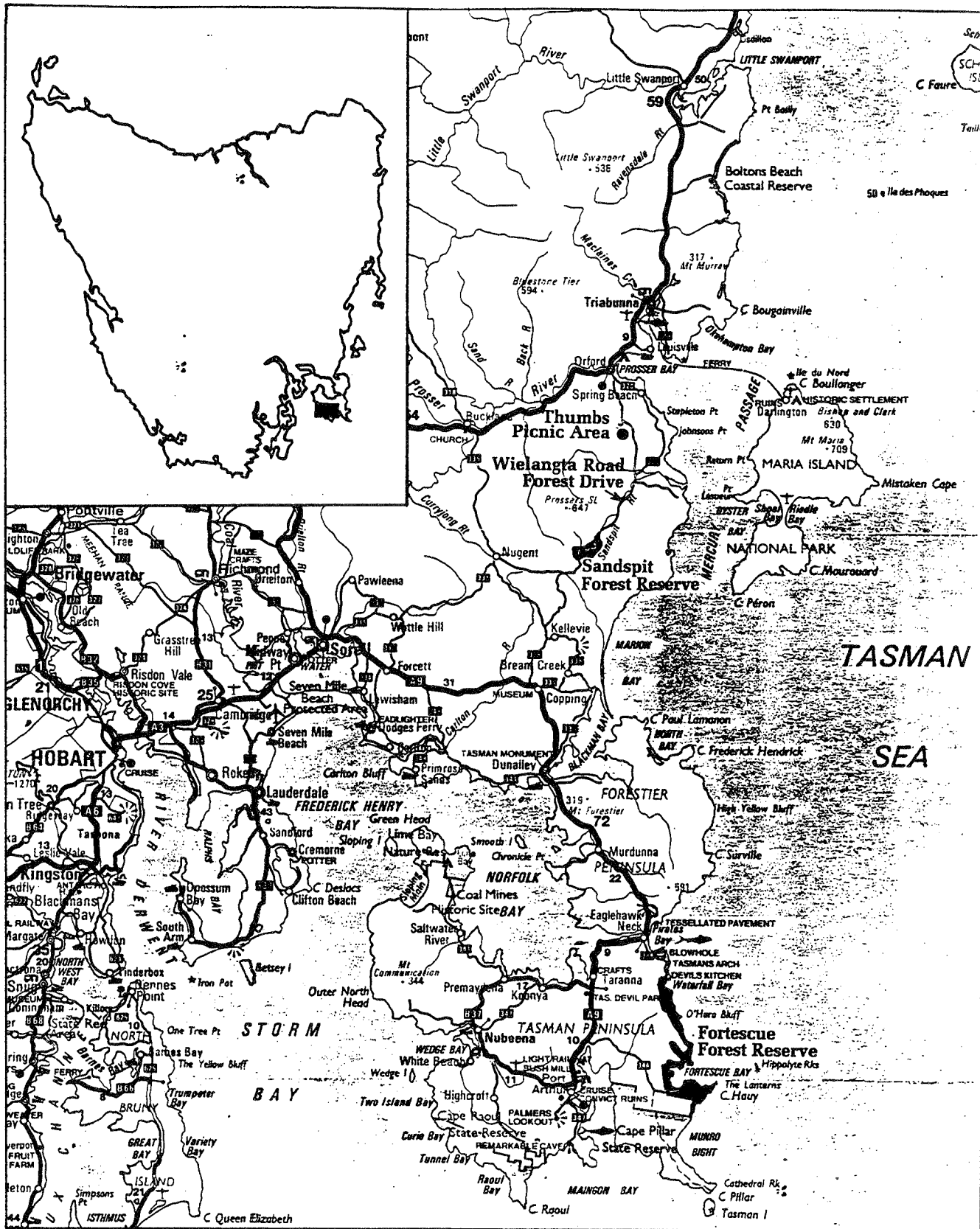


Figure 2.1 Location of Wedge Island in the south-eastern region of Tasmania.

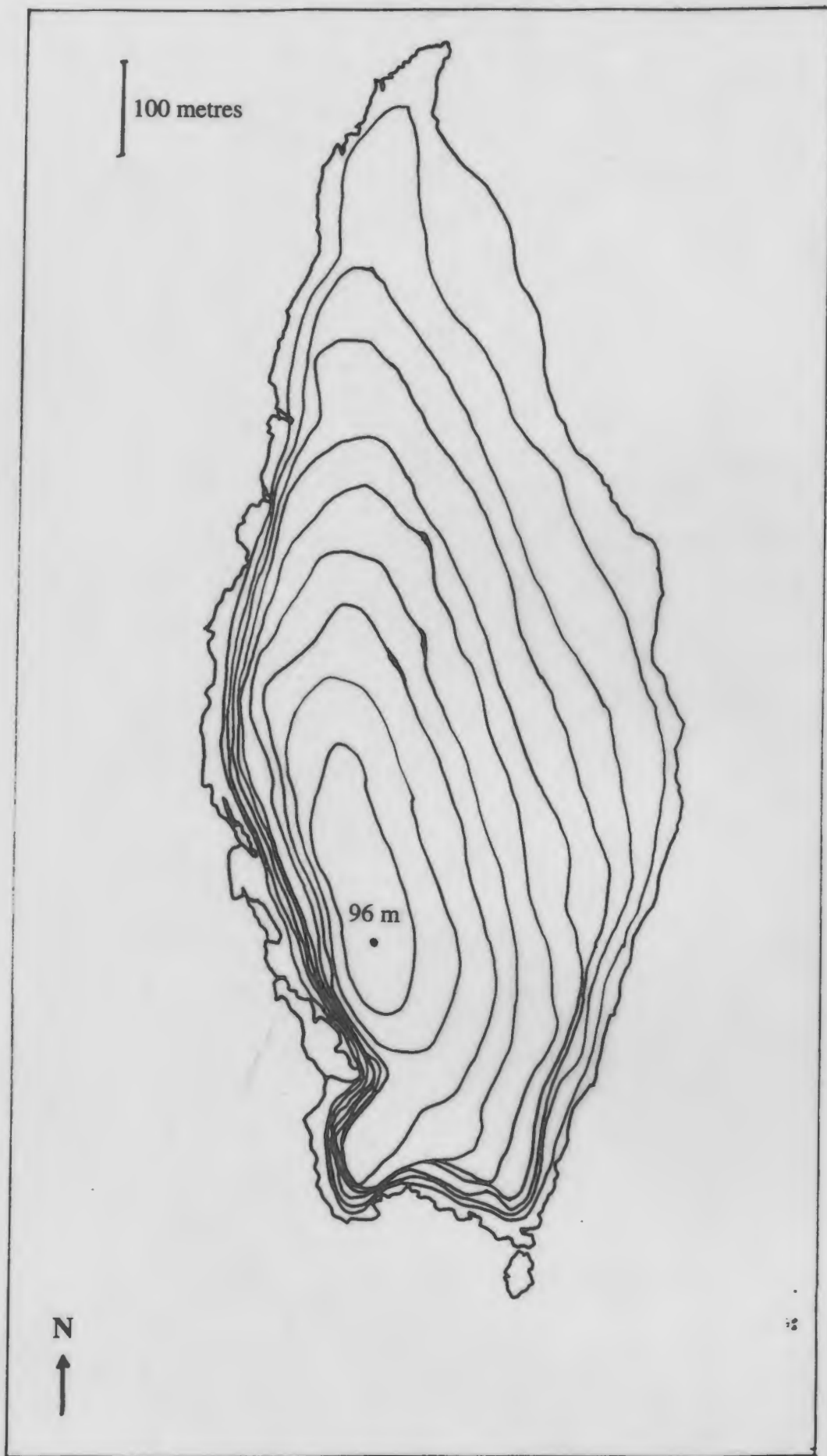
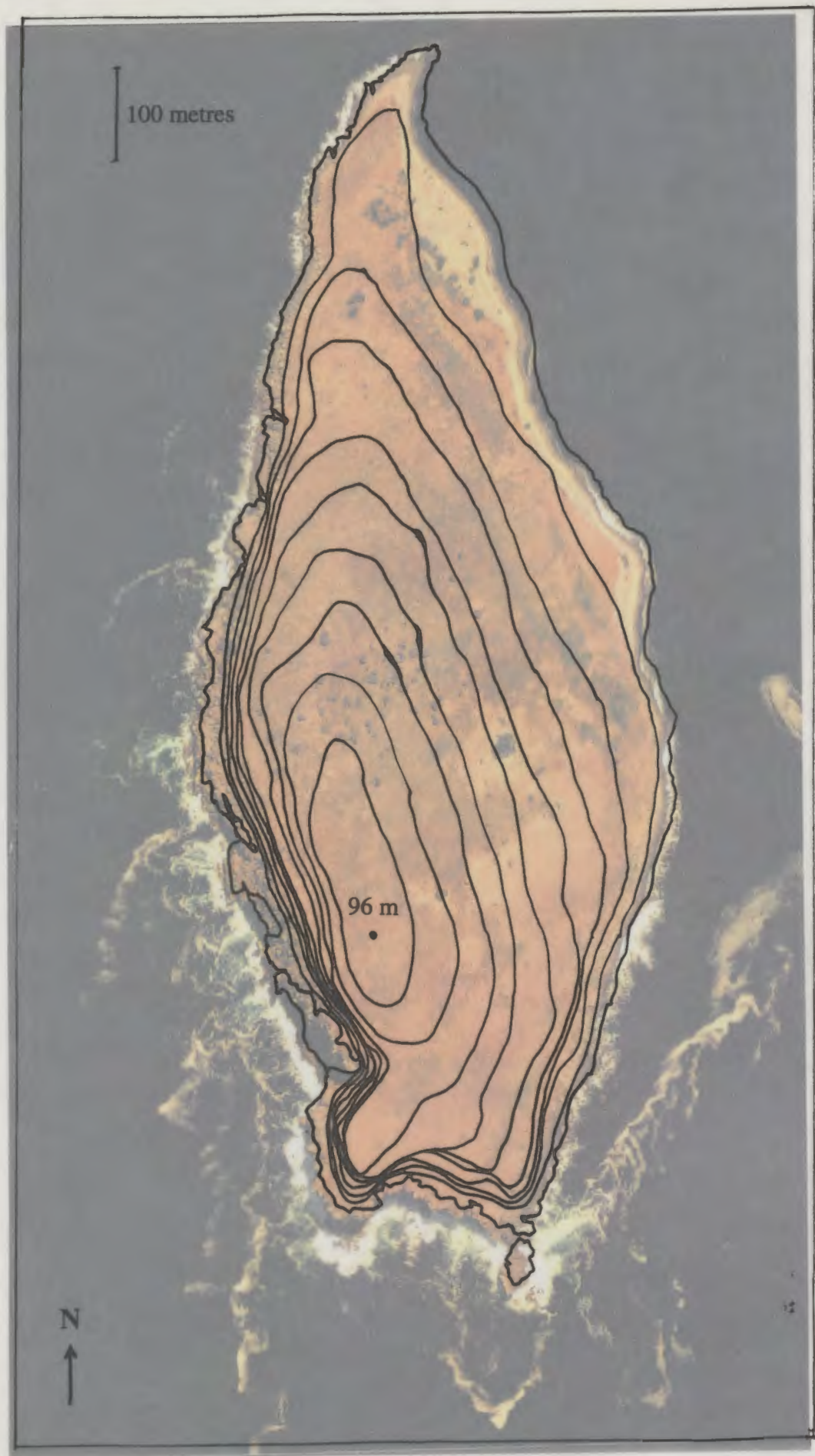


Figure 2.2 Topographic contours of Wedge Island with location of the peak point on



Aerial photograph of Wedge Island; February 1984 (Department of Environment and Land Management).



Aerial photograph of Wedge Island; February 1984 (Department of Environment and Land Management).

Figure 2.2 Topographic contours of Wedge Island with location of the peak point on ridge line

The rookeries are dominated by succulent vegetation of the genera *Rhagodia*, *Tetragonia*, *Carflobrotus* and native grasses of the genus *Poa*. The remaining areas of the island support extensive growth of bracken (genus *Pteridium*) and short-sword grass fields of the genus *Lomandra*. Few trees are present on the island and most of these are concentrated below the ridge line around the central area of the island. Low hanging shrubs (unidentified species) are present with growth along both shorelines and the lower regions of both rookeries (aerial photograph, Figure 2.2).

Table 2.1 List of principal plant species identified on Wedge Island.

Vegetation Species
1. <i>Rhagodia baccata</i>
2. <i>Tetragonia inflexicoma</i>
3. <i>Carflobrotus edulis</i>
4. <i>Carflobrotus rossi</i>
5. <i>Poa poiformis</i> var. <i>ramifer</i>
6. <i>Lomandra longifolia</i>

This study was conducted on Wedge Island in the period between May and September 1995, during which six field trips were conducted (Table 2.2). Access to Wedge Island was gained by a departmental research vessel from White Beach, Nubeena. Due to adverse weather conditions, the duration of field trips was variable and field work was often difficult.

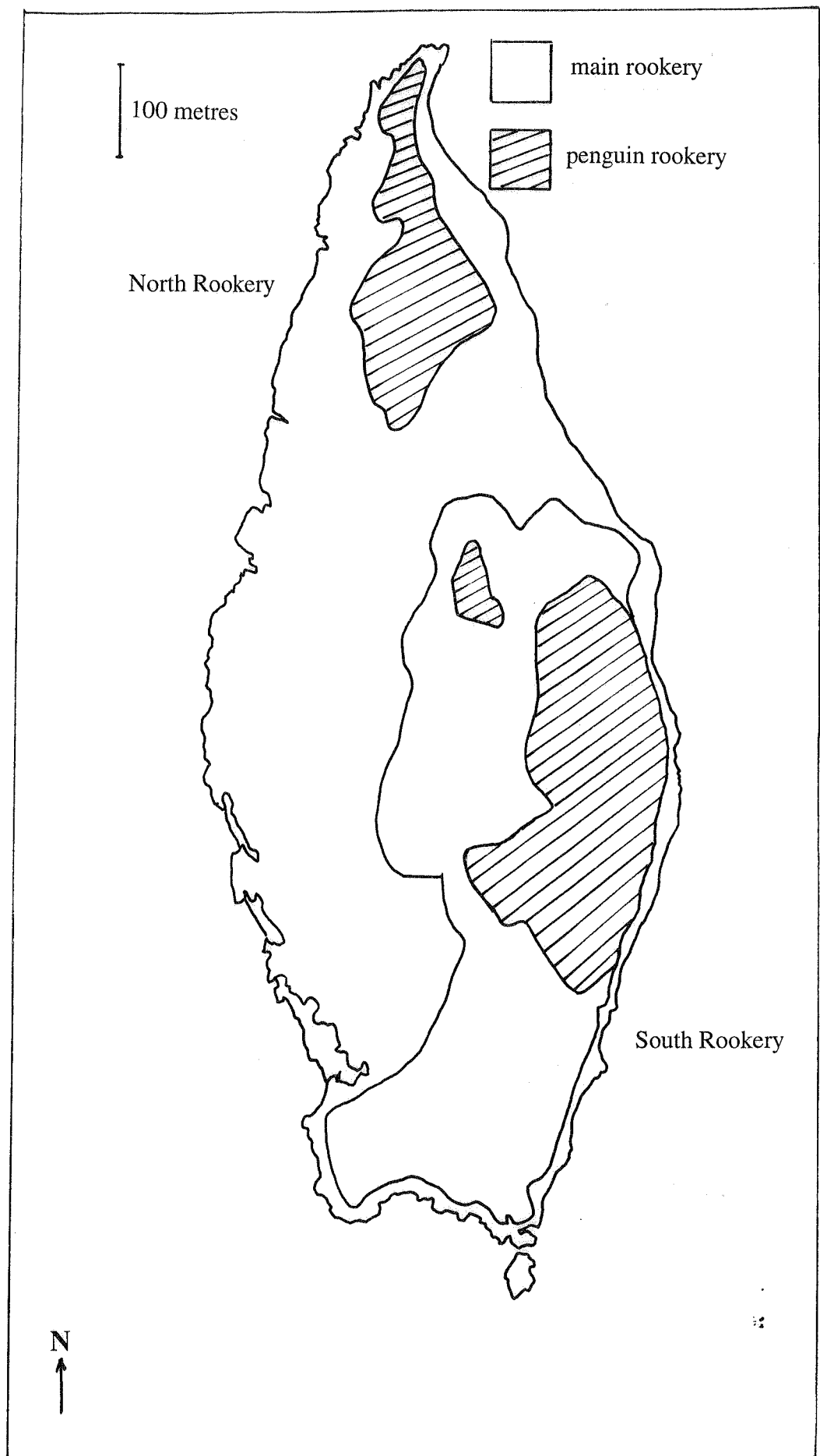


Figure 2.3 North and South Rookeries: utilised by little penguin and petrel colonies.



Aerial photograph of Wedge Island; February 1984 (Department of Environment and Land Management).



Aerial photograph of Wedge Island; February 1984 (Department of Environment and Land Management).

Figure 2.3 North and South Rookeries: utilised by little penguin and petrel colonies.

Table 2.2 Dates and durations of field trips to Wedge Island between May and September 1995.

Field trip number	Dates	Duration/Days
1	8-22 May	15
2	5-13 June	9
3	25 July-1 August	8
4	10-15 August	6
5	28 August-1 September	5
6	25-29 September	5

Vertebrate prey on Wedge Island

Wedge Island is an important rookery for nesting seabirds. These seabird species include the little penguin (*Eudyptula minor*) and two species of petrel: the short tailed shearwater (*Puffinus tenuirostris*) and the fairy prion (*Pachyptila turtur*). Short-tailed shearwaters or muttonbirds, as these birds are more commonly known, migrate in late autumn to spend the Australian winter months along the Siberian coast to feed. Fairy penguins and fairy prions utilise Wedge Island throughout the year.

The combined areas of both the North and South Rookeries comprise approximately 0.27 square kilometres. With an average of 85 to 110 burrows within a 400 square metre transect, the entire rookery area on the island contains more than half a million burrows. During the mating and breeding season, the total number of burrows in both rookeries may be considered to represent a similar number of sea birds present on the island, each burrow in the rookery supporting two seabirds with their chick. However, the total number of the birds present on the island may fluctuate considerably, particularly with the departure of the short-tailed shearwaters over winter.



Figure 2.4 Northern end of Wedge Island, overlooking North Rookery and base camp at north tip.



Figure 2.5 Cliff face at the northern end of Wedge Island.



Figure 2.6 Mid island ridge-line view towards southern end of Wedge Island; vegetation dominated by short sword grassfields and native grass tussocks.



Figure 2.7 Ridge line view towards southern end of Wedge Island.



Figure 2.8 Cliff face at the southern tip of Wedge Island.



Figure 2.9 Rocky outcrops at southern tip of Wedge Island.



Figure 2.10 View of South Rookery from eastern shoreline.



Figure 2.11 View of South Rookery, mid island.



Figure 2.12 South Rookery seabird burrows with native grass tussocks and succulent vegetation.



Figure 2.13 South Rookery seabird burrows dominated by native grass tussocks and succulent vegetation.

***Little penguin Eudyptula minor* (Forster, 1781)**

Bluish-grey above and white below, lacking any conspicuous markings, and the smallest of penguins, this species is virtually unmistakable. Widely known as the fairy penguin or little blue penguin in New Zealand, it is the only penguin to breed in mainland Australia. (Schodde 1986). The range of the little penguin extends from near Perth in Western Australia, around the southern coast of Australia to about Port Stephens, New South Wales but it is most numerous in Tasmania and Victoria; it is also common and widespread in New Zealand waters (Schodde 1986). Hardly synchronous or cohesive enough to be called colonies, most breeding aggregations are found on offshore islands where introduced foxes, dogs and cats are absent. In comparison with most other penguins, breeding colonies are not large; there are some 5000-10,000 burrows on Gabo Island in Victoria and St. Helens Island in Tasmania had an estimated 30,000 birds in 1978 (Schodde 1986). The total population breeding at eighteen known colonies in New South Wales has been assessed at about 17,000 pairs, most occurring in the large colonies on Montague, Tollgate and Brush Islands. However, the birds often breed as scattered pairs (Blakers *et al.* 1984).

The little penguin is a sedentary bird. Breeding adults visit their burrows intermittently throughout the year (although those in Tasmanian waters tend to disperse more widely), whereas young birds wander extensively after leaving their natal island (Schodde 1986). As well as being subject to predation by feral cats and foxes, the little penguin is sensitive to human disturbance and many colonies in populated areas have dwindled or disappeared. Much of this interference results from soil erosion, inadvertent collapse of burrows or the disruption of the breeding activities of birds, but in some parts of the country little penguin flesh is valued as bait by lobster fishermen (Lindsey 1986). Although the colony on Phillip Island is completely protected and access is carefully controlled, disturbing signs of decline are now evident: active burrows numbered 617 in 1980-1981, 587 in 1981-1982 and 481 in 1982-1983, the decline strongly attributed to the predation impacts of foxes and cats (McManus 1979).

Compared with other seabirds of temperate regions, the onset of the breeding season of the little penguin is unusually flexible, varying widely from year to year and not



Figure 2.14 Adult little penguin with chick; Albatross Island, Tasmania, November 1983 (G. Robertson).

even closely synchronised within colonies in any one year. However, in Tasmania the breeding schedule is more synchronised and it begins two or three months after the commencement of the breeding season in Victoria (Blakers *et al.* 1984). Unusually for penguins, two or three broods may be raised successfully in a season. The clutch invariably consists of two eggs but more than one chick is seldom raised. Little penguins show a strong attachment to the same burrow (or another in close proximity) and to the same mate, year after year (Reilly and Cullen 1982).

For some time before breeding begins (generally in late July, August or September), birds visit the colony with increasing frequency and for longer periods, occasionally remaining all day in their burrows. Most eggs are laid in September or October and incubation is shared by both sexes and lasts about thirty-five days (Blakers *et al.* 1984). One or the other of the parents remains with the chicks continually for about fifteen days after hatching, after which the young are left unattended while both parents forage for food. The growing period varies considerably but most young fledge and leave their burrows within nine weeks (Schodde 1986).

***Short-tailed shearwater Puffinus tenuirostris* (Temminck, 1835)**

This is one of the very few Australian birds to support a well established growing industry. Known in its range as the 'muttonbird', short-tailed shearwaters breed in huge numbers on islands in and around Bass Strait where chicks are harvested for their flesh, oil and feathers. Taking into consideration an estimated annual crop of 3.2 million chicks and at least 1.7 million immature birds and non-breeding adults, a new total figure of 16.3 million birds has been suggested to comprise the muttonbird population in Tasmania (Lindsey 1986).

The migration routes of the short-tailed shearwater describe a huge figure of eight path across the Pacific, taking the birds north through Japanese waters to reach the main wintering area off the Aleutian Islands as early as mid-May. A few continue eastwards to the coast of British Columbia and south as far as California. The return route is through the central Pacific, curving westward to the Australian coastline. Birds arrive in the Bass Strait in mid-September, normally about a week before the



Figure 2.17 Short-tailed shearwater adults leaving colony; Cat Island, Tasmania.
(J. Warham).

birds first visit their breeding islands (Schodde 1986). The arrival at the breeding sites is relatively consistent from year to year, although it appears to vary by a few days from colony to colony. The first animals to arrive are adults; birds younger than five or six years (too young to breed) also visit the colonies but arrive later in the season and leave before the breeding birds. For five or six weeks the birds are occupied with refurbishing their old burrows or digging new ones. The courtship period begins in the first few days of November and lasts twenty-one days, during which the female forms her single egg, a process thought to take about eighteen days, this formation period being spent at sea (Lindsey 1986). The birds return on or about the 25th of November and eggs are laid almost immediately. Egg laying may span about seven days but there is a marked peak at the 27-28th of November. Parents take turn incubating, in shifts of about fourteen days. The egg hatches after about 53 days, and hatching success is very high, varying about 92 and 95%, except in those colonies where feral cats are common (Blakers *et al.* 1984). Chicks are fed daily for the first seven to ten days, after which the feeding frequency declines to such an extent that in late March the chick is fed only once every ten to fourteen days. In early April, the chicks leave their burrows at night and begin moving about the colony, often congregating in open areas and flapping their wings. Adults desert the colonies in mid-April, generally within a period of a few days; the young leave several weeks later (Schodde 1986).

***Fairy prion* *Pachyptila turtur* (Kuhl, 1820)**

This is the only species of prion known to breed in Australian waters, with colonies on Moncoeur and Lady Julia Perry Islands, at Lawrence Rocks in Victoria and a number of islands in the Bass Strait and around Tasmania (Harris and Norman 1981, Serventy *et al.* 1971). Almost 50,000 birds breed at each end of the Tasman and Ile de Golf Islands and about 20,000 at Flat Witch Island (Brothers 1979, White 1981, White 1979). Fairy prions also breed on Macquarie Island and offshore islands around New Zealand and at Marion Island in the Indian Ocean (Blakers *et al.* 1984).

Fairy prions that breed in New Zealand are believed to be migratory but the Australian population is relatively sedentary, significant numbers visiting their colonies



Figure 2.18 Fairy prion chick; The Snares, New Zealand, February 1975 (G. Robertson).



Figure 2.19 Adult fairy prions; Albatross Island, Tasmania, November 1982 (G. Robertson).

throughout the year (Harper 1980). The breeding cycle has not been studied in Australia but has been substantially investigated by L.E Richdale in New Zealand (Schodde 1986). Birds return to their colonies in late August, older birds often returning to the same burrows used in previous years. Egg laying reaches a peak in early November and both parents incubate the egg until it hatches after about 56 days (Lindsey 1986). The chick is brooded by both parents for the first few days, then neglected, except for feeding visits (which may be as brief as fifteen minutes) towards the end of the nesting period. After 44 to 55 days in the nest, the chick leaves for the sea during February (Schodde 1986).

***Tasmanian native hen Gallinula mortierri* (Dubois, 1840)**

Fossil remains show that the Tasmanian native hen once lived on mainland Australia but this plump, dull coloured bird is now found only in Tasmania. The Tasmanian native hen is endemic to the Tasmanian mainland but was introduced to Maria Island in 1969 (Green 1977). This bird is almost twice the size of its closest relative, the black-tailed native hen *Gallinula ventralis* of the mainland (Lindsey 1986). It is flightless but is able to run extremely fast, aided by stubby wings which it uses for balance when pursued. The habitat of Tasmanian native hens comprises swampy short-sword grassfields, intermingled with creek-side tussocks and thickets in which they shelter (Blakers *et al.* 1984). Resting in cover most of the day, the hen emerges at dawn and dusk to feed on plant shoots and various insects. An analysis of the gut contents of 4477 specimens showed that the native hen feeds principally on plants (90 % by volume) but the parents feed many insects to young chicks (Ridpath 1972). The Tasmanian native hen is sedentary; individuals rarely move more than three kilometres from their parents' nest; the recorded maximum movement is 40 kilometres (Australian Bird Banding Scheme, CSIRO 1985). The hens live in small groups of one female with one or two occasionally more males, as well as the young of the previous season. Breeding is often communal (Ridpath 1972). Pairs and trios occur in about equal proportions; the males of one nesting group are often brothers. The group operates as a unit, establishing a permanent territory that can grow from 5000 square metres to 15000 square metres. Tasmanian native hens breed in July to December, rearing two broods in good years. The number of eggs in each clutch



Figure 2.15 Tasmanian native hens, Wedge Island.



Figure 2.16 Tasmanian native hen, Wedge Island.

varies from four to nine. Incubation is shared within the communal group which begins when the clutch is completely laid. Chicks are attended for approximately eight weeks (Schodde 1986).

The Tasmanian native hen is not a native of Wedge Island; it is suspected by rangers in the Tasmanian Department of Parks, Wildlife and Heritage (TPWH) that this species was introduced to the island around the same period as rabbits and sheep. A decline was reported in the numbers of native hens in the Tasmanian Midlands after the introduction of myxomatosis and the consequent reduction of rabbits (Green 1965). It is probable that native hens originally lived on 'lawns' maintained by the grazing of marsupials and benefited from the introduction of the rabbit, as well as sheep (Ridpath 1972). The large initial colony of native hens on Wedge Island may have diminished due to the relocation of sheep from the island and the subsequent decline and demise of the rabbit population affected by the myxomatosis virus (Ridpath 1972). Sightings and subjective recordings of the presence of native hens throughout this study lead to an estimation of not more than thirty birds representing the island population.

Other vertebrate fauna

Other vertebrate fauna present on Wedge Island which are potential prey items for feral cats include two species of skinks: *Niveoscincus metallicus* and *Niveoscincus ocellatus*. *N. ocellatus* is found in abundance in its habitat along the eastern rocky shoreline of the island, indicated by sightings on warm days, of up to three individuals per square metre. *N. metallicus* is relatively less abundant in comparison with *N. ocellatus* and this species is located in the vegetated areas of native grass tussocks and bracken of the island.

CHAPTER 3

Feral cats on Wedge Island: past and present

Island background and history

European rabbits (*Oryctolagus cuniculus*) and sheep were introduced by fishermen to Wedge Island in 1930 (N.P. Brothers, Tasmanian Department of Parks, Wildlife and Heritage, pers. comm.). In the following years the rabbit population grew and flourished to such an extent that in 1939 the entire sheep population had to be relocated from the island due to lack of food and suitable grazing pasture (N.P. Brothers, TPWH, pers. comm.) There is some uncertainty about to the exact date regarding the initial introduction of cats to Wedge Island. According to local historians in Nubeena, the first sightings of cats were reported in 1939. However, this fledgling population of cats died out 'sometime' a few years later due to unknown reasons. Cats were reintroduced back onto Wedge Island in 1976, when a pregnant female was released on the island. Two years after the reintroduction, the rabbit population of the island disappeared. The demise of the rabbit population may be attributable to feral cat predation, coupled with resource shortage from severe overgrazing. In addition, in the years leading up to the demise of the rabbit population, the dissemination of the myxomatosis virus was continually undertaken by wildlife rangers of the Tasmanian Department of Parks, Wildlife and Heritage within the island rabbit population; anecdotal reports detail that the virus was effective and very active at times (N.P. Brothers, TPWH, pers. comm.).

Seabird colonies on the island were reported to have been much smaller in size in the early years but subsequently evidenced great expansion after 1950. Only one previous study (unpublished) has been conducted on the Wedge Island feral cat population. Between the years of 1984-1986 (inclusive), N.P Brothers (Tasmanian Department of Parks, Wildlife and Heritage) and Brian Green (CSIRO) conducted a study which attempted to quantify the energetic requirements of feral cats. Throughout that period of investigation, N.P Brothers estimated the total number of feral cats on the island to be between approximately 40 to 50 individuals. It was observed that the main areas of

high feral cat activity and density concentrated at the two extremities of the island. Cats captured in that study were collared and ear tagged for individual identification.

Methods

Live Trapping

A total of 817 trap nights was amassed over the course of the study. Feral cats were captured by live trapping in treadle operated wire Mascot cages. A variety of trap baits, consisting of different brands of canned cat food, fresh fish, frozen fish heads, sheep hearts and fish meal pellets were tested as bait throughout the early stages of the investigation. Initially, trap lines were laid selectively, concentrating on the North Rookery and from the central area to the south end of the island, in accordance with information obtained from N.P. Brothers (TPWH, pers comm.). As the study progressed trap lines were continually relocated to areas that yielded high density of feral cats. A total of 19 trap cages were utilised at all times. The traps were baited in the late afternoon between 1700 and 1800 hours.

Captured cats were removed from the cages and restrained in hessian bags. The animals were then sedated with an intramuscular injection of Zoletil™ 100 (10-15 mg/kg) in the femoral area. The volume of administered Zoletil™ varied for every individual captured, the maximum amount injected was 0.45 ml. When subjects were sedated, several body measurements were taken. All animals were sexed and weighed by suspension, then body length measurements such as skull, tibia, head to tail tip and head to tail base lengths were recorded. Juvenile and adult cats were distinguished by criteria of body size and length. Body temperature was obtained by rectal readings. The cats were also examined for evidence of external parasitic infections and the general condition status was noted for each individual. Finally, individuals were identified with a number tattooed applied to either one or both ears.

Spotlighting

Spotlighting was performed nightly on each field trip between the hours of 1830 and 2130 hours for an average of 45 minutes to one hour. The spotlighting transect began from base camp and continued along the eastern shoreline to the South Rookery. The

transect was approximately 900 metres in length, bordering both rookeries and offering an unobstructed view of each rookery area up to the ridge line. In addition, subjective observations of locations relative to other individual cats were made.

Results

Live trapping

Over 817 trapping nights beginning from the 8th of May and concluding on the 28th September 1995, a total of seven feral cats was captured by live trapping. The sex, age, weight and frequency of recaptures of all individual cats were recorded. These demographic attributes are listed in Table 3.1.

Table 3.1 Demographic attributes of all feral cats captured throughout the study.

Cat	Age	Sex	Weight	Recapture
001	juvenile	female	2.4 kg	0
002	adult	female	4.55 kg	0
004	adult	female	4.78 kg	1
005	juvenile	female	2.4 kg	9
003	adult	male	5.0 kg	0
006	adult	male	4.3 kg	0
007	juvenile	male	2.73 kg	4

Extensive trials of different feral cat baits resulted in the use of fish meal pellets which were found to be the most practical, durable and effective bait. All captured feral cats were physically examined and found to be lean and in good overall body condition. No female cats were found to be carrying litters or lactating. The mean weight of adult female cats was calculated to be 4.67 ± 0.163 kg and mean weight for adult males was 4.65 ± 0.49 kg (standard deviation). The mean weight of juveniles was 2.4 kg for females and 2.73 kg for males. No abnormalities were noted with respect to the body temperatures recorded from all the animals; the temperature range was confined to a narrow bracket from 37.5 °C to 39.3 °C. Over the course of the



Figure 3.1 Feral cat caught by live trapping and sedated.



Figure 3.2 Feral cat identified by ear tattoo.

period of live trapping, the body weights of individual animals in recaptures were closely monitored and no substantial fluctuations of body weights were recorded for any individual. No major increase in body measurements was observed for either juveniles or adult cats.

Spotlighting

Figure 3.1 illustrates the number of feral cats spotlighted on each field trip throughout the duration of the study. Results of the spotlighting study are expressed as feral cats spotlighted per hour on each field trip. The number of individuals identified by this procedure peaked in the month of June when 2.44 cats/hour were recorded; this decreased to 0.44 cats/hour in the months of August/September and then further declined to no cats being observed during the sixth field trip in the last week of September.

Data analysis

A two way analysis of variance was considered as an option to determine if significance of weight differences between male and female cats existed. It was decided not to apply this statistical procedure due to the small sample size of cats in the study; the analysis would have resulted in standard errors of considerable magnitude which would have biased the interpretation of data and comparison with other studies.

Discussion

Results from live trapping of feral cats and spotlighting strongly suggested that the feral cat population on Wedge Island was not extensive, in contrast with the estimation made by N.P. Brothers (pers. comm., TPWH) during his joint study with B. Green (CSIRO) on the island in 1984 to 1986. In the two year study, Brothers (TPWH, pers. comm.) estimated approximately fifty cats living in the island population. However, evidence obtained from this study lead to a more conservative estimate of not more than a total of fifteen individuals present on the island.

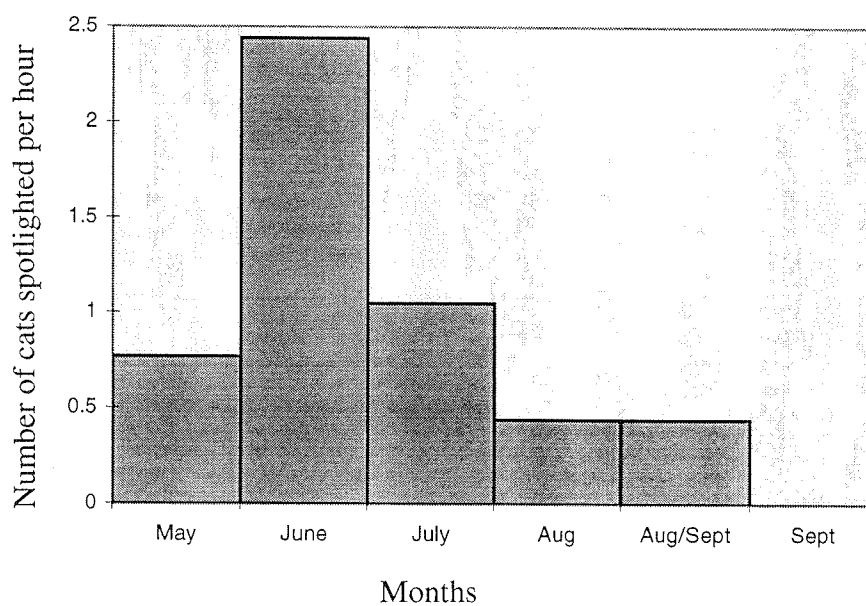


Figure 3.1 Number of feral cats spotlighted on each field trip throughout the winter study.

The body weights of cats in this study did not differ greatly from those reported by Jones and Horton (1984) for feral cats on Macquarie Island (4.46 ± 0.087 kg for males and 2.95 ± 0.093 kg for females). However, it should be noted that their sample size was almost seven-fold that obtained in this study and their samples were collected over a period of two years. Jones and Horton (1984) also reported that a highly significant difference existed in weight between sexes and for feral cats sampled from Macquarie Island and other sites on the Australian mainland. The differences in body weights of feral cats from different localities could be attributed to variable environmental factors. For example, winter nutritional stresses were suggested to be population limiting mechanisms for feral cats on Macquarie Island (Jones 1977) and in the Hattah-Kulkyne Park (Jones and Coman 1982) in the Victorian Mallee; such a factor could well be the major cause behind the decline of the feral cat population on Wedge Island since 1984. The possible effects of changes in resource availability and abundance as a limiting factor for the feral cat population on Wedge Island are further discussed in the following chapter in relation to the results of the dietary analysis.

CHAPTER 4

Feral cat population: dietary analysis

Introduction

Few studies of the diet of feral cats have been made on islands off the coast of Australia. However, several investigations have been based on islands elsewhere in the Pacific region (Appendix 1). On islands such as Macquarie, Raoul and Stewart, feral cat diets comprise mostly of the introduced European rabbit and rats (Appendix 2). The range of food taken on islands is generally less than that on the Australian mainland and this reflects the absence of prey such as marsupials and, on some islands, amphibians, large reptiles or bats.

Because of restricted availability of prey types, feral cats on some islands make extensive use of alternative food sources. For example, on the tiny (28 hectare) Herekopare Island in New Zealand, there are no introduced or native species of mammals. Prior to the elimination of feral cats from the island in 1970, the fairy prion *Pachyptila turtur* comprised the bulk of the feral cat diet, other seabirds and occasional land birds making up most of the remainder (Fitzgerald and Veitch 1985). Terrestrial orthopterans, wetas, appeared to be important to individual cats and two stomachs were found to contain over 100 insects. On Christmas Island the introduced black rat *Rattus rattus* comprised almost one third of the diet of feral cats by weight (Tidemann *et al.* 1994). However, 21% of the diet comprised the large (350 grams) flying fox *Pteropus melanotus*, while the large (524 grams) imperial pigeon *Ducula whartoni* constituted a further 28% (Tidemann *et al. op. cit.*).

The results of studies of feral cat diets on islands elsewhere in the world conformed to the pattern evident from the Pacific: that island cats often have a restricted diet comprising local prey. On the sub-antarctic Marion Island, petrels are a major prey item, many chicks of the great winged petrel *Pterodroma macroptera* being taken directly by feral cats from nesting burrows (van Aarde 1980). On the Galapagos Islands cats sometimes take birds of a larger mass than themselves, such as frigate birds (*Fregata* spp.), pelicans (*Pelecanus* spp.) and flightless cormorants

(*Phalacrocorax* spp.) (Konecny 1987). Iguanids feature prominently in the diet on islands of the Caribbean (Rand 1967), while on Aldabra Atoll, Seychelles, hatchlings of green turtles *Chelonia mydas* are seasonally predominant (Seabrook 1990).

In Tasmania, the orange bellied parrot, swift parrot, forty spotted pardalote, ground parrot, eastern barred bandicoot, long nosed potoroo, Tasmanian bettong and the New Holland mouse are believed to be potentially threatened by feral cat predation. On the offshore islands, species seabirds are locally vulnerable. Wedge Island supports colonies of short-tailed shearwaters, fairy prions and little penguins among other fauna and it is strongly suspected that introduced cats may have a significant impact on the population dynamics of the local fauna.

Aims

The primary aim of the present study was to quantify the diet of the feral cat population on Wedge Island. This investigation was undertaken to determine the entire range of prey that was taken by feral cats over the winter period. Dietary analysis was also expected to show the frequency with which prey were taken while simultaneous changes in prey items over the winter months could be monitored. The results of the dietary analysis were intended to establish possible relationships with regard to the availability and abundance of prey over the period of the study.

Methods

Scats of feral cats were collected from transects spanning both North and South rookeries. Minor fragments of scats located in close proximity were taken as a collective specimen. The precise location and freshness of the scats were recorded as they were collected. The samples were kept individually in resealable bags and transported back the laboratory for analysis. Each scat was dissected and prey items were identified to the nearest taxonomic group. Microscopic identification was used to categorise bird feathers found in the materials. Prey items present in each scat were then sorted by volume and assigned a category ranking from 1 to 5, each rank representing the percentage volume of the total scat (Table 4.1).

Table 4.1 Category ranking of prey items found in scat analysis.

Category Ranking	Per Cent Volume
1	0-20
2	21-40
3	41-60
4	61-80
5	81-100

Results

Scat Collection

A total of 527 scats was collected over 6 field trips from the 8th of May to the 29th of September 1995. The number of scats collected on each field trip was variable.

Figure 4.1 shows the breakdown of scats collected over the entire study period. Scat collection was rendered difficult by inclement weather during field trips in the months of June, August and August/September. During these trips, scats were either eroded or dislodged by heavy rains and strong winds.

Scat analysis

The collected scats were transported back to the laboratory where they were individually dissected and different prey items examined and identified. Table 4.2 lists the entire range of prey items that were identified in the cat scats. The frequency of occurrence of each prey item was calculated (Table 4.3). The volume of each prey item found in each individual scat was estimated and given a category ranking (Appendix 3).

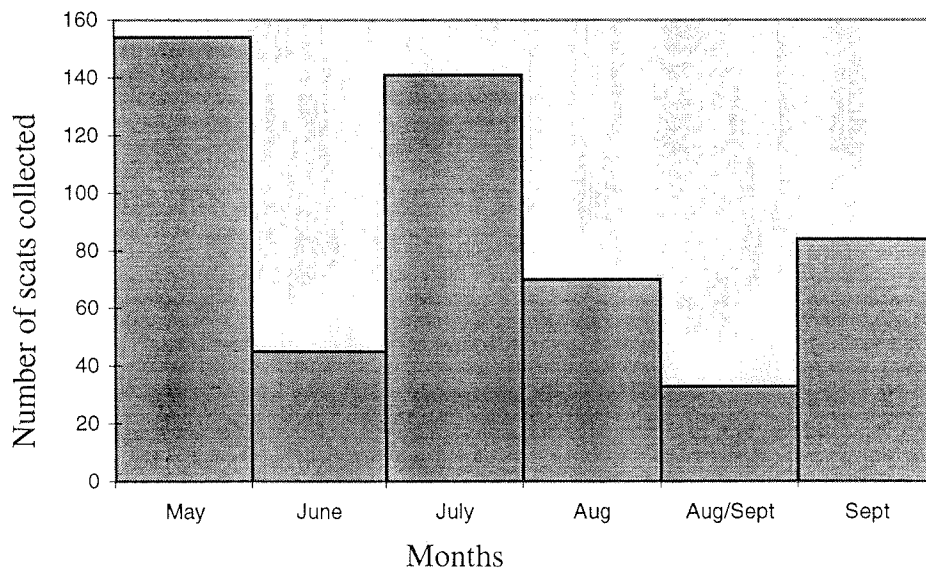


Figure 4.1 Breakdown of scats collected over six field trips conducted over the winter study period.

Table 4.2 Range of prey items identified in scats. (n=527)

Prey Categories	Prey Items
P1	petrels: short-tailed shearwater (<i>Puffinus tenuirostris</i>) fairy prion (<i>Pachyptila turtur</i>)
P2	little penguin (<i>Eudyptula minor</i>)
P3	Tasmanian native hen (<i>Gallinula mortierii</i>)
P4	coleopterans
P5	other insects: ants, crickets, grasshoppers,
P6	skinks: <i>Niveoscincus metallicus</i> <i>Niveoscincus ocellatus</i>
P7	caterpillars: Noctuidae: <i>Rictonis</i> Anthelidae: <i>Pterolecera</i>
P8	eggshell fragments and egg residues
P9	vegetation: grass, bark, leaves, small twigs, berries
P10	crab shell fragments
P11	other items: bivalves, molluscs, fish, starfish, chitons, scorpions, dirt, and foreign material (unidentified or miscellaneous)



Figure 4.4 Remains of a short-tailed shearwater killed by feral cat.



Figure 4.5 Remains of a little penguin killed by feral cat.

Table 4.3 Frequency of occurrence of prey items in scats. (n=527)

Prey Categories	Percentage	Mean volume and standard deviation
P1 petrels	21.63 %	4.54 ± 0.894
P2 little penguins	50.28 %	4.25 ± 1.11
P3 native hens	11.76 %	3.84 ± 1.217
P4 coleopterans	16.51 %	1.38 ± 1.035
P5 other insects	4.36 %	1.0 ± 0
P6 skinks	1.52 %	4.0 ± 1.852
P7 caterpillars	16.13 %	2.58 ± 1.282
P8 eggshell fragments	18.79 %	2.22 ± 1.401
P9 vegetation	54.46 %	1.26 ± 0.720
P10 crab fragments	4.74 %	1.4 ± 0.913
P11 other items	8.54 %	1.49 ± 1.014

Table 4.3 indicates that of the vertebrate fauna, the most common prey item found in scats were little penguins, followed by petrels and native hens. Overall, vegetation comprised of tussock grass, leaves, bark, berries and succulent vegetation were the most common items discovered, occurring in over half of all scats analysed. Of the invertebrate fauna, eggshell fragments and residue were the most common items recorded followed by beetles and caterpillars. Minor components of the feral cat diet included crab fragments and other insects. Skinks represented the least frequent prey item encountered in the scat analysis.

Every prey item identified in the scats exhibited fluctuations of mean volumes over the winter months. Figure 4.2 illustrates the changes in mean volumes of vertebrate prey (petrels, little penguins and native hens) found in scats during the period of the investigation.

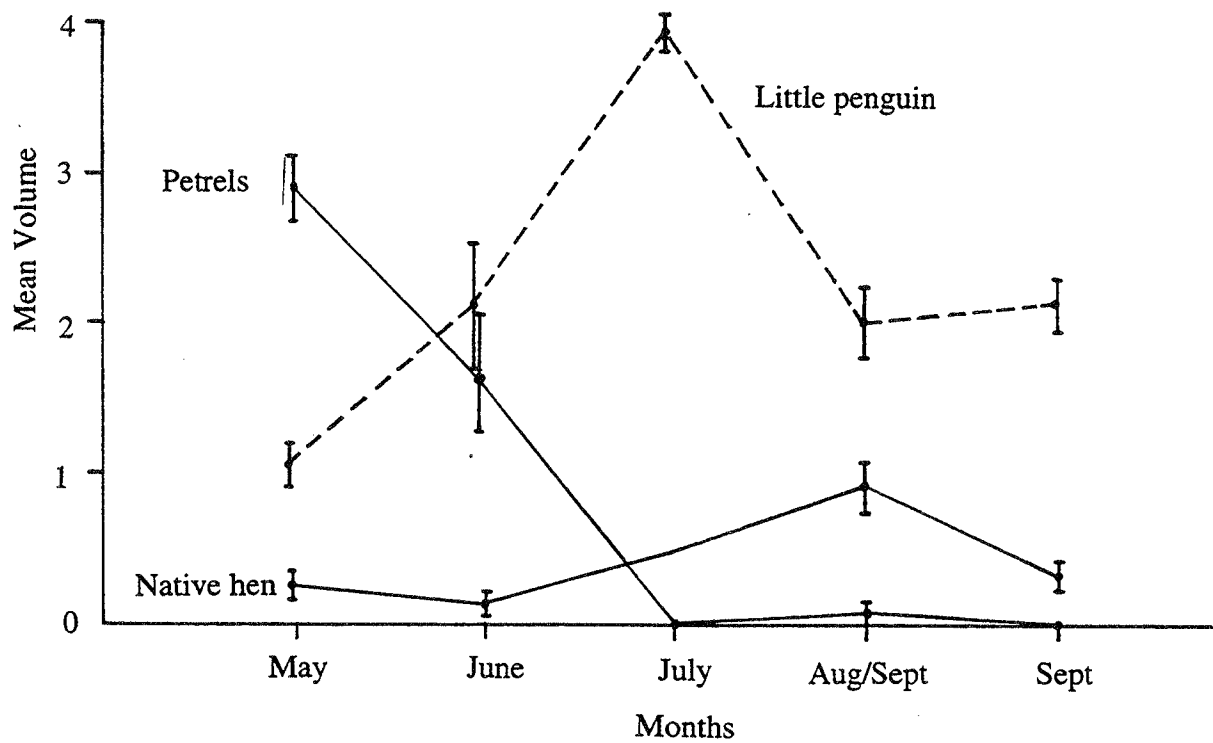


Figure 4.2 Mean volumes of vertebrate prey items: petrels, little penguins and native hens analysed in scats throughout the winter study. (n=527)



Figure 4.6 Skeletal remains of Tasmanian native hen killed by feral cat.



Figure 4.7 Skeletal remains of prey items found at a feral cat feeding site on the eastern shoreline, north end of the island.

Scat analysis from the first field trip indicated that petrels were less important than penguins as prey items; the mean volume of petrels decreased from a mean volume of 3 (41-60%) in May falling to zero in July and subsequently remaining at an almost negligible level to September. There was a corresponding sharp increase in the mean volume of little penguins in the scats from a value of 1 (0-20%) in May which then peaked in July (mean volume between 3 and 4 [41-80%]) coinciding with the period when mean petrel values fell to zero. The mean volume of little penguins in scats decreased after the month of July and stabilised at around a mean volume of 2 (21-40%) in August/September.

The mean volume of remains of native hens was initially lower than those of fairy penguins and petrels; the values obtained for the former were more constant and exhibited no major fluctuations. The pattern showed a slight increase with a peak in the period of August/September which coincided with the decline in the mean little penguin values obtained for the corresponding period (Fig. 4.2).

The mean volumes of coleopterans, caterpillars and egg fragments are illustrated in Figure 4.3. Coleopteran mean volumes remained low and constant over the six field trips (0-21%), while sharp increases were observed in the mean volumes of egg fragments and caterpillars from the month of June onwards. The mean volume of egg fragments peaked in July and subsequently stabilised, while the values estimated for caterpillars exhibited a constant and steep increase from July to September.

Data analysis

A Kruskal-Wallis non-parametric one-way analysis was applied to the mean volumes of all prey items analysed in scats (Appendix 4). The Kruskal-Wallis test is the most suitable procedure to test nonparametrically for intergroup differences with regard to data which is obtained according to a completely randomised design where $k > 2$ (Zar 1984). This process examined the significance of each individual prey item with regard to changes in volume over the period of the study (Table 4.4).

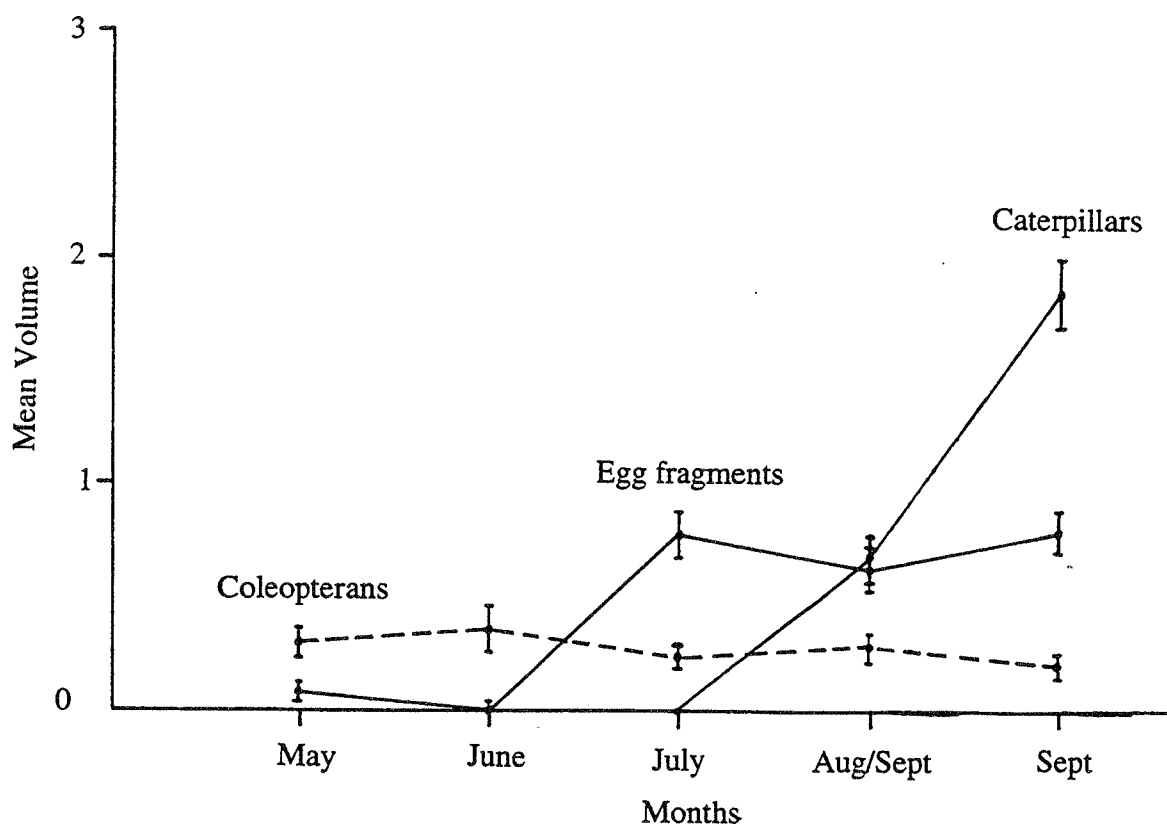


Figure 4.3 Mean volumes of invertebrate prey items: coleopterans, caterpillars and egg fragments/residue analysed in scats throughout the winter study. (n=527)

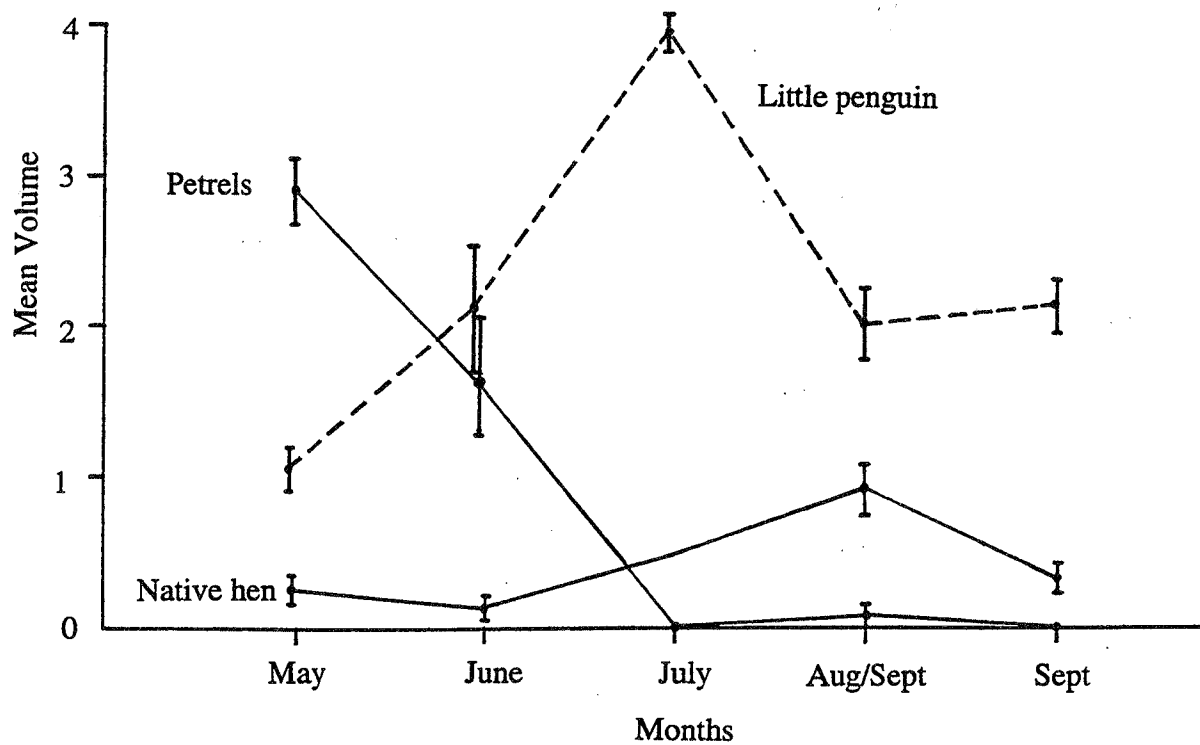


Figure 4.3 Mean volumes of invertebrate prey items: coleopterans, caterpillars and egg fragments/residue analysed in scats throughout the winter study. (n = 527)

Table 4.4 Results of Kruskal-Wallis one-way non-parametric analysis of variance on the mean volumes of prey items analysed in scats from six separate time groups.
(n=527)

Dependent Variable	Test Statistic
P1 petrels	245.586
P2 little penguins	115.451
P3 native hen	36.877
P4 coleopterans	0.504
P5 other insects	16.083
P6 skinks	12.184
P7 caterpillars	235.261
P8 egg fragments	45.164
P9 vegetation	26.234
P10 crab fragments	39.391
P11 other items	20.777

The results of the Kruskal-Wallis analysis revealed that the mean volumes of all individual prey items analysed varied significantly over the study period, with the exception of coleopterans. The three most significant results from the analysis were represented by petrels, followed by caterpillars and little penguins. Variations in the mean volumes of the other prey items over the winter period were less pronounced, although they were still significant (Table 4.4).

Discussion

Scat analysis conducted in the dietary study identified a large range of prey items which constituted the winter diet of the feral cat population on Wedge Island (Table 4.2). The range of prey items included the majority of the seabirds and extended to most the other island fauna comprising insects, caterpillars, vegetation and skinks.

The two species of seabirds (short-tailed shearwaters and little penguins) and the Tasmanian native hen were found to represent a major part of the feral cat diet although varying in importance. Overall, native hens were present in relatively low and constant volumes in the scats which suggested that these birds represent a major supplementary part of the feral cat diet after the shearwater migration. However, remains of the second species of petrel, the fairy prion, were not discovered in scats; the absence of this species and its implications are discussed in more detail in Chapter 5. The most common vertebrate prey items (*i.e.* with the highest frequency of occurrence) found in scats were little penguins, doubling that of short-tailed shearwaters. Mean volumes of little penguins in scats increased and peaked in July; this coincided with the period immediately after the departure of the shearwaters in their annual migration in May. This pattern suggests that increased numbers of little penguins were taken by the feral cat population to compensate for the sudden change in overall prey availability attendant upon the migration of shearwaters. The same pattern was evident for native hens; mean volumes of this prey item exhibited a slight but significant increase in the period following the shearwater migration. However, this species did not constitute a major prey item, unlike little penguins; this was evident from the low mean volumes of native hens in comparison with values of little penguins throughout the study (Figure 4.2).

Of the invertebrate prey, coleopterans were the only prey items which did not change significantly over the winter months; mean values for this group remained low throughout the study and did not exhibit any fluctuations. This suggests that coleopterans possibly represent only a minor component of the feral cat diet or alternatively it might mean that beetles and other insects do not exist in abundance on Wedge Island over the winter period. In contrast, the mean volumes of egg fragments and residue and also caterpillars showed highly significant increases from the month of June onwards, in the period after the shearwater migration. As little penguins do not begin nesting and laying until late July, the initial presence of egg fragments and residue in the scats and its subsequent sharp rate of increase could most probably coincided with the commencement of the native hen laying and brooding period. The same explanation may apply to the sudden increase of caterpillars in the diet; this pattern essentially conforms to an opportunistic diet of the feral cat in taking

advantage of seasonal variation of prey abundance and availability. The animals are generally considered to be opportunistic predators, their feeding being influenced by the availability, rather than active selection of prey (Jones 1977, Fitzgerald and Karl 1979, van Aarde 1980, Jones and Coman 1981, Karl and Best 1982, Alls 1983, Liberg 1984, van Rensburg 1985). The results of this dietary analysis are further discussed with regard to prey abundance and availability in the following chapter.

It is surprising that the two species of skinks *N. metallicus* and *N. ocellatus* available on the island were not present prominently in the feral cat diet. These two species were present in relative abundance on the rocky eastern shoreline and in the peripheral areas of both rookeries yet were represented by low values in the total number of scats analysed. This result contrasts strongly with the reported status of rock iguanas *Cyclura carinata* inhabiting Pine Clay in the Caicos Islands, West Indies. The decline of an estimated adult population of nearly 5500 individuals was suspected to be caused primarily by predation by domestic cats introduced to the island; it was also suggested that population declines on other islands in the group are also attributable to predation by these feral animals (Iverson 1978). In semi-arid Australia, many species of skinks and lizards are presently under threat from feral cat predation; in a predator removal study currently in progress in the Simpson Desert, south-west Queensland, one stomach of a feral cat alone was found to contain seventeen military lizards (C.R. Dickman, *pers. comm.*). It is possible that skinks on Wedge Island obtain a large degree of protection from their environment; these lizards inhabit rocky areas and dense vegetation of the island, areas which afford a high degree of camouflage and shelter and are not conducive to or selected for foraging by feral cats.

CHAPTER 5

Bird populations

Introduction

The impact of cat predation on wildlife has been most clearly demonstrated on islands, which tend to be relatively simple ecosystems. The effects of alien vertebrates on small insular environments with depauperate native faunas are generally greater than those in larger, less isolated areas as on the Australian mainland (Hengeveld 1989). On Macquarie Island, Marion Island and other subantarctic islands, Jarvis Island (Central Pacific), Little Barrier Island, Herekopare Island and numerous other New Zealand islands, the Galapagos Islands, the West Indies, Socorro Island (Mexico), Carribean Islands and Fiji, feral cats are believed to have caused extinctions and considerable reductions in populations of indigenous fauna. Seabirds and ground nesting birds have been particularly affected, although some endemic rodents and have also been eliminated. Chicks and fledglings are extremely vulnerable to predation just prior to flying (Brothers and Copson 1988, Fitzgerald *et al.* 1990, Fitzgerald and Veitch 1985, Flux 1993, Rauzon 1985, Veitch 1983, Veitch and Moors 1985, Veitch *et al.* 1989, Wodzicki and Wright 1984).

Wedge Island has long been unofficially recognised as an important island rookery for the little penguin, short-tailed shearwater and the fairy prion. Wedge Island also provides habitats for other species of seabirds such as little pied cormorants, white faced herons, sea eagles, peregrines, kites, brown falcons as well as a few species of finches and the Tasmanian native hen.

There have been no systematic faunal surveys of Wedge Island. The sole sources of known information regarding Wedge Island and its fauna are derived from anecdotal evidence gathered from local historians in Nubeena and from rangers in the Tasmanian Department of Parks, Wildlife and Heritage (TPWH).

According to historians, seabird rookeries on the island were not extensive in the early years around 1930 and the actual rookeries were only represented as small areas at

both ends of the island. The rookeries expanded during the following years, with the addition of extensive new areas around both ends of the island which spread towards the central region of the island. The fastest growth of both island rookeries was observed in periods after 1950, culminating with their present size; this expansion occurred with a corresponding increase in the number of seabirds observed to use the island as a nesting base.

Aims

The aims of the rookery census was to monitor and identify the main species of seabirds along with other fauna which utilise the rookeries on Wedge Island. This component of the study attempted to quantify the seabird population of both the North and South Rookeries and to relate population changes and fluctuations to the results of the dietary analysis of feral cats.

Methods

Rookery census

Three twenty metre by twenty metre transects were established in both the North and South Rookery. One transect was located in each of the upper, central, and lower regions respectively of each rookery. This arrangement was structured to obtain an overall representation the population density of each rookery. Each transect contained between 85 to 110 burrows. All burrows were hand searched and their occupants were identified and recorded. Rookery surveys were performed twice on each field trip, once on arrival and again before departure. These surveys were conducted throughout the winter period in attempts to monitor changes in the rookery population. In addition to the rookery survey, other avian fauna sighted on the island were also recorded.

Results

The two main species of seabirds which inhabit Wedge Island rookeries are little penguins *Eudyptula minor* and short-tailed shearwaters *Puffinus tenuirostris*. In addition to these seabirds, a population of Tasmanian native hens was relatively abundant in the rookeries and around the periphery of both rookery areas. From incidental sightings of native hens over the study period, the population of these birds was estimated to comprise between 40 and 50 individuals. A brood of approximately eight to ten newly hatched chicks was observed in late September.

There were no sightings of any fairy prions *Pachyptila turtur* during this study. The presence of this species was not evident in the transect surveys of burrows in either the North or South Rookeries, although a few skeletal remains of weathered fairy prion skulls were discovered among rocks and shrubs along the eastern shoreline.

Late juvenile and fledgling short-tailed shearwaters were present only during May. No adult shearwaters were encountered until the fourth week of September. Little penguins were present on Wedge Island throughout the winter study period although nightly sightings of the penguin populations of both rookeries varied considerably between each field trip throughout the winter months. Little penguins were the only seabirds that were continually present in the island rookeries in all of the winter months.

The burrow occupancies of all three transects in each rookery, obtained from burrow surveys, were combined. These data were then evaluated and expressed as a percentage value representing the overall burrow occupancy of each respective rookery at that time of the rookery survey. The burrow occupancy rates of each rookery were then plotted against each survey date (Julian Dates) of the study period (Figure 5.1).

The burrow occupancy of the North Rookery was estimated to be 21.79 % in mid May while the corresponding value at the South Rookery was higher (36.56 %). In the first week of June, the occupancy rate at the North Rookery was 27.22 %. However, from the second survey onwards, both the North and South Rookeries exhibited a

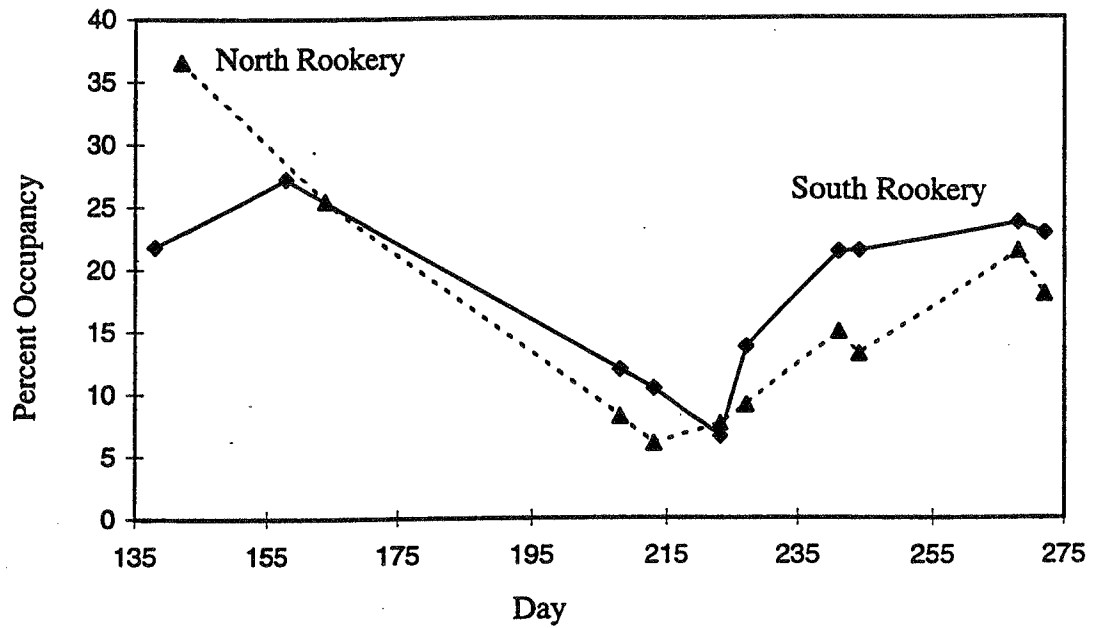


Figure 5.1 Burrow occupancy rates of North and South Rookeries throughout the winter survey period.

constantly declining trend in burrow occupancies. The decrease in occupancy rates at both rookeries continued this trend until August. The lowest levels of occupancy rates were approximately similar at both rookeries and occurred within ten days of each other. The lowest levels occurred at day 223 for the North Rookery and at day 213 for South Rookery. Occupancy rates at both rookeries gradually increased to peak at day 268 for both rookeries. The burrow occupancies had begun to decrease again at the last survey conducted on day 272.

Using burrow occupancy data from transect surveys, the population of little penguins present in each of the two rookeries on each survey date was estimated. In comparing North and South Rookeries, it was clear that the estimated number of little penguins at the South Rookery was constantly higher than at the North Rookery; this pattern did not exhibit pronounced variations throughout the duration of the survey (Table 5.1). Combined data from population estimates of penguins of both North and South Rookery were also utilised to estimate the overall total number of penguins present on the island on each survey date (Table 5.1).

The data illustrated in Table 5.1 exhibit a salient feature of the pattern of the Wedge Island little penguin population dynamics. A steep decline was evident in the overall number of penguins estimated on Wedge Island in the middle of the study; the island population of little penguins decreased from 2166 individuals at the beginning of the survey in mid-May to the lowest point on Day 223 in August, the difference between the two survey periods representing a decrease of nearly 1700 individuals. By the completion of the study on day 272 in September, the estimated number of penguins in both rookery populations had increased to 1291 individuals although the population change was on a downward trend again.

Data analysis

Analysis of variance was applied to data obtained from the two rookery sites, the North and South Rookery. A significant spatial difference ($df=2$, $F=4.37$, $P=0.043$), but no significant temporal difference ($df=9$, $F=2.04$, $P=0.059$) was found (Appendix 6).

Table 5.1 Estimated total number of little penguins on Wedge Island (North and South Rookeries) on each survey date (Julian Dates).

Day	North Rookery	Day	South Rookery	Total number
138	400	142	1766.5	2166.5
158	491.75	164	1216.5	1708.25
208	216.75	208	383.5	600.25
213	191.75	213	283.5	475.25
223	125	223	350	475
227	258.25	227	400	658.25
241	391.68	241	616.5	1008.18
244	400	244	616.5	1016.5
268	433.25	268	1033.5	1466.75
272	425	272	866.5	1291.5

Discussion

Seabird abundance and availability on Wedge Island did not remain constant throughout the year. This interseasonal variation was represented primarily by the migration of short-tailed shearwaters at the beginning of the winter season in May, although some late juveniles and fledgling chicks were abandoned by the colony and these birds remained behind and starved. No adult muttonbirds were sighted on the island; neither were any individuals discovered in the rookery surveys from the month of May onwards. The migration of the short-tailed shearwaters represented a significant change in prey availability and abundance for feral cats in winter; this sudden depletion of shearwaters numbering several thousands at the beginning of winter means that the enduring little penguin population and native hen colonies have to sustain the majority of the food requirements of the feral cat population throughout the winter months.

Little penguins were the only species of seabird resident in the rookeries throughout the year. However, the burrow occupancies of little penguins in both rookeries were variable and exhibited a major decline in the months of late July and early August. The existence of population fluctuations was additionally supported by sightings of the penguins nightly during each field trip; observed numbers of penguins varied considerably between each field trip. The survey revealed that the burrow occupancy rates of the South Rookery were constantly higher than the North Rookery. This bias could have been affected by the presence of more shearwater burrows at the North Rookery or simply by the difference of colony size between both rookeries. Little penguins do not constantly occupy their burrows but spend several days at a stretch foraging at sea, returning to brood in their burrows for periods up to a week or more. This behavioural pattern meant that the total number of penguins estimated on the island at any survey date did not necessarily represent the number of penguins available to feral cats as prey. The few occasions when these penguins were susceptible to predation include the period when returning from foraging from the ocean in the late evening or at dusk and while traversing the rocky eastern shoreline back to their burrows. These seabirds are similarly at risk throughout the night when they periodically position themselves outside their burrows and call to other

individuals in their colony and also at dawn when these birds abandon their burrows and move to the sea.

The Tasmanian native hen population of Wedge Island was not substantial. Although native hens were sighted regularly during the field trips, the island population was estimated to be only between forty to fifty individuals. Native hens were taken as prey by feral cats although this species did not represent a major component of the feral cat diet during the winter months since the native hen population numbers were not as high as those of the little penguins; hence feral cat predation was limited by prey abundance. However, the dietary analysis revealed that native hens constituted a constant prey item, albeit in low numbers throughout winter. This meant that native hens were an important supplementary component to main prey.

Throughout the duration of the study, there were no sightings of fairy prions on Wedge Island nor was there any evidence of the presence these seabirds in the burrow surveys. The absence of fairy prions on Wedge Island is cause for concern, since past reports indicate that this species of seabird was present in considerable numbers in the previous decade (N.P. Brothers, TPWH, pers. comm.). The only evidence of the species on the island was the discovery of a number of fairy prion skulls along the eastern shore among rocks and low hanging shrubs. It is highly probable that the fairy prion is now extinct on Wedge Island, possibly due to extensive predation in the last decade by the feral cat population. The absence of fairy prions from Wedge Island clearly demonstrates that certain species of seabirds are more susceptible and at risk to feral cats compared to other species such as penguins. Risk of predation could be further enhanced by certain behavioural traits such as ground nesting or brooding behaviour and compounded by low population numbers and small reproductive outputs.

The results of the dietary analysis described in Chapter 4 together with the results from the rookery survey draw strong parallels with other similar studies of islands which support colonies of nesting seabirds. On Macquarie Island the grey petrel *Procellaria cinerea*, which formerly bred there is now extinct, while the blue petrel *Halobaena caerulea* and common diving petrel *Pelecanoides urinatrix*, both formerly

abundant and present all year, are now rare breeders (Brothers 1984). The three most abundant petrel species on Macquarie Island, the antarctic prion *Pachyptila desolata*, white-headed petrel *Pterodroma lessoni* and sooty shearwater *Puffinus griesus* are absent during the winter months (Brothers *et al.* 1985). Chicks of *Pterodroma macroptera* and *Preocellaria aequinoctialis* on subantarctic Marion Island were especially vulnerable to feral cat predation, as cats were observed to enter nesting burrows (van Rensburg and Bester 1988). Prior to the introduction of feline panleucopaenia virus in 1977 (van Rensburg *et al.* 1977) the 1975 feral cat population of 2139 ± 290 cats consumed an estimated 450,000 burrowing petrels *Procellariidae* spp. (van Rensburg and Bester 1988). In the Central Pacific Ocean, feral cat stomach contents collected on Howland and Jarvis Island revealed that sooty terns *Sterna fuscata* represented the primary species of seabird taken, with a 67% frequency occurrence in scats. Temporal changes were observed in feral cat diets on Dassen Island, South Africa and it seemed likely that this pattern in the cat diet, at least in part was due to a functional response by feral cats to changes in relative availability of two food resources. The island is saturated by Cape cormorants for a similar period every year and a dietary specialisation by feral cats on this species was clearly indicated. Feral cats were observed to feed exclusively on Cape cormorant chicks for the brief time those birds were available and the emphasis in diet reverted to the European rabbit after the departure of the cormorant (Apps 1983).

These studies clearly show that the feral cat is a highly opportunistic predator and is very able in adapting to changing or fluctuating resource availability and abundance. In this study, the dietary analysis demonstrated that the feral cat population readily switched to the penguin population as the staple prey; a change in response to the sudden decrease of an important and substantial prey item when the shearwaters migrated in early winter. However, even with this ability to switch prey to compensate for resource fluctuations, the feral cat population seems to suffer a resource bottleneck at a certain stage in winter. This limiting factor or nutritional stress could be effected by the limited availability of little penguins as prey. Even though the rookery census showed that little penguins occur in relative abundance on Wedge Island; it is the limited factor of availability which seems to be the primary reason which suppresses the growth of the feral cat population in winter.

CHAPTER 6

Reproductive status

Introduction

Reproduction in feral cats is very similar to domestic cats except that it is more likely to be influenced by environmental factors. Females usually produce two litters a year, one in spring and the second in late summer/early autumn in south-eastern Australia (Jones and Coman 1982). Anoestrus is believed to occur in most but not all female cats in late autumn and winter. In their first breeding season, females usually only produce one litter. Comparison of reproductive parameters such as breeding season, litter size and age at sexual maturity have shown no major differences between feral and domestic colony cats (Moodie 1994).

Aims

There are few quantitative data available on reproductive status of feral cats in offshore populations. It was attempted to determine the reproductive condition of male feral cats throughout the winter period by the monitoring of blood plasma testosterone levels; the reproductive status of cats could be very possibly governed by environmental factors such as seasonal availability of food resource, shelter or mating opportunities.

Methods

Approximately 1.0 ml of blood was drawn from the caudal vein (tail base, ventral) of captured male cats. The blood sample was then centrifuged and the blood plasma removed and stored in liquid nitrogen (in the field). Blood plasma samples were subsequently analysed in assays for testosterone levels in the laboratory.

Results

A total of three male feral cats was captured during the study. Blood samples were drawn from two male cats, one juvenile and one adult. The results of the testosterone assays are shown in Table 6.1 below.

Table 6.1 Blood plasma testosterone levels in male feral cats captured during the study.

Cat	Sample Date	Testosterone Level
006	13/August	1.92 ng/ml
007	14/August	3.3 ng/ml
	01/September	3.63 ng/ml
	29/September	1.95 ng/ml

006: adult male

007: juvenile male

The mean blood plasma testosterone level for the juvenile male cat (007) was 2.96 ± 0.890 ng/ml. The overall mean blood plasma testosterone for the entire sample size was 2.7 ± 0.89 ng/ml.

Discussion

Seasonal control of reproduction in mammals has been documented in twenty two species of carnivores representing eight orders (Sadleir 1972). However, the vast majority of these studies have focussed only upon females. Among the non-domestic species of Felidae inhabiting the northern hemisphere such as the European wild cat (*Felis silvestris*), bobcat (*Felis rufus*) and the mountain lion (*Felis concolor*), females show consistent photoperiodic control of reproduction (Asdell 1964). However, little is known about seasonal influences upon the males of the genus (Kirkpatrick 1985). There are few studies which attempt to establish or define the effects of seasonal

influences such as fluctuating resources on reproductive condition or its effects on fecundity.

It is a well known clinical fact that domestic male cats are consistently fertile throughout the year. Kirkpatrick (1985) examined the seasonal testosterone levels in 46 male cats; plasma testosterone levels were 3.1 ± 0.6 ng/ml in March, 3.5 ± 0.7 ng/ml in June, 3.3 ± 0.4 ng/ml in September and 2.9 ± 0.5 ng/ml in December and no significant differences were noted. In Kirkpatrick's (1985) study, the plasma testosterone values for September (3.3 ± 0.4 ng/ml) compared favourably with the value obtained for the juvenile male (2.96 ± 0.89 ng/ml : cat 007) in this winter study. However, the plasma testosterone of the adult male (1.92 ng/ml) was much lower in comparison to the juvenile male.

The mean plasma testosterone concentration (2.7 ± 0.894 ng/ml) estimated in this study did not fall within the range (3.7 - 8.0 ng/ml) and mean of 5.6 ng/ml reported by Olmstead *et al.* (1982) and is considerably less than the mean in the range (0 - 23.5 ng/ml) reported by Johnstone *et al.* (1984). Hence, although the juvenile male feral cat examined in this study is fertile and possesses a plasma testosterone level which is constant throughout the winter months, the same cannot be said for the adult male cat. A higher level of plasma testosterone in the juvenile compared to the adult male strongly suggests that the adult male was not reproductively active in winter. Two explanations could be used to explain the difference in reproductive status with regard to resource availability in winter. Firstly, the juvenile male could have been in the last stages of being weaned and the majority of its nutritional needs were still supplied through maternal care; hence it would be in reasonably good body condition and sexually mature. On the other hand, a resource bottleneck in mid to late winter would adversely affect the reproductive status of the adult male; nutritional stress would serve to suppress production of testosterone to a large degree. Although Bronson (1985) has pointed out that there is a strong genetic advantage imparted to the male which is reproductively ready all year round, reproductive ability would be one of the first primary traits to be suppressed should there occur a resource bottleneck.

Few quantitative data on factors influencing reproductive success of feral cats in different environments and at different population densities are available. Various facets of male and female reproductive behaviour are discussed below with regard to the winter months on Wedge Island.

Seasonality of breeding

Feral cats are most generally seasonal breeders although most females experience a short period of winter anoestrus. Litters are produced throughout the year; however, most are born in a spring peak and a second smaller summer peak (Love 1972, Wilson *et al.* 1992). There may also be slight differences between populations in timing of the peaks in births (van Aarde 1978). Seasonality of breeding is influenced by day length, genetics and more importantly food supply. Anoestrus coincides with reduced day length, usually beginning three to five weeks after the longest day in the year. Male cats may experience seasonal changes in testes mass, tubule diameter and epididymal mass. In many habitats, there is a seasonal decline in the availability of prey over winter, undoubtedly influencing the reproductive physiology of the animals (Herron and Burke 1986, van Aarde 1978, Wildt *et al.* 1991). Jones (1977) reported that the winter months at Macquarie Island were most probably a period of nutritional stress for the feral cat population when several species of petrels migrate and there is a scarcity of suitable sized rabbits under 600 grams. A marked decrease in food abundance and availability of prey due to seasonal factors would suppress the reproductive output of both male and female cats. The same scenario would apply to the feral cat population on Wedge Island as the population experiences a similar seasonal fluctuation of prey. In addition, the availability of little penguins as staple prey after the migration of shearwaters would represent a limiting factor to reproduction in the winter months.

Onset of sexual maturity

Domestic cats exhibit first oestrus at six to nine months of age, although this may occur as early as four months or as late as 12 months (Herron and Burke 1986, Wildt *et al.* 1991). Feral females take a little longer to reach maturity, usually at about seven

to twelve months, or at a weight of over 2500 grams in south- eastern Australia. The sexual development of males is slower. Feral males achieve maturity at about seven months and engage in sexual activity at ten to eighteen months. In south- eastern Australia, the lightest male feral in which spermatozoa were detected weighed 2600 grams and sexual maturity was attained at a mean body weight of 3250 grams. Size appears to be the major factor governing the attainment of reproductive status (Huxley 1987, Jones and Coman 1982, van Aarde 1978). For example, the age at first breeding in bobcats has been shown to be influenced by food availability, a common feature in carnivores (Rolley 1985).

Even though some juveniles in the Wedge Island feral cat population may have reached sexual maturity by winter, food availability and abundance would be of critical importance in determining breeding. Nutritional requirements of female cats increase three fold during pregnancy and in lactation (Moodie 1994); fluctuating and unreliable food resources would not be conducive to raising litters successfully.

Reproductive lifespan

Female cats are at their sexual prime between two and eight years of age and seldom produce kittens after 14 years (Jones 1989). A decline in the number of young per litter has been noted from litter 17 onwards (Moodie 1994). All female feral cats captured on Wedge Island were estimated to be less than five years old (by criteria of body size) and in good body condition. Feral cats rarely survive beyond eight to nine years, due to harsh environmental constraints such as resource availability, predation and disease and the majority die well before this (Robinson and Cox 1970, van Aarde 1978). Repeated seasons of resource bottlenecks on Wedge Island would effectively cull old and weak individuals as well as juveniles. This repeated pattern would possibly result in a continual reduction of cat numbers in the population.

Fertility and fecundity

At their maximum reproductive potential, a female cat and her offspring can in principle produce 420,000 cats in seven years (Thornton 1993). In actuality, the maximum potential may rarely be reached. Mean prenatal litter sizes recorded for feral cats vary from 3.3 on the Kerguelen Islands to 4.7 on Marion Island. In south-eastern Australia, the mean prenatal litter size is somewhere between at 4.35. The number of kittens per litter ranged from two to seven (Brothers *et al.* 1985, Jones and Coman 1982, van Aarde 1993, van Aarde 1978, Veitch and Moors 1985). Post partum litter sizes are very difficult to determine for feral populations as locating the kittens at this time is extremely difficult. In domestic and rural populations, post partum litter sizes of 3.9 to 4.4 kittens have been recorded (Robinson and Cox 1970, van Aarde 1978, Warner 1985).

In unmodified, stable, feral populations, most kittens die before reaching maturity (Veitch and Moors 1985). Mortality rate to weaning (about eight weeks) has been estimated at 27.5 % in the Kerguelen Islands. Mortality rate in the first ten weeks of life on Marion Island was estimated at about 42%. On Macquarie Island, the mortality rate in juveniles up to 1.8 kilogram in weight (about six months of age) was estimated at 57% (Brothers *et al.* 1985, van Aarde 1978). Post weaning litter size on Marion Island decreased significantly from 2.7 in 1957 to 1.7 in 1982 after the introduction of feline parvovirus (van Rensburg 1986). The mortality rate of juveniles is not known for the feral cat population on Wedge Island. However, given the occurrence of resource shortages in the winter months, it would be reasonable to assume that the mortality rate would be comparable to similar feral populations on other offshore islands. The feral cat population on Wedge Island was estimated to be not more than fifteen individuals sharing an total area of approximately 50 hectares. Feral cat populations living in such isolated and close proximities are extremely susceptible to diseases such as feline panleucopaenia and 'cat flu' which are easily transmitted by close contact. Diseases would therefore represent a major role in regulating population growth. The feral population on Wedge Island is derived from a narrow genetic lineage with limited genetic diversity. Harsh environmental constraints would cause genetic bottlenecks to occur from time to time; genetic mutations would also act as a natural population growth regulator.

In comparison to populations of urban strays, mortality rates to weaning appear similar to those in feral populations. Huxley recorded 42-71% loss of kittens between birth and weaning in Melbourne. This increased to 61-81% of kittens from the first post partum oestrus while 43% mortality has been recorded elsewhere (Huxley 1987). In the Melbourne study, only 13% of kittens have survived more than 6 months. Of those known to have died, half succumbed to disease and half were killed by traumatic injury due to humans or cars. Domestic cats are significantly more successful than ferals or strays in raising their kittens. Over a 10 year period, Robinson and Cox reported a survival rate to weaning of 87% of kittens born in a domestic cat colony. Increased preweaning loss occurred in large litters and there was an inverse relationship between incidence of stillbirths and subsequent loss before weaning. The average number of litters per queen per year was 2.5 (Robinson and Cox 1970).

In feral populations, queens rarely have more than two litters per year. Up to 100% of queens may become pregnant during the breeding season (van Aarde 1983). The first litter is usually smaller and less successfully weaned than subsequent litters. Very old cats also have smaller litters. Large females tend to produce large litters (Brothers *et al.* 1985, Huxley 1987, van Aarde 1978). When population density has been lowered by external factors, for example control measures, there is some evidence for a compensatory increase in the fecundity and survival of kittens. Van Rensburg *et al.* (1987) and Rolley (1985) suggested that the higher fecundity in cats of some age classes (2,8 and 9 years) on Marion Island may have been a reaction to lowered population density after the introduction of feline parvovirus. More research is needed in this area.

Reproductive success

Food supply, the availability of shelter for raising kittens and the density of cats are thought to be factors limiting reproduction in feral populations. Low and uncertain prey availability was thought to be responsible for reduced fecundity in feral cats on Jarvis Island; after the seasonal arrival of the primary prey species, sooty terns, an increase in pregnancy rates and number of kittens *in utero* was noted (Rauzon 1985). Food abundance was thought to influence breeding potential on Marion Island (van

Aarde 1978). At high densities, the availability of breeding shelters was suggested as a limiting factor for two year old cats on the island (van Rensburg *et al.* 1987). The results of the dietary analysis and rookery survey of this study strongly describes a situation similar to Jarvis and Marion Island. The decrease in the feral cat population from 1984 (N.P. Brothers, TPWH, pers. comm.) to the present estimated population suggests that reproductive success of the population has been affected by resource bottlenecks which has suppressed the cat density on the island. The adverse effect on reproductive success could be further amplified by a skewed ratio of male to female cats. However, further study is required to quantify the mortality rates of different sexes to establish cause and effect relationships with reproductive success.

Where populations have been dramatically reduced in density, cats may have problems finding partners. Fewer females were breeding and the number of litters per female declined on Marion Island when population density decreased to very low levels. A similar phenomenon has been described during eradication of cats from New Zealand islands and Coypu from Britain (Bell 1989, Eason and Jolly 1993). Although cats have a reputation for reproducing well in nature, the propagation of laboratory cats is often difficult due to problems with poor libido and sexual incompatibility under controlled conditions (Wildt *et al.* 1991). Known predators of cats and kittens in Australia other than humans include foxes, dingoes probably dogs and the wedge-tailed eagle; however, little is known about the effects of such predation on reproductive success in feral populations (Brooker and Ridpath 1980, Newson *et al.* 1983).

CHAPTER 7

Home range

Introduction

There is enormous variation in the social behaviour of the cat, *Felis catus*. The activities of male, female, old, young, dominant and sub-dominant cats within any population all differ with regard to various ecological facets. The ecology of male and female cats may be similar in certain respects or vastly differ to others. Individuals may switch between contrasting spatial and social arrangements on a seasonal basis as resource availability or abundance changes (Kerby *et al.* 1990).

The social structure of the animals tends to vary from group to group. Factors influencing social organisations may include population density, age, structure, ecological conditions and genetic differences (Bradshaw 1992, Leyhausen *et al.* 1990). The availability of food and other factors including prey density, access to shelter or refuge places, sunning spots and places suitable for breeding might influence the form and size of an individual's home range (Liberg 1980). During the breeding season, the home ranges of males may possibly expand in size (Liberg and Sandell 1990).

Aims

The aim of this study was to assess whether or not a consistent pattern existed in the spatial organisation of the feral cat in an offshore island population. Individual features of home range and home range sizes will provide insight into the ecology of the feral cat over the winter months as well as information with regard to social interactions between individuals in the population. Since the cat is a promiscuous species, it is expected that male cats do compete primarily for access to receptive females, while females compete over food and other environmental resources to improve their production and rearing of their offspring (Trivers 1972, Clutton-Brock and Harvey 1978).

Methods

A total of three feral cats was captured and equipped with radio transmitter collars. Radio telemetry was performed through triangulation by obtaining accurate location fixes of an individual from different angles. Telemetry distances ranged from ten to 200 metres. Radio tracking was undertaken four times per day at six-hour intervals beginning at 2400, 0600, 1200 and at 1800 hours. Radio tracking would begin from base camp at the northern extremity of the island and proceed along the eastern shore and to the south end.

Results

A total of three feral cats was captured and tagged with individual radio-transmitter collars for the spatial organisation/home range study. The demographic attributes of these three cats are listed in Table 7.1 below. Raw data of location fixes of individual cats obtained by radio telemetry on field trips are provided in Appendix 5.

Table 7.1 Demographic attributes of individual feral cats tagged with radio-transmitter collars in home range study.

Cat	Status	Sex
004	adult	female
005	juvenile	male
006	adult	male

A summary of calculated home range sizes of each individual cat in the study is listed in Table 7.2. The largest home range size of 32.5 hectares was recorded for the adult male cat (006), which covers an area approximately two-thirds of the island. This is followed by the adult female cat (004) which possesses a home range size of 23 hectares, approximately half the area of the island. The smallest home range of 14 hectares was recorded for the juvenile male cat (005).

Table 7.2 Home range sizes of individual cats in the study.

Cat	Age	Sex	Home Range Size
004	adult	female	23 hectares
005	juvenile	female	14 hectares
006	adult	male	32.5 hectares

Home range area overlaps of the three individual cats over the entire area of the island is illustrated in Figure 7.1. The range overlaps reveal that the greatest degree of overlap between the three cats occurs in the southern region of the island which extends upwards through the south rookery towards the central region of Wedge Island. The den sites of the adult male cat (006) and adult female cat (004) are situated on the cliff face on the eastern side of the island, on the southern tip; the den sites of these two adult cats are approximately 25 to 30 metres apart. The den site of the juvenile female cat (005) is situated at approximately mid-south rookery at the lower regions of the rookery bordering the eastern shoreline; the den of the juvenile female cat is a burrow well hidden by clumps of low hanging shrubs and vegetation. Degrees of home range overlap between all three individual cats were variable. Table 7.3 is a matrix detailing the per cent overlap of home ranges between the three individual subjects.

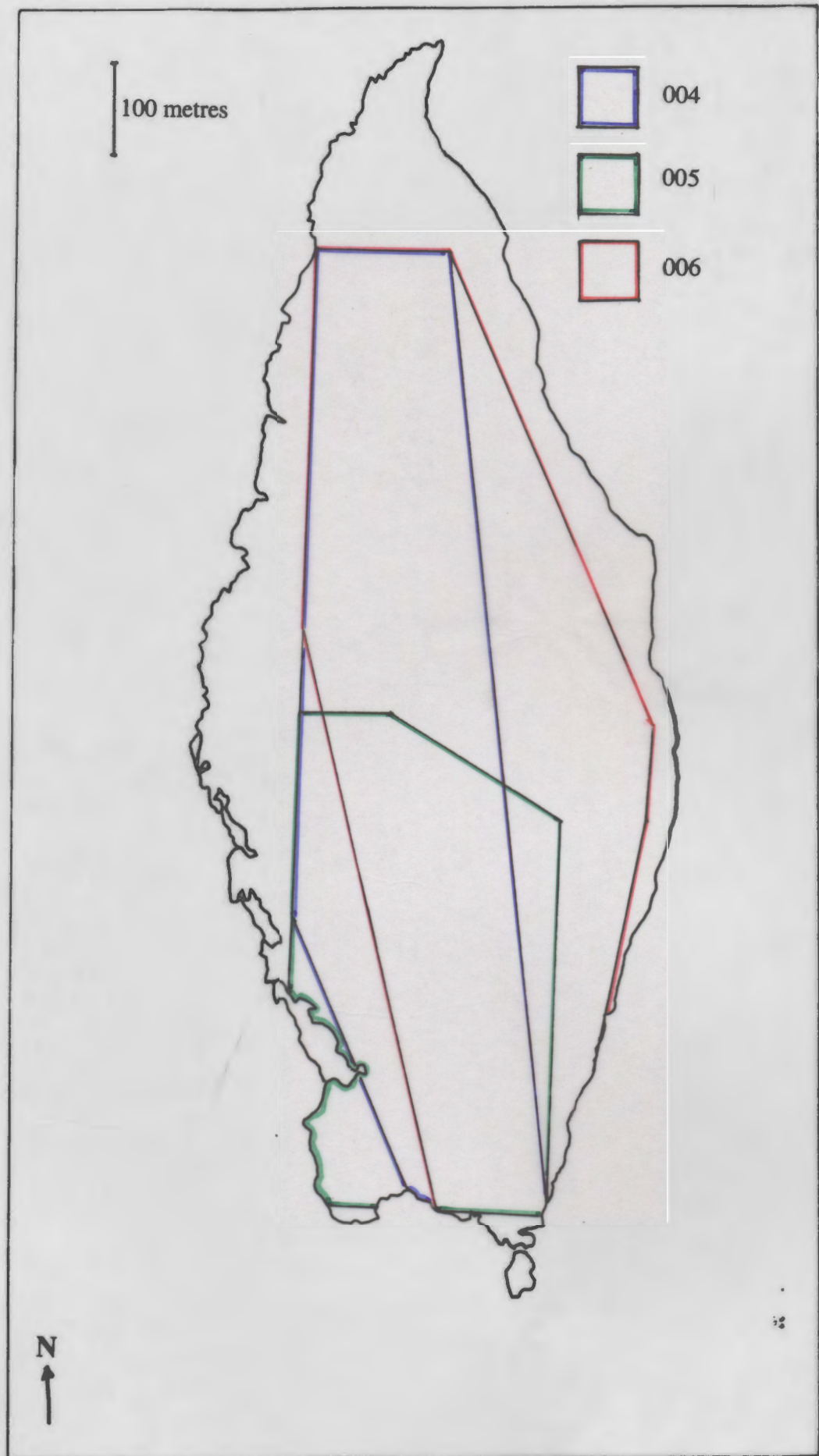


Figure 7.1 Home range overlaps of adult male (006), adult female (004) and juvenile female (005) on Wedge Island



Aerial photograph of Wedge Island; February 1984 (Department of Environment and Land Management).



Aerial photograph of Wedge Island; February 1984 (Department of Environment and Land Management).

Figure 7.1 Home range overlaps of adult male (006), adult female (004) and juvenile female (005) on Wedge Island.

Table 7.3 Matrix of home range overlap of all three individuals in the study. Range areas in rows are overlapped by range areas in columns.

	004	005	006
004	100%	44.8%	88.3%
005	73.3%	100%	67.4%
006	64.1	28.9%	100%

The largest degree of home range area overlap occurs between the adult male cat (006) and the adult female cat (004); both home range areas overlap by 88.3% (Table 8.3). The least degree of overlap occurs between the adult male cat (006) and the juvenile female cat (005); the degree of home range overlap is 28.5% (Table 7.3).

Data analysis

Home range analysis

In most studies, two basic methods have been used to determine home range size: radio tracking and sightings of identified individuals. Radio telemetry naturally gives a less biased result, since locating the subjects is not dependent on habitat quality. In addition the risk of missing less frequented parts of the home range is higher when range size is only based on sightings. It is therefore expected that the sighting method will yield smaller home range estimates than radio tracking, supported by data from Izawa, Doi and Ono (1982). With very large samples, as in the study by Dards (1978), the sighting method will also yield reliable results. However this is only if the study is conducted in a confined area and all parts evenly searched by the observer.

Due to a difference in sampling methods, lengths of tracking periods, sample size and, especially, the methods used to calculate range size, there is a great variation in the data on home range size. Therefore, radio telemetry data from the home range study

was analysed by a home range analysis method termed 'minimum convex polygon' in which the outermost or peripheral location points or fixes obtained by radio tracking are used to calculate the maximum home range size and spacing pattern of any individual (Mohr and Stump, 1966). This method of analysis is most suitable for studies in which sample sizes are small and where radio tracking data is most extensive. Matrices of home range overlaps and maximum home range sizes were calculated using this method.

Discussion

Spatial organisation

The spacing pattern in a population is the result of the tactics chosen by the individual animals in their attempts to survive and maximise reproductive success. It is assumed that female spacing patterns are determined by the abundance and dispersion of food, whereas male spatial organisation, at least during the mating season, is determined by the distribution of females (Erlinge and Sandell, 1986).

Female home range size

As with density, there is a 1000-fold variation in mean home range size reported in different studies. Female ranges span from 0.1-1.8 hectares in a Japanese fishing village (Izawa *et al.*, 1982) to 170 hectares in the Australian bush (Jones and Coman, 1982). Because females in non-cooperative or solitary species must rear their young by themselves, their reproductive success is closely correlated with the amount of energy they can allocate to reproduction. In turn, this amount mainly depends on the food resources available during the rearing period. Thus, for solitary females, food is the most important resource, and females should follow a behavioural tactic that maximises the chance of securing the required food resources for reproduction and survival.

Range size is expected to be flexible and adjustable so that a female maintains the minimum food requirements when resources are low. Hence, range size should be determined by food availability during the most critical period, though food dispersion

may also be of some influence. When two or more different food sources are used during the year, the dispersion or availability of these resources in relation to each other may influence range size. For example, black bears in the Great Smoky Mountains National Park feed on berries and fruits during summer, whereas their staple food diet during autumn is the acorn (Garshelis and Pelton 1981). Many of the radio tracked bears showed ranges completely disjunct from their summer ranges and thus their annual or seasonal ranges are determined more by the distribution of the two resources than by their abundance. Generally, when one food source is utilised throughout the year, its dispersion probably has relatively little influence on range size. A patchily distributed resource also usually has a lower total abundance when calculated over the whole area. Konecny (1983) found that when food occurred in patches, the feral cats in the study moved over longer areas than when it was evenly distributed, in spite of a lighter overall food abundance in the former case. In this study, the change in prey abundance and availability on Wedge Island effected by the winter migration of short-tailed shearwaters could very possibly be a determining factor of the female home range size; unfortunately there is a lack of summer and autumn data on prey abundance and availability for comparison. However, it can be strongly assumed that, with such a dramatic change in prey availability in winter (beginning in the months of June and July), females do expand their home range size (winter range size: 23 hectares) to compensate for the reduction in prey abundance available in the original home range. It can therefore be predicted that female range size is correlated with food abundance, and especially with food biomass during the most critical period of the year.

A correlation between prey density and range size has been found in the cases of the bobcat (Litvaitis *et al.* 1985) and the Canadian lynx (Ward and Krebs 1985). In both studies it was demonstrated that the predators altered home range and habitat use to concentrate on areas of highest prey abundance. Van Orsdol *et al.* (1985) discovered that for the African lion, the range size was correlated with lean-season prey biomass, but not with good-season prey biomass. Since many studies do not present data on food abundance, the prediction cannot be tested directly. There is, however, a way to test it indirectly. Density is expected to be directly correlated with food abundance. For the lion, three measurements of density (overall mean, adult females and pride

members) were correlated with lean-season prey biomass (Van Orsdol *et al.* 1985). A correlation between density and home range size would indicate the dependence of both variables on food abundance, although causality is not clear. A strong correlation between density and female range size is apparent in the data of solitary carnivores (Sandell 1989). Thus, range size in females is mainly determined by food abundance.

One of the main characteristics of the spacing pattern in a population is the extent of range overlaps between individuals. For ranges to be exclusive, the food resource must be so evenly distributed and stable that an area just large enough to support the animal during the most critical period contains food enough to satisfy energetic needs throughout the year. If food resource varies in space and time, the range must be larger to provide for the animal for the animal at all times. This larger area may contain a surplus of food for most of the year; thus, several animals are able to utilise the same area, and a system of overlapping ranges develops (Sandell 1989). With this theory in consideration, it could be proposed that the home ranges of both the adult male and adult female cat in this study are essentially maintained at the same size all year round; a further factor is that the area of the island is finite and not extensive (approximately 50 hectares). Home ranges of both adult cats extend to over at least two-thirds of the island and cover the entirety of the extensive South Rookery (Figure 9.1). Essentially the same explanation has been proposed by Macdonald (1983) for the evolution of group living in some carnivores. The same scenario may, however, lead to a system of solitary animals with overlapping ranges, indicating that this hypothesis is not sufficient to explain the evolution of group living in these species.

Whereas overlapping ranges are easy to detect, it is more difficult to prove that ranges are exclusive. Either there must be a high level of confidence that all animals within an area are radio collared, or data must be acquired on several animals with adjacent ranges. The latter criterion is used here, and three to four animals with adjacent ranges and overlaps of less than 10% (measured on minimum convex polygons) is considered to be a strong indication of exclusivity.

From the discussion above, it follows that exclusive ranges are expected when food resources are stable and evenly distributed, whereas a system of overlapping ranges is likely when the timing and spacing of available food varies. As it can be seen from the results of this home range/spatial distribution study (Figure 9.1), the home ranges of all three individuals: adult male, adult female and juvenile female overlap more than 40%. This pattern strongly implies that availability and abundance of food does vary, and in turn, this factor could also represent increases in home ranges for both the adult male and female in winter to compensate for the shearwater migration and patchy distribution of penguins.

So long as there are no methods to measure resource distribution, this prediction cannot be satisfactorily tested. Exclusive ranges are, however, not common among female solitary carnivores; in his review, Sandell (1989) reported that exclusive ranges existed only in seven of twenty-four studies, and the trend was that range sizes were mainly small.

Male home range size

The variation in range size between different areas is just as large for males as for female cats (Table 9.4). According to the basic hypothesis, male spatial organisation is influenced by two resources: food outside the mating season and receptive females during the mating season. It follows that during a substantial part of the year, male and female spacing patterns are determined by different factors, and range size in males should be a function not only of food requirements but also of female distribution. Since food ranges are minimised whereas mating ranges are expected to be maximised, it follows that male ranges should be larger than predicted by energy requirements (Sandell 1989). On the average male ranges are 3.5 times larger than those of females (Liberg and Sandell 1988). Energetically this increase in range size corresponds to a body weight 5.3 times that of females (Liberg 1981). This is interpreted as a clear indication that food is not a determining factor for male range sizes, at least not directly.

According to the basic assumption that males compete for access to females; it can be predicted that the primary factor determining male range size is female density and distribution. It is expected that males will maximise access to females; this means that male ranges will generally be larger than those of females. In most polygamous species, both dominant breeding males and subordinate males that are partly or totally excluded from breeding occur. When such a situation exists in a cat population, it would be expected that breeding males would have larger ranges than non-breeding males, if they are living under otherwise similar conditions. The adult male (006) in this study could very possibly be the dominant member or alpha male of the cat population on the island, with its home range of 37.5 hectares extending to almost the entire island; this overlaps the adult female home range by 88.3% (Table 7.3, Figure 7.1). In contrast, the home range of the juvenile female (005) is only 14 hectares (Table 7.2) and overlaps with the adult male cat (006) by only 28.9% (Table 7.3).

Liberg (1981, 1984) recognised six categories of adult males based on dominance and ecological status (home-based or feral). In home based cats, breeding males had ranges of 350-380 hectares; ranges of subordinate, non-breeding males were approximately 80 hectares, or not much larger than those of females. Turner and Mertens (1986) also reported that the male they presumed to be the 'breeder' of their small population possessed the largest male range in their study.

If breeding is seasonal, it would be expected that female density and dispersion would be important for male home range extension during the mating season. At other times throughout the year, breeder male ranges might be determined by the same factors as those of females and subordinate males. Unfortunately this study only presented data of home ranges during the winter/breeding season, although it could be argued because Wedge Island is a relatively small island of 50 hectares, male and female home ranges are maintained at constant size throughout the year and no difference is effected on a seasonal basis. The main advantage of maintaining a permanent home range size is that there is no need for additional energetic expenditure spent in foraging to compensate for changes in prey abundance. There are few studies that have presented data on differences in range size between mating and non-mating seasons. Corbett (1979) illustrated that male ranges in his Herbrides study were

largest in spring, when presumably mating activities were at their highest, and declined as the year proceeded. Izawa *et al.* (1982) also showed that male ranges were larger during the mating season compared with the rest of the year; unfortunately neither author presented separate data for breeding versus non-breeding males.

CHAPTER 8

General discussion and conclusions

This study has investigated selected aspects of the ecology of the feral cat *Felis catus* on Wedge Island over the winter period. The winter diet of the feral cat population was quantified through scat analysis and related to the seabird population survey where prey abundance and availability were monitored throughout the study. In addition, two other parameters of the feral cat winter ecology of home range and reproductive condition were studied. The study estimated that not more than fifteen individuals represented the feral cat population on Wedge Island. Live trapping yielded captures of seven feral cats, four adults and three late juveniles. The study was therefore characterised by small sample sizes and the results from each component of the study should be interpreted conservatively.

The results of the study highlight the fact that the feral cat population of Wedge Island was regulated to a certain degree by prey abundance and availability over the winter period. The seabird survey revealed sudden and continued fluctuations occurring within the seabird population in winter. This occurred firstly when short-tailed shearwaters embarked on their annual migration in late May and the trend continued with a decline in the little penguin populations of both North and South rookeries in late July and early August. Dietary analysis of the feral cat population revealed significant increases of little penguin and native hen remains in scats after the departure of the shearwaters, although native hens represented only a smaller component of the feral cat diet. Little penguins were taken as major prey, possibly compensating for the overall decline in prey abundance. Significant increases of caterpillar, egg fragment and insect remains were also recorded from the month of July onwards; these increases strongly suggest that these invertebrates and eggs (presumably of little penguin and native hens) comprise an important supplementary component to the staple prey of little penguins. Remains of crab fragments, chitons, barnacles, fish bones and scales, with various residues of plant material in the scats also suggested that the feral cats scavenged on the shoreline and around the rookeries to further supplement their winter food requirements.

Other studies have clearly demonstrated that feral cats are opportunistic predators, the act of predation being a function of prey availability rather than prey selection (Jones 1977, Fitzgerald and Karl 1979, van Aarde 1980, Jones and Coman 1981, Karl and Best 1982, Apps 1983, Liberg 1984, van Rensburg 1985). This study clearly demonstrated that the feral cat population adopted a similar approach in response to seasonal changes of prey availability. The ability to switch to other prey species as the latter became available or abundant extended to invertebrates such as coleopterans, scorpions, crickets, ants, caterpillars and included bird eggs and vegetation. Scat analysis indicated that these prey items were increasingly taken as abundance increased.

Brothers *et al.* (1985) reported that feral cat numbers on subantarctic islands fluctuated seasonally following corresponding variations in the abundance and availability of prey; European rabbits and burrow nesting petrels are the chief source of food and, when rabbits are absent, winter breeding burrow nesting petrels or species sedentary all year round sustain cats through winter. Jones (1977) suggested that the absence of white headed petrels and antarctic prions from Macquarie Island from late May to September, together with the scarcity of rabbits under 600 grams during the same period, must severely limit prey availability to the feral cat population; evidence from gut contents indicated that, although rabbits were eaten throughout the year, the diet changed in winter to include scavenging on dead elephant seals and increased predation on wekas. This change of diet also suggested a movement, at least for foraging of cats from the plateau to the slopes and coastal terrace during winter. Jones (*op. cit.*) also reported evidence of carcasses of feral cats that had starved to death during successive winters. At the onset of winter, with a rapidly decreasing supply of available food, old, debilitated and young cats in particular may be unable to capture the larger prey present and be forced to scavenge on a very limited supply of carrion (Jones 1977).

A somewhat similar situation has been reported from Ascension Island, where feral cats rely predominantly on wideawake terns *Sterna fuscata* for food; during the terns' three month absence each year, feral cats were seen at garbage bins and dumps more frequently than the rest of the year; this starvation period kept feral cat numbers well

below the level that the large tern population could otherwise have supported (Stonehouse 1962).

The seasonal fluctuation of prey availability and abundance on Wedge Island may represent the major factor in limiting the growth of the feral cat population. Although this immediate resource shortage was overcome by switching the main emphasis of the feral cat diet to little penguins to compensate for the absence of the short-tailed shearwaters, it is possible that the number of penguins present at any time on the island was not sufficient to sustain the energetic requirements of individual cats with regard to reproductive needs over winter. This was strongly supported by evidence from the hormonal analysis of the population which revealed that the blood plasma testosterone levels of adult male individuals in winter were not sufficiently high to maintain an active reproductive status. There were also no captures of lactating or pregnant females, nor were there any sightings of early juveniles throughout the course of the study. This leads to a tentative conclusion that the reproductive status of male and female cats was suppressed or adversely affected throughout the winter months.

The total number of little penguins estimated on each survey date could be easily misinterpreted as the net estimation would not represent the actual number of penguins available to the feral cats as prey. The little penguins are at a major risk from predation on two occasions. The most vulnerable during the transitional period on the shoreline at dusk when returning from the sea after foraging or conversely at dawn when part of the colony sets off to sea. The other period when penguins were apparently exposed to high risks of predation was during the night when individuals seemed to position themselves around their burrows calling out to conspecifics within the colony. Spotlighting revealed that most of the feral cats foraged actively along the shoreline and concentrated around the lower regions of both rookeries bordering the eastern shore. However, further studies need to quantify the amount of transitional shoretime spent by the little penguins and also the corresponding rates of predation by feral cats before the full extent of prey availability as limiting factor on the feral cat population can be ascertained.

The overlap of home range areas for the three feral cats (one adult male and female, one juvenile male) in the study was extensive. The spatial organisation of these animals were comparable to those reported by Apps (1986) in his study of feral cat home ranges on Dassen Island, South Africa; the mean range size of five adult males was 44 hectares with a range of 32 -63 hectares and female cats moved over a mean area of 19 hectares (range 11-32 hectares) while three juveniles possessed a mean of 18 hectares (range 12-24 hectares). Apps (*op. cit.*) observed that overlap between all range areas was complete for all cats; no cat had an exclusive area and approximately twelve cats were observed in each identified range. A similar pattern was observed for the home ranges of the three cats in this study; the ranges of these feral cats fall outside both Wilson's (1975) and Kaufmann's (1983) definitions of territory; these areas were neither exclusive nor defended but it appeared that the adult male cat tolerated the presence of the adult female and juvenile male over a substantial part of its range. This large degree of tolerance is further suggested by the location of the den of the adult female which was positioned approximately twenty metres away from the den site of the adult male on the southern end of the island. Another possible explanation for the close proximity observed between these cats is that all the individuals may have been genetically closely related due to repeated founder effects caused by resource bottlenecks or the effects of diseases on the population structure. Further long term studies, monitoring growth and changes in the feral cat population with regard to resource availability may reveal the full extent of the effects of resource bottlenecks on the island.

Conclusions

The decline of the feral cat population on Wedge Island is evident from this study. The present population was conservatively estimated to be less than a third of the estimated population of 1984 - 1986. A major seasonal fluctuation of feral cat prey occurred with the winter migration of short-tailed shearwaters. Although the feral cats demonstrated an ability to switch to little penguins as the alternative major prey in a functional response to the shearwater departure, it is possible that the feral cat population experiences a resource bottleneck in winter. Although little penguins occurred in relative abundance on Wedge Island throughout the year, the availability

of these seabirds to feral cats as prey represented an important limiting parameter to the cat population over the winter months. Nutritional stresses in winter would also adversely affect reproductive condition of individual feral cats and suppress reproductive success. This factor of resource availability ultimately determines the extent to which the feral cat population can be sustained over the winter period. Hence, the type and structure of different island faunas could well regulate the impact of introduced predators such as feral cats in different ways. This study clearly demonstrated that the feral cat population of Wedge Island was regulated to an extent by the structure of the seabird community.

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APPENDIX 1.

Impacts of feral cats *Felis catus* on native terrestrial mammals and birds on islands off the coast of Australia (after Dickman 1995).

Island	Area (ha)	Species	Effect	Source
St. Francis SA	809	<i>Bettongia penicillata</i> <i>Isodon obesulus</i> <i>Macropus eugenii</i> 24 species of birds	Ex S Ex S	Robinson & Smyth (1976)
Reevesby SA	344	<i>Macropus eugenii</i> <i>Leporillus conditor</i> <i>Pelagodroma marina</i> Other sea and land birds	Ex Ex D? S	Robinson <i>et al.</i> (1985) Robinson (1989)
Flinders SA	3642	<i>Macropus eugenii</i>	Ex	Robinson (1989)
Kangaroo SA	435000	<i>Phascogale tapoatafa</i> <i>Dasyurus maculatus</i> 11 other species native mammals <i>Leipoa ocellata</i> 214 other species native birds	Ex Ex S Ex S	Ford (1979) Inns <i>et al.</i> (1979) Robinson (1989)
Hermite WA	1010	<i>Lagorchestes conspicillatus</i> <i>Isodon auratus</i> <i>Hydromys chrysogaster</i> <i>Malurus leucopterus</i> <i>Eremiorinis carteri</i> <i>Chrysococcyx basalis</i> <i>Pachycephala rufiventris</i> <i>Ephthannura tricolor</i> <i>Charadrius mongolus</i> 35 other species of native birds	Ex Ex S Ex Ex Ex Ex Ex Ex S	Burbidge (1971, 1989); Burbidge & McKenzie (1989)
Dirk Hartog WA	54360	<i>Bettongia lesueur</i> <i>B. penicillata</i> <i>Lagostrophus fasciatus</i> (?) <i>Dasyurus cristicauda</i> <i>Dasyurus geoffroii</i> <i>Parantechinus apicalis</i> <i>Sminthopsis dolichura</i> <i>Perameles bougainville</i> <i>Leporillus conditor</i> <i>Pseudomys albocinereus</i> <i>P. fieldi</i> <i>P. hermannsburgensis</i> <i>P. shortridgei</i> 84 species native bird	Ex Ex Ex Ex Ex Ex S Ex Ex S Ex S Ex S	Burbidge & George (1978) Baynes (1990)

Angel WA	880	<i>Zyzomys argurus</i>	S	Burbidge & McKenzie (1989)
Dolphin WA	3200	<i>Petrogale rothschildi</i> <i>Dasyurus hallucatus</i> <i>Zyzomys argurus</i>	D S S	“ “
Gidley WA	845	<i>Z. argurus</i>	S	“ “
Legendre WA	1300	<i>Z. argutrus</i> <i>Rattus tunneyi</i>	S S	“ “
Garden WA	1170	<i>Macropus eugenii</i> 60 species native birds	S S	“ “ Abbott (1980)
Rottneet WA	1550	<i>Setonix brachyurus</i> 113 species native birds	S S	Burbidge & McKenzie (1989) Saunders & de Rebeira (1983, 1989)
North Stradbroke QLD		Not specified	D	Sinclair (1989)
Muttonbird NSW	8	<i>Pelagodrama marina</i> 4 other species sea birds	D? S?	Smith & Dodkin (1989)
Broughton NSW	138	<i>P. marina</i> 6 other species sea birds	D S?	“ “

Notes. S = stable, D = declined, Ex = extinct. ? indicates that an effect is suspected but not quantified. Tammar wallabies *Macropus eugenii* were probably extinct prior to settlement on St. Francis and Reevesby Islands, and hence may not have been eliminated by cats (Robinson & Smyth, 1976; Robinson, 1989). On Hermite Island, Burbidge (1971) emphasised the disappearance only of *E. carteri* and *M. leucopterus*. However, the four other named species of birds have not been recorded since 1912 and may thus be presumed extinct.

APPENDIX 2.

Diet of the feral cat *Felis catus* on Australian, New Zealand and Pacific region islands (after Dickman 1995).

Data are taken from 12 published and unpublished studies and represent diet as % volume of occurrence of food categories (Roamn type) or % frequency of occurrence of food categories (italic). Samples (n) were obtained from stomachs (s), faeces (f), or both sources combined (b).

Food Category	Little Barrier Is. New Zealand (Marshall, 1961)	Campbell Is. New Zealand (Dilks, 1979)	Raoul Is. New Zealand (Fitzgerald et al., 1991)	Lord Howe Is. south-west Pacific (Miller & Mullette, 1985)	Jarvis Is. central Pacific (Kirkpatrick & Rauzon, 1986)	Howland Is. central Pacific (Kirkpatrick & Rauzon, 1986)
	n = 94 (f)	n = 20 (f)	n = 57 (s)	n>=14 (b)	n = 73 (s)	n = 5 (s)
Rabbit						
House mouse				3.0	2.0	
Other rodent < 50g						
Other rodent >=50g	39.4	95.0	86.0	14.0		
Bats						
Diprotodont						
Marsupial >=100g	39.4		88.0			
All mammals						
Passerines	24.5				97.0	92.0
Non-passerines	50.0			35.0	97.0	92.0
All birds		35.0	35.0	35.0		
Lizards < 100g					<1.0	8.0
Lizards > 100g						
Snakes < 100g						
Snakes >=100g						
All reptiles					<1.0	
Amphibians						
Fish						
Invertebrates	31.9	60.0	~20		<1.0	
Scavenge & carrion			16.0			
Other			23.0		<1.0	<1.0

APPENDIX 3.

Range of prey items identified in scats. (n=527)

Prey Categories	Prey Items
P1	petrels: short-tailed shearwater (<i>Puffinus tenuirostris</i>) fairy prion (<i>Pachyptila turtur</i>)
P2	little penguin (<i>Eudyptula minor</i>)
P3	Tasmanian native hen (<i>Gallinula mortierii</i>)
P4	coleopterans
P5	other insects: ants, crickets, grasshoppers
P6	skinks: <i>Niveoscincus metallicus</i> <i>Niveoscincus ocellatus</i>
P7	caterpillars: Noctuidae: <i>Rictonis</i> Anthelidae: <i>Pterolecera</i>
P8	eggshell fragments and egg residues
P9	vegetation: grass, bark, leaves, small twigs, berries
P10	crab shell fragments
P11	other items: bivalves, molluscs, fish, starfish, chitons, scorpions, dirt and foreign material (unidentified or miscellaneous)

Category ranking of prey items found in scat analysis.

Category Ranking	Per Cent Volume
1	0-20
2	21-40
3	41-60
4	61-80
5	81-100

Abbreviations

Berry seeds: b.seeds

Eggshell fragments and residue: egg frags

Bone fragments: b.frags

Tasmanian native hen: n.hen

Little penguin: penguin

Short-tailed shearwater and fairy prion: petrel

33	May	3,4	T		F	5	0	0	0	0	0	0	0	0	0	0	0	1	petrel, fish bones		
34	May	3,4	T		F	0	0	5	0	0	0	0	0	0	0	1	0	0	petrel, b. frags, b. seeds		
35	May	3,4	T		O	5	0	0	0	0	0	0	0	0	0	1	1	0	petrel, crab frags, b. seeds		
36	May	3,4	T		O	5	0	0	0	0	0	0	0	0	0	1	1	0	petrel, crab frags, b. seeds, b. frags		
37	May	3,4	T		O	5	0	0	0	0	0	0	0	0	0	1	0	0	petrel, b. frags, grass		
38	May	4,5	T		O	5	0	0	0	0	0	0	0	0	0	1	0	0	petrel, b. frags, b. seeds		
39	May	4,5	T		O	5	0	0	0	0	0	0	0	0	0	0	0	0	petrel, b. frags		
40	May	4,5	T		O	5	0	0	0	0	0	0	0	0	0	1	0	0	petrel, b. seeds, b. frags		
41	May	3,4	T		O	5	0	0	0	0	0	0	0	0	0	1	2	0	petrel, crab frags, b. seeds		
42	May	3,4	T		O	5	0	0	0	0	0	0	0	0	0	0	0	0	petrel, b. frags,		
43	May	4,5	T		O	5	0	0	0	0	0	0	0	0	0	0	0	0	petrel		
44	May	4,5	T		O	5	0	0	0	0	0	0	0	0	0	0	0	0	petrel, b. frags		
45	May	4,5	T		O	5	0	0	0	0	0	0	0	0	0	0	0	0	petrel, b. frags		
46	May	4,5	T		O	5	0	0	0	0	0	0	0	0	0	0	0	0	petrel, b. frags		
47	May	4,5	T		O	5	0	0	0	0	0	0	0	0	0	0	2	0	petrel, crab frags, b. frags		
48	May	4,5	T		F	5	0	0	0	0	0	0	0	0	0	0	0	0	petrel, b. frags		
49	May	3,5	T		O	5	0	0	0	0	1	0	0	0	0	0	0	0	petrel, b. frags, ant		
50	May	3,5	T		O	5	0	0	0	0	0	0	0	0	0	0	0	1	petrel, fish bones, b. frags		
51	May	4,5	T		F	0	0	0	0	0	0	0	0	0	0	2	5	0	crab frags, b. seeds		
52	May	3,14	R		O	5	0	0	0	1	0	0	0	0	0	0	0	0	petrel, b. frags, beetles		
53	May	3,13	T		F	5	0	0	0	0	0	0	0	0	0	1	2	0	petrel, crab frags, b. frags, b. seeds		
54	May	4,5	G		F	1	0	0	5	0	0	0	0	0	0	0	0	0	petrel, beetles, b. frags		
55	May	3,13	T		O	3	0	0	0	0	0	0	0	0	0	3	0	0	petrel, b. frags, b. seeds		
56	May	4,5	G		O	5	0	0	0	0	0	0	0	0	0	0	2	0	petrel, b. frags, crab frags		
57	May	3,13	T		O	4	0	0	0	0	0	0	0	0	1	0	0	2	petrel, egg frags, dirt		
58	May	3,13	T		F	5	0	0	0	0	0	0	0	1	0	1	0	0	petrel, b. frags, b. seeds		
59	May	3,13	T		O	5	0	0	0	0	0	0	0	0	0	0	1	1	petrel, crab frags, bivalve		
60	May	3,13	T		O	5	0	0	0	0	0	0	0	0	0	0	0	0	petrel, b. frags		
61	May	3,13	G		F	4	0	0	0	0	0	0	0	0	0	0	0	3	petrel, b. frags, dirt		
62	May	3,13	T		O	5	0	0	0	0	0	0	0	0	0	1	1	0	petrel, crab frags, grass		
63	May	4,4	G		O	3	0	0	0	0	0	0	0	0	0	0	3	0	petrel, crab frags		
64	May	3,13	T		O	4	0	0	0	0	0	0	0	0	0	0	2	0	petrel, b. frags, b. seeds		
65	May	3,13	T		O	5	0	0	0	0	0	0	0	0	0	0	1	0	petrel, crab frags, b. frags		

132	May	5,9	G	O	0	4	0	0	0	0	0	0	1	0	0	penguin, grass		
133	May	5,9	G	O	0	5	0	0	0	0	0	0	0	0	0	penguin, b. frags		
134	May	6,9	G	F	0	5	0	0	0	0	0	0	0	0	0	penguin, b. frags		
135	May	6,9	G	O	0	5	0	0	0	0	0	0	0	0	0	penguin, b. frags		
136	May	6,9	G	O	0	1	0	0	0	0	0	2	1	0	0	penguin, b. frag, egg frag, grass		
137	May	5,8	G	F	0	4	0	0	0	0	0	0	1	0	1	penguin, b. frag, grass, dirt		
138	May	5,9	G	F	0	0	5	0	0	0	0	0	1	0	0	n. hen, grass		
139	May	6,9	G	F	0	5	0	0	0	0	0	0	0	0	0	penguin, b. frags		
140	May	5,9	G	F	0	5	0	0	0	0	0	0	0	0	0	penguin, b. frags		
141	May	5,9	G	O	0	2	0	0	0	0	0	0	2	0	1	penguin, b. frags, grass, dirt		
142	May	5,9	G	F	0	4	0	0	0	0	0	0	0	0	0	penguin, b. frags		
143	May	6,9	G	O	3	0	0	0	0	0	0	2	1	0	0	petrel, egg frags, grass, b. frags		
144	May	6,9	G	F	0	4	0	0	0	0	0	0	1	0	0	penguin, b. frags, grass		
145	May	6,9	G	O	0	4	0	0	0	0	0	0	0	0	0	penguin, grass		
146	May	5,9	G	F	0	0	5	0	0	0	0	0	0	0	0	n. hen, b. frags		
147	May	5,9	G	O	0	3	0	0	0	0	0	1	3	0	0	penguin, egg frags, b. frags, grass		
148	May	5,9	G	F	0	0	5	0	0	0	0	0	1	0	0	n. hen, b. frags, grass		
149	May	5,9	G	F	0	0	4	0	0	0	0	0	0	0	0	n. hen, b. frags		
150	May	3,14	G	F	4	0	0	0	0	0	0	0	1	1	1	petrel, bivalve, chiton, crab frags, b. frags, b. seeds		
151	May	3,14	G	F	3	0	0	0	0	0	0	0	3	0	0	petrel, b. seeds, b. frags		
152	May	3,14	G	F	4	0	0	0	0	0	0	0	3	1	0	petrel, crab frags, b. frags, b. seeds		
153	May	3,14	G	O	0	0	0	0	0	0	0	0	4	1	0	crab frags, b. seeds		
154	May	3,14	G	F	3	0	0	0	0	0	0	0	3	1	0	petrel, crab frags, b. seeds		
1	June	5,6	T	O	0	0	5	1	0	0	0	0	0	0	0	n. hen, b. frags, beetles		
2	June	5,6	T	O	5	0	0	0	0	0	0	0	1	0	0	petrel, b. seeds, b. frags		
3	June	5,6	T	O	5	0	0	1	0	0	0	0	1	0	0	petrel, b. seeds, b. frags		
4	June	3,9	T	O	5	0	0	0	0	0	0	0	1	0	0	petrel, b. seeds, beetles		
5	June	3,9	T	O	0	0	0	0	0	0	0	0	5	0	0	b. seeds, grass		
6	June	5,6	T	O	5	0	0	0	0	0	0	0	2	0	0	petrel, b. seeds, b. frags		
7	June	3,4	T	O	0	0	0	5	0	0	0	0	0	0	0	beetles, b. frags		
8	June	5,6	T	O	0	0	4	0	0	0	0	0	0	1	1	n. hen, crab frags, bivalve		
9	June	5,6	T	O	5	0	0	0	0	0	0	0	1	0	0	petrel, b. seeds, b. frags		
10	June	5,6	T	O	5	0	0	0	0	0	0	0	1	1	0	petrel, b. frags, crab frags, b. seeds		

11	June	5,3	R	F		1	3	0	1	0	0	0	0	0	0	0	petrel,penguin,beetle,b.frag		
12	June	5,4	G	F		0	0	0	0	0	0	0	0	5	0	0	berries,grass		
13	June	5,10	G	F		0	5	0	0	0	0	0	0	0	0	0	penguin		
14	June	5,4	G	F		5	0	0	0	0	0	0	1	1	0	0	petrel,egg frag,grass		
15	June	5,10	G	F		0	5	0	0	0	0	0	0	0	0	0	penguin		
16	June	6,6	G	F		0	4	0	2	0	0	0	0	0	0	0	penguin,beetle		
17	June	5,10	G	F		0	5	0	0	0	0	0	0	0	0	0	penguin		
18	June	5,4	G	F		4	5	0	0	0	0	0	0	2	0	0	petrel,b.frag,b.seeds,grass		
19	June	5,10	G	F		0	0	0	0	0	0	0	0	0	0	0	penguin		
20	June	4,4	G	F		5	0	0	0	0	0	0	0	1	0	0	petrel,berries,b.frag		
21	June	4,12	G	F		0	5	0	0	0	0	0	0	0	1	0	penguin,crab frag,b.frag		
22	June	6,6	G	F		0	3	0	0	0	0	0	0	3	0	0	penguin,grass,berries		
23	June	5,10	G	F		0	5	0	0	0	0	0	0	0	0	0	penguin		
24	June	6,6	G	F		0	5	0	0	0	0	0	0	1	0	0	penguin,grass		
25	June	5,4	G	O		0	5	0	0	0	0	0	0	0	0	0	penguin		
26	June	4,13	R	O		5	0	0	0	0	0	0	0	1	0	0	petrel,b.frag,b.seeds		
27	June	5,4	G	F		5	0	0	0	0	0	0	0	1	0	0	petrel,berries,		
28	June	5,4	G	F		0	3	0	1	0	0	0	0	1	0	0	penguin,beetle,grass		
29	June	6,7	R	F		3	2	0	0	0	0	0	0	0	0	0	penguin,petrel,		
30	June	5,4	G	F		4	0	0	0	0	0	0	0	2	0	0	petrel,berries		
31	June	5,4	G	F		5	0	0	0	0	0	0	0	1	0	0	petrel,grass,berries,b.frag		
32	June	5,4	G	F		5	0	0	0	0	0	0	0	0	0	0	petrel		
33	June	4,12	G	F		0	5	0	0	0	0	0	0	0	0	0	penguin		
34	June	5,3	G	F		0	2	0	0	0	0	0	0	1	0	0	penguin,b.frag,grass		
35	June	5,3	G	F		0	2	0	1	0	0	0	0	0	0	0	penguin,beetle,grass		
36	June	5,3	G	F		2	0	0	0	1	0	0	0	2	0	0	petrel,ant,berries,grass		
37	June	5,3	G	F		0	3	0	0	0	0	0	0	1	0	0	penguin,grass,b.frag		
38	June	4,12	R	O		0	4	0	0	0	0	0	0	0	0	0	penguin,b.frag		
39	June	5,4	G	O		0	5	0	0	0	0	0	0	0	1	0	penguin,crab frag		
40	June	5,3	G	F		0	3	0	0	0	0	0	0	1	0	0	penguin,b.frag,grass		
41	June	5,3	G	F		0	5	0	0	0	0	0	0	0	0	0	penguin		
42	June	4,3	G	O		0	4	0	1	0	0	0	0	1	0	0	penguin,beetle,grass		
43	June	4,3	G	F		0	0	0	0	0	0	0	0	1	0	5	dirt,grass		

32 July	5,5	G	F	0	0	5	0	0	0	0	0	1	0	0	0	n.hen,egg frags		
33 July	3,13	G	F	0	5	0	0	0	0	0	0	0	0	0	0	penguin,b.frags		
34 July	6,5	G	F	0	5	0	0	0	0	0	0	0	1	0	0	penguin,b.seeds		
35 July	3,13	G	F	0	5	0	0	0	0	0	0	0	0	0	0	penguin		
36 July	5,6	G	O	0	3	0	0	0	0	0	0	0	1	0	0	grass,b.frags		
37 July	5,5	G	F	0	5	0	1	0	0	0	0	0	1	0	0	penguin,beetles,grass		
38 July	6,6	G	F	0	5	0	0	0	0	0	0	0	0	0	0	penguin,b.frags		
39 July	6,6	G	O	0	5	0	0	0	0	0	0	0	0	0	0	penguin		
40 July	6,6	G	F	0	5	0	0	0	0	0	0	0	0	0	0	penguin,b.frags		
41 July	5,6	G	F	0	5	0	0	0	0	0	0	0	0	0	0	penguin,b.frags		
42 July	5,6	G	F	0	3	0	0	0	0	0	0	0	1	0	2	penguin,b.frags,grass		
43 July	4,4	G	F	0	0	0	0	0	0	0	0	3	2	0	0	grass,dirt		
44 July	3,13	G	F	0	4	0	0	0	0	0	0	0	2	0	0	penguin,b.frags,grass		
45 July	5,3	G	F	0	3	0	0	0	0	0	0	0	1	0	0	penguin,b.frags,grass		
46 July	5,6	G	F	0	5	0	0	0	0	0	0	0	1	0	0	penguin,b.seeds		
47 July	3,13	G	F	0	5	0	0	0	0	0	0	0	0	0	0	penguin,b.frags		
48 July	3,13	G	F	0	5	0	0	0	0	0	0	0	0	0	0	penguin,b.frags		
49 July	4,11	G	F	0	5	0	0	0	0	0	0	0	0	0	0	penguin		
50 July	5,4	G	F	0	0	5	0	0	0	0	0	0	0	0	0	n.hen,b.frags		
51 July	5,4	G	F	0	5	0	0	0	0	0	0	0	0	0	0	penguin		
52 July	5,5	G	F	0	5	0	0	0	0	0	0	0	1	0	0	penguin,grass		
53 July	5,5	G	F	0	0	0	0	0	0	0	5	1	0	0	0	egg frags,grass		
54 July	3,14	G	F	0	5	0	0	0	0	0	0	0	0	0	0	penguin		
55 July	5,5	G	F	0	0	0	0	0	0	0	5	1	0	0	0	egg frags,grass		
56 July	3,13	G	F	0	5	0	0	0	0	0	0	0	0	0	0	penguin		
57 July	5,4	G	F	0	5	0	0	0	0	0	0	0	1	0	0	penguin,grass		
58 July	5,6	G	F	0	5	0	0	0	0	0	0	0	0	0	0	penguin,b.frags		
59 July	5,3	G	F	0	5	0	1	0	0	0	0	0	1	0	0	penguin,beetle,grass		
60 July	5,5	G	F	0	5	0	0	0	0	0	0	0	0	0	0	penguin,b.frags		
61 July	5,4	G	F	0	0	5	0	0	0	0	0	3	0	0	0	n.hen,egg frags		
62 July	5,5	G	F	0	0	5	0	1	0	0	0	0	1	0	0	n.hen,ant,grass		
63 July	5,5	G	F	0	5	0	1	0	0	0	0	1	0	0	0	penguin,egg frags,beetle		
64 July	4,11	G	F	0	5	0	0	0	0	0	0	0	1	0	0	penguin,grass,b.frags		

65	July	5,5	G	F	0	0	0	0	0	0	0	0	0	0	0	0	0	0	egg frags,grass		
66	July	5,5	G	F	0	0	0	0	0	0	0	0	0	0	0	0	0	0	egg frags,grass		
67	July	5,4	G	F	0	0	0	0	0	0	0	0	0	0	0	0	0	0	grass,egg frags		
68	July	3,13	G	F	0	5	0	0	0	0	0	0	0	0	0	0	0	0	penguin		
69	July	5,3	G	F	0	0	0	0	0	0	0	0	0	0	0	0	0	0	egg frags,grass		
70	July	5,10	G	F	0	0	0	0	0	0	0	0	0	0	0	0	0	0	berries,grass		
71	July	3,14	G	O	0	5	0	0	0	0	0	0	0	0	0	0	0	0	penguin,b.frags,grass		
72	July	3,13	G	O	0	5	0	0	0	0	0	0	0	0	0	0	0	0	penguin,b.frags		
73	July	3,13	G	O	0	5	0	0	0	0	0	0	0	0	0	0	0	0	penguin,grass,b.frags		
74	July	4,5	G	F	0	0	4	0	0	0	0	0	0	0	0	0	0	0	n.hen,egg frags,		
75	July	3,14	G	F	0	5	0	0	0	0	0	0	0	0	0	0	0	0	penguin,b.frags		
76	July	4,4	G	F	0	5	0	0	0	0	0	0	0	0	0	0	0	0	penguin,grass,b.seeds,berries		
77	July	4,4	G	F	0	5	0	0	0	0	0	0	0	0	0	0	0	0	penguin,grass		
78	July	5,5	G	F	0	0	0	0	0	0	0	0	0	0	0	0	0	0	egg frags,grass		
79	July	3,14	G	F	0	5	0	1	0	0	0	0	0	0	0	0	0	0	penguin		
80	July	4,4	G	F	0	5	0	0	0	0	0	0	0	0	0	0	0	0	penguin,beetle,grass		
81	July	4,4	G	F	0	5	0	0	0	0	0	0	0	0	0	0	0	0	penguin,egg frags		
82	July	3,14	G	O	0	5	0	0	0	0	0	0	0	0	0	0	0	0	penguin		
83	July	5,4	G	F	0	5	0	0	0	0	0	0	0	0	0	0	0	0	penguin,grass		
84	July	5,4	G	F	0	5	0	0	0	0	0	0	0	0	0	0	0	0	penguin,grass		
85	July	4,4	G	F	0	5	0	0	0	0	0	0	0	0	0	0	0	0	penguin,grass		
86	July	5,4	G	F	0	5	0	1	0	0	0	0	0	0	0	0	0	0	penguin b.frags,beetle,grass		
87	July	5,4	G	F	0	0	0	0	0	0	0	0	0	0	0	0	0	0	egg frags,scorpion		
88	July	5,3	G	O	0	5	0	0	0	0	0	0	0	0	0	0	0	0	penguin,grass		
89	July	5,3	G	F	0	3	0	1	1	0	0	0	0	0	0	0	0	0	egg frags,b.frags,penguin,ant		
90	July	5,3	G	F	0	2	0	0	0	0	0	0	0	0	0	0	0	0	penguin,egg frags,grass		
91	July	5,11	G	F	0	5	0	0	0	0	0	0	0	0	0	0	0	0	penguin,b.frags		
92	July	5,3	G	F	0	5	0	0	0	0	0	0	0	0	0	0	0	0	penguin,grass		
93	July	5,11	G	F	0	5	0	0	0	0	0	0	0	0	0	0	0	0	penguin,b.frags		
94	July	3,13	G	F	0	5	0	0	0	0	0	0	0	0	0	0	0	0	penguin,b.frags		
95	July	5,2	G	F	0	5	0	0	0	0	0	0	0	0	0	0	0	0	penguin,egg frags		
96	July	5,3	G	F	0	0	5	0	0	0	0	0	0	0	0	0	0	0	n.hen,grass		
97	July	5,11	G	F	0	5	0	0	0	0	0	0	0	0	0	0	0	0	penguin,b.frags		

98 July	4,4	G	F	0	0	0	0	0	0	0	4	1	0	0	egg frags,grass		
99 July	5,4	G	F	0	4	0	0	0	0	0	2	1	0	0	penguin,egg frags,grass,b.frags		
100 July	5,3	G	F	0	0	5	0	0	0	0	0	0	0	0	n.hen,b.frags		
101 July	5,3	G	F	0	2	0	1	0	0	0	0	1	0	0	penguin,beetle,grass		
102 July	3,13	G	F	0	5	0	0	0	0	0	0	1	0	0	penguin,b.frags,grass		
103 July	3,14	G	F	0	5	0	0	0	0	0	0	0	0	0	penguin		
104 July	3,14	G	F	0	5	0	0	0	0	0	0	0	0	0	penguin,b.frags		
105 July	4,12	G	F	0	5	0	0	0	0	0	0	0	0	0	penguin,b.frags		
106 July	3,13	G	F	0	5	0	0	0	0	0	0	0	0	0	penguin,b.frags		
107 July	3,13	G	F	0	5	0	0	0	0	0	0	0	0	0	penguin,b.frags		
108 July	5,10	G	F	0	5	0	0	0	0	0	0	0	0	0	penguin,b.frags		
109 July	5,10	G	F	0	5	0	0	0	0	0	0	0	0	0	penguin,b.frags		
110 July	5,10	G	F	0	5	0	1	0	0	0	0	0	0	0	penguin,b.frags		
111 July	4,3	G	F	0	4	0	0	0	0	0	0	1	0	0	penguin,beetle,grass		
112 July	5,10	G	F	0	5	0	0	0	0	0	0	1	0	0	penguin,grass,b.frags		
113 July	5,10	G	F	0	5	0	0	0	0	0	0	1	0	0	penguin,grass		
114 July	5,10	G	F	0	5	0	0	0	0	0	0	1	0	0	penguin,berries,claw		
115 July	5,10	G	F	0	5	0	1	0	0	0	0	0	0	0	penguin,b.frags,beetle		
116 July	5,10	G	F	0	5	0	1	0	0	0	0	1	0	0	penguin,grass,beetle		
117 July	5,10	G	F	0	5	0	1	0	0	0	0	1	0	0	penguin,beetle,grass		
118 July	5,10	G	F	0	5	0	0	0	0	0	0	0	0	0	penguin,b.frags		
119 July	5,5	G	F	0	5	0	1	0	0	0	0	0	0	0	penguin,grass		
120 July	5,10	G	F	0	4	0	1	0	0	0	0	2	0	0	penguin,b.frags,beetle,grass		
121 July	5,10	G	F	0	5	0	0	0	0	0	0	0	0	0	penguin		
122 July	5,10	G	F	0	5	0	0	0	0	0	0	0	0	0	penguin		
123 July	5,9	G	F	0	5	0	0	0	0	0	0	0	0	0	penguin,b.frags		
124 July	5,4	G	O	0	5	0	0	0	0	0	0	1	0	0	penguin,grass		
125 July	5,5	G	O	0	4	0	1	0	0	0	0	0	0	0	penguin,b.frags		
126 July	5,4	G	F	0	5	0	1	0	0	0	0	1	0	0	penguin,beetle,egg frags		
127 July	5,10	G	F	0	4	0	1	0	0	0	0	2	1	0	penguin,beetle,grass,egg frags		
128 July	5,4	G	F	0	5	0	1	0	0	0	0	0	1	0	penguin,beetle,grass		
129 July	5,4	G	F	0	5	0	1	0	0	0	0	1	1	0	penguin,beetle,grass,egg frags		
130 July	5,4	G	F	0	3	0	1	0	0	0	0	1	0	0	penguin,beetle,grass		

131	July	5,4	G	F	0	3	0	0	0	0	0	0	2	1	0	1	penguin, grass, scorpion, egg frags		
132	July	3,13	G	F	0	3	0	0	0	0	0	0	0	0	0	0	penguin, b. frags		
133	July	5,3	G	F	0	0	0	0	0	0	0	0	5	2	0	0	egg frags, grass		
134	July	3,13	G	F	0	4	0	0	0	0	0	0	1	0	0	1	egg frags, penguin, plastic gauze		
135	July	3,13	G	F	0	3	0	0	0	0	0	0	0	1	0	0	penguin, berries, b. frags		
136	Aug	3,14	G	F	0	5	0	0	0	0	0	0	0	0	0	0	penguin, b. frags		
137	Aug	3,14	G	F	0	5	0	0	0	0	0	0	2	0	0	0	penguin, egg frags		
138	Aug	3,14	G	F	0	5	0	0	0	0	0	0	0	0	0	1	penguin, b. frags, plastic shreds		
139	July	5,9	G	F	0	5	0	0	0	0	0	0	0	0	0	0	penguin, b. frags		
140	July	6,5	G	F	0	5	0	0	0	0	0	0	0	1	0	0	penguin, grass		
141	July	5,4	G	F	0	5	0	1	0	0	0	0	2	0	0	0	penguin, beetle, egg frags		
1	Aug	5,4	G	O	0	2	0	0	0	0	0	0	3	1	0	0	egg frags, penguin b. frags, grass		
2	Aug	5,2	G	O	0	2	0	5	0	0	0	0	0	1	0	0	beetle, penguin, grass		
3	Aug	4,5	G	F	0	5	0	0	1	0	0	0	0	0	0	0	penguin, b. frags, ant, egg frags		
4	Aug	3,5	G	F	0	0	1	0	0	0	0	0	3	2	0	0	egg frags, grass		
5	Aug	4,6	G	F	0	3	0	0	1	0	0	0	0	1	0	0	penguin, b. frags, ant, grass, styrofoam piece		
6	Aug	5,2	G	F	0	5	0	0	0	0	0	0	1	1	0	0	penguin, grass, egg frags		
7	Aug	3,13	G	F	0	0	3	0	0	0	0	0	2	0	0	0	n. hen, egg frags		
8	Aug	3,5	G	F	0	5	0	0	0	0	0	0	0	0	0	0	penguin		
9	Aug	6,7	R	F	0	0	5	0	0	0	0	0	1	1	0	1	n. hen, crab frags, grass, b. frags, berries		
10	Aug	3,13	T	F	0	5	0	0	0	0	0	0	0	0	0	0	penguin		
11	Aug	5,3	G	F	0	5	0	1	0	0	0	0	0	0	0	0	penguin, beetle		
12	Aug	6,7	R	F	0	5	0	0	0	0	0	0	1	1	0	0	penguin, b. frags, grass		
13	Aug	5,4	G	F	0	5	0	0	0	0	0	0	0	1	0	0	penguin, b. frags		
14	Aug	5,3	G	O	0	5	0	0	1	0	0	0	0	2	0	0	penguin b. frags, grass, ant		
15	Aug	5,5	G	F	0	4	0	0	0	0	0	0	1	1	0	0	penguin, grass, b. frags		
16	Aug	3,14	R	F	0	0	5	0	0	0	0	0	0	0	0	0	n. hen, berries		
17	Aug	3,13	G	F	0	5	0	0	0	0	0	0	0	0	0	0	penguin, b. frags		
18	Aug	5,5	G	F	0	1	0	0	0	0	0	0	1	1	0	0	penguin b. frags, grass		
19	Aug	2,6	G	F	0	5	0	1	0	0	0	0	0	1	0	0	penguin, grass, beetle		
20	Aug	3,5	G	F	0	0	5	0	0	0	0	0	0	0	0	0	n. hen, b. frags		
21	Aug	4,6	G	F	0	5	0	0	0	0	0	0	0	0	0	0	penguin, b. frags		
22	Aug	5,11	G	F	0	5	0	0	0	0	0	0	0	0	0	0	penguin, b. frags		

56 Aug	5,2	G	F	0	0	4	0	0	0	0	0	1	1	0	0	n. hen, grass, egg frags		
57 Aug	5,2	G	F	0	0	0	0	0	0	3	0	2	0	0	0	caterp, grass		
58 Aug	4,5	G	F	0	0	4	0	0	0	0	2	1	0	0	0	n. hen, grass, b. frags		
59 Aug	5,2	G	F	0	0	2	1	0	0	0	0	1	0	0	0	n. hen, egg frags, beetle, grass		
60 Aug	5,3	G	F	0	0	0	0	0	0	3	0	2	0	0	0	caterp, grass		
61 Aug	5,2	G	F	0	0	0	0	0	0	3	0	2	0	0	0	caterp, grass		
62 Aug	3,13	G	F	0	5	0	0	0	0	0	0	1	0	0	0	penguin, grass		
63 Aug	5,2	G	F	0	0	4	0	0	0	1	0	0	0	0	0	n. hen, caterpillar, grass		
64 Aug	5,5	G	F	0	0	0	0	0	0	0	0	2	0	0	0	grass, dirt		
65 Aug	6,6	G	F	0	0	0	0	0	5	0	0	0	0	0	0	skink		
66 Aug	6,6	G	F	0	0	0	0	0	5	0	0	0	0	0	0	skink		
67 Aug	6,6	G	F	0	0	0	0	0	5	0	0	0	0	0	0	skink		
68 Aug	6,6	G	F	0	0	0	0	0	5	0	0	0	0	0	0	skink		
69 Aug	6,6	G	F	0	0	0	0	0	5	0	0	0	0	0	0	skink		
70 Aug	3,13	G	O	0	3	0	0	0	0	0	0	1	0	0	0	penguin, grass		
1 Aug	6,5	G	F	0	5	0	0	0	0	0	0	0	0	0	0	penguin		
2 Aug	6,5	G	F	0	0	2	0	0	0	2	0	1	0	0	0	n. hen, caterpillar, grass		
3 Aug	5,2	G	O	0	0	0	2	0	0	0	0	2	0	0	0	beetle, grass		
4 Aug	5,3	G	O	0	2	0	1	0	0	2	0	2	0	0	0	penguin, b. frags, beetle, grass, caterpillar		
5 Aug	5,2	G	F	0	3	0	0	0	0	2	0	1	0	0	0	penguin, grass, caterpillar		
6 Aug	5,2	G	F	0	0	3	1	0	0	1	0	1	0	0	0	n. hen, beetle, grass, caterpillar		
7 Aug	5,2	G	F	0	0	0	0	0	0	5	0	1	0	0	0	caterp, grass		
8 Aug	6,7	G	F	0	5	0	0	0	0	0	0	1	0	0	0	penguin, grass		
9 Aug	3,14	G	F	0	5	0	0	0	0	0	0	1	0	0	0	penguin, grass		
10 Aug	5,3	G	F	0	2	0	0	0	0	4	0	1	0	0	0	caterp, grass, penguin, b. frags		
11 Aug	5,2	G	F	0	0	4	1	1	0	1	0	1	0	0	0	n. hen, egg frags, beetle, ant, caterpillar		
12 Aug	5,3	G	F	0	2	0	1	0	0	1	0	1	0	0	0	penguin, b. frags, beetle, grass, caterpillar		
13 Aug	5,3	G	F	0	0	4	0	0	0	0	0	1	0	0	0	n. hen, caterpillar, grass		
14 Aug	5,2	G	F	0	4	0	0	0	0	0	1	1	0	0	0	penguin, egg frags, grass		
15 Aug	5,2	G	O	0	0	4	0	0	0	1	1	1	0	0	0	n. hen, grass, caterpillar, egg frags		
16 Aug	5,3	G	F	0	0	0	0	0	0	2	0	2	0	0	0	grass, caterpillar		
17 Aug	5,3	G	F	0	0	0	1	0	0	4	0	0	0	0	0	beetle, caterpillar		
18 Aug	5,7	G	F	0	5	0	0	0	0	0	0	0	0	0	0	penguin		

19 Aug	5,2	G	F	0	0	0	1	0	0	1	4	1	0	0	egg frags,grass,caterpillar,beetle		
20 Aug	5,2	G	F	0	2	0	0	1	0	2	0	0	0	0	penguin b. frags,ant,caterpillar		
21 Aug	5,3	G	F	0	0	0	1	0	0	0	5	0	0	0	beetle,egg frags		
22 Sept	5,2	G	F	0	2	0	0	0	0	2	0	1	0	0	penguin b. frags,grass,caterpillar		
23 Sept	5,3	G	F	0	0	5	1	0	0	0	1	0	0	0	n.hen,beetle,egg frags		
24 Sept	5,3	G	F	0	3	0	0	0	0	2	1	0	0	1	penguin b. frags,egg frags,scorpion,beetle,caterpillar		
25 Sept	5,3	G	F	0	0	0	0	0	0	1	5	1	0	0	egg frags,caterpillar,grass		
26 Sept	5,2	G	F	0	3	0	1	0	0	2	0	1	0	1	penguin b. frags,grass,scorpion,beetle,caterpillar		
27 Sept	5,2	G	F	0	0	3	0	1	0	1	0	0	0	0	n.hen,ant,caterpillar		
28 Sept	5,2	G	F	0	0	4	1	0	0	1	0	1	0	0	n.hen,grass,beetle,caterpillar		
29 Sept	5,2	G	F	0	0	3	0	0	0	1	2	1	0	0	n.hen,egg frags,caterpillar,grass		
30 Sept	5,4	G	F	0	0	0	0	0	0	3	1	1	0	0	egg frags,caterpillar,grass		
31 Sept	5,2	G	F	0	5	0	0	0	0	1	0	0	0	0	penguin,caterpillar		
32 Sept	3,13	G	F	0	0	2	0	0	0	2	0	1	0	0	n.hen,caterpillar,grass		
33 Sept	3,13	G	F	0	5	0	0	0	0	0	0	1	0	0	penguin,grass		
1 Sept	3,13	G	F	0	0	0	1	0	0	4	0	1	0	0	caterp.beetle,grass		
2 Sept	3,13	G	F	0	3	0	0	0	0	2	0	1	0	1	penguin b. frags,grass,scorpion		
3 Sept	5,5	G	F	0	5	0	0	0	0	0	0	1	0	0	penguin,grass		
4 Sept	4,6	G	F	0	5	0	0	0	0	0	0	0	0	0	penguin		
5 Sept	5,3	G	F	0	5	0	1	0	0	1	2	0	0	0	penguin,egg frags,caterpillar,beetle		
6 Sept	4,6	G	F	0	5	0	0	0	0	0	0	0	0	0	penguin		
7 Sept	3,14	G	F	0	5	0	0	0	0	0	0	0	0	0	penguin		
8 Sept	4,7	G	F	0	3	0	0	0	0	1	1	0	0	0	penguin,caterpillar,grass		
9 Sept	5,2	G	F	0	5	0	0	0	0	0	0	0	0	0	penguin		
10 Sept	5,3	G	F	0	0	0	0	0	0	2	1	1	0	0	caterpillar,egg frags,grass		
11 Sept	5,2	G	F	0	0	0	0	0	0	5	0	0	0	0	caterpillar		
12 Sept	5,3	G	F	0	3	0	0	0	0	2	0	1	0	0	penguin,caterpillar,grass		
13 Sept	5,3	G	F	0	0	0	1	1	0	2	0	1	0	0	beetle,ant,caterpillar,grass		
14 Sept	5,10	G	F	0	5	0	0	0	0	0	0	1	0	0	penguin,grass		
15 Sept	5,3	G	F	0	0	0	0	0	0	4	0	1	0	0	caterpillar,grass		
16 Sept	3,14	G	F	0	5	0	0	0	0	0	0	1	0	0	penguin,b. frags,grass		
17 Sept	5,2	G	F	0	0	0	0	0	0	5	0	1	0	0	caterpillar,grass		
18 Sept	5,3	G	F	0	0	0	0	0	0	0	5	0	0	0	egg frags		

19 Sept	5,2	G	F	0	0	0	0	0	0	0	3	1	0	0	caterpillar,egg frag,grass		
20 Sept	5,2	G	F	0	0	0	1	1	0	4	0	1	0	0	caterpillar,beetle,ant,grass		
21 Sept	5,2	G	F	0	3	0	0	0	0	2	0	1	0	0	penguin,caterpillar,grass		
22 Sept	5,2	G	F	0	0	0	0	0	0	4	0	1	0	0	caterpillar,grass		
23 Sept	3,14	G	F	0	5	0	0	0	0	0	0	0	0	0	penguin		
24 Sept	5,2	G	F	0	2	0	0	0	0	3	2	1	0	0	penguin,egg frags,caterpillar,grass		
25 Sept	5,3	G	F	0	3	0	0	0	0	3	0	1	0	0	penguin,caterpillar,grass		
26 Sept	5,4	G	F	0	5	0	0	0	0	0	0	0	0	0	penguin		
27 Sept	5,5	G	F	0	3	0	0	0	0	0	0	0	0	1	penguin b.frags,scorpion		
28 Sept	4,7	G	F	0	0	2	1	0	0	0	3	0	0	0	n.hen,egg frags		
29 Sept	5,4	G	F	0	0	0	1	0	0	2	2	0	0	0	egg frags,caterpillar,beetle		
30 Sept	5,3	G	F	0	0	0	0	0	0	2	0	0	0	1	caterpillar,beetle,scorpion		
31 Sept	5,13	G	F	0	0	0	0	0	0	0	0	2	0	2	grass,dirt		
32 Sept	5,2	G	F	0	0	0	1	0	0	3	0	1	0	0	caterpillar,beetle,grass		
33 Sept	5,2	G	F	0	0	0	0	1	0	3	0	1	0	1	caterpillar,scorpion,grass,ant		
34 Sept	4,5	G	F	0	0	0	0	0	0	4	1	1	0	0	caterpillar,egg frags,grass		
35 Sept	5,3	G	F	0	0	0	0	0	0	0	2	1	0	0	egg frags,grass		
36 Sept	5,4	G	F	0	5	0	0	0	0	0	0	0	0	0	penguin		
37 Sept	5,3	G	F	0	0	0	0	0	0	5	0	1	0	0	caterpillar,grass		
38 Sept	6,6	G	F	0	5	0	0	0	0	0	0	1	0	0	penguin,grass,b.frags		
39 Sept	3,14	G	F	0	2	0	1	0	0	0	0	2	0	0	beetle,grass,penguin b.frags		
40 Sept	4,6	G	F	0	3	0	1	0	0	0	0	1	0	0	penguin,beetle,grass		
41 Sept	5,3	G	F	0	0	0	0	0	0	3	2	1	0	0	caterpillar,grass,egg frags		
42 Sept	3,13	G	F	0	3	0	0	0	0	2	1	1	0	0	penguin,caterpillar,egg frags,grass		
43 Sept	5,3	G	F	0	3	0	0	0	0	2	1	1	0	1	penguin b.frags,egg frags,scorpion,caterpillar,grass		
44 Sept	5,3	G	F	0	0	0	0	0	0	4	0	1	0	0	caterpillar,grass		
45 Sept	3,14	G	F	0	5	0	0	0	0	0	0	0	0	0	penguin		
46 Sept	5,4	G	F	0	2	0	0	0	0	2	0	1	0	1	penguin b.frags,caterpillar,grass,scorpion		
47 Sept	5,4	G	F	0	5	0	0	0	0	0	0	0	0	0	penguin		
48 Sept	4,6	G	F	0	3	0	1	0	1	0	2	1	0	0	penguin,skink,egg frags,grass,beetle		
49 Sept	5,5	G	F	0	0	0	0	0	0	0	5	1	0	0	egg frags,grass		
50 Sept	5,3	G	F	0	0	3	0	0	0	0	2	0	0	0	n.hen,egg frags		
51 Sept	5,4	G	F	0	3	0	0	0	0	1	0	1	0	0	penguin b.frags,caterpillar,grass		

52	Sept	5,2	G	F	0	0	0	0	0	0	5	0	0	0	0	0	0	caterpillar	
53	Sept	5,3	G	F	0	5	0	0	0	0	1	0	0	0	0	0	1	penguin, caterpillar, scorpion	
54	Sept	5,3	G	F	0	2	0	0	0	0	0	5	0	1	0	0	0	penguin b. frags, caterpillar, grass	
55	Sept	5,3	G	F	0	0	0	0	0	0	0	0	5	1	0	0	0	egg frags, grass	
56	Sept	4,7	G	F	0	3	0	0	0	0	0	2	1	1	0	0	0	penguin, caterpillar, egg frags, grass	
57	Sept	4,6	G	F	0	2	0	0	0	0	0	2	0	1	0	0	0	penguin, caterpillar, grass	
58	Sept	5,2	G	F	0	0	0	0	0	0	0	5	0	1	0	0	0	caterpillar, grass	
59	Sept	4,2	G	F	0	0	0	1	1	0	2	0	1	0	0	0	0	caterpillar, grass, beetle, ant	
60	Sept	3,13	G	F	0	3	0	0	0	0	0	2	0	1	0	0	0	penguin, caterpillar, grass	
61	Sept	5,2	G	F	0	0	0	0	1	0	5	1	1	0	0	0	0	caterpillar, ant, egg frags, grass	
62	Sept	5,4	G	F	0	0	4	0	1	0	1	0	1	0	1	0	0	n. hen, ant, caterpillar, grass	
63	Sept	5,2	G	F	0	0	0	0	0	0	0	5	1	1	0	0	0	caterpillar, egg frags, grass	
64	Sept	5,2	G	F	0	0	0	0	0	0	0	2	1	0	0	2	0	egg frags, caterpillar, dirt, grass	
65	Sept	5,2	G	F	0	3	0	0	0	0	0	0	0	1	0	0	0	penguin, b. frags, grass	
66	Sept	3,13	G	F	0	5	0	0	0	0	0	0	0	0	0	0	0	penguin	
67	Sept	5,4	G	F	0	3	0	0	0	0	0	4	0	1	0	0	0	penguin, caterpillar, grass	
68	Sept	4,6	G	F	0	3	0	0	0	0	0	0	1	1	0	0	0	penguin, b. frags, grass, egg frags	
69	Sept	3,7	G	F	0	3	0	0	0	0	0	1	0	1	0	0	0	penguin, b. frags, caterpillar, grass	
70	Sept	5,2	G	F	0	5	0	0	0	0	0	0	0	0	0	0	0	penguin	
71	Sept	5,2	G	F	0	3	0	0	0	0	0	0	0	1	0	0	0	penguin b. frags, grass	
72	Sept	5,2	G	F	0	2	0	0	0	0	0	4	0	1	0	1	0	penguin, caterpillar, grass, scorpion	
73	Sept	5,5	G	F	0	2	0	0	0	0	0	2	0	1	0	0	2	penguin b. frags, caterpillar, grass, scorpion	
74	Sept	5,2	G	F	0	0	0	0	0	0	0	2	1	0	0	0	0	egg frags, caterpillar, grass	
75	Sept	5,3	G	F	0	0	0	0	0	0	0	0	5	1	0	0	0	egg frags, grass	
76	Sept	5,3	G	F	0	2	0	0	0	0	0	4	0	1	0	0	0	penguin, caterpillar, grass	
77	Sept	3,13	G	F	0	3	0	1	1	0	3	0	1	0	0	0	0	penguin b. frags, beetle, ant, caterpillar, grass	
78	Sept	3,6	G	F	0	3	0	0	1	0	3	0	1	0	0	0	0	penguin b. frags, caterpillar, grass	
79	Sept	5,2	G	F	0	3	0	0	0	0	0	3	0	1	0	0	0	penguin b. frags, caterpillar, grass	
80	Sept	5,2	G	F	0	3	0	0	1	0	2	1	1	0	0	1	0	penguin b. frags, beetle, caterpillar, egg frags, scorpion, grass	
81	Sept	5,4	G	F	0	0	0	1	0	0	4	0	1	0	0	1	0	caterpillar, beetle, scorpion, grass	
82	Sept	5,2	G	F	0	3	0	1	0	0	3	0	1	0	0	0	0	penguin b. frags, grass	
83	Sept	5,2	G	F	0	3	0	0	0	0	0	3	0	1	0	0	1	penguin b. frags, caterpillar, grass, scorpion	
84	Sept	3,13	R	F	0	0	5	0	0	0	0	0	0	0	0	0	1	n. hen, chiton, b. frags	

APPENDIX 4.

Kruskal-Wallis one-way analysis of variance on the mean values of eleven prey items recorded in 527 scats collected over the winter study period.

KRUSKAL-WALLIS ONE-WAY ANALYSIS OF VARIANCE FOR 527 CASES

DEPENDENT VARIABLE IS P1

GROUPING VARIABLE IS DATE\$

GROUP	COUNT	RANK SUM
May	154	57399.000
June	45	13719.000
July	138	28497.000
Aug	94	19689.000
Sept	96	19824.000

KRUSKAL-WALLIS TEST STATISTIC = 245.586

PROBABILITY IS 0.000 ASSUMING CHI-SQUARE DISTRIBUTION WITH 4 DF

KRUSKAL-WALLIS ONE-WAY ANALYSIS OF VARIANCE FOR 527 CASES

DEPENDENT VARIABLE IS P2

GROUPING VARIABLE IS DATE\$

GROUP	COUNT	RANK SUM
May	154	29681.000
June	45	11361.500
July	138	50550.500
Aug	94	23309.000
Sept	96	24226.000

KRUSKAL-WALLIS TEST STATISTIC = 115.451

PROBABILITY IS 0.000 ASSUMING CHI-SQUARE DISTRIBUTION WITH 4 DF

KRUSKAL-WALLIS ONE-WAY ANALYSIS OF VARIANCE FOR 527 CASES

DEPENDENT VARIABLE IS P3

GROUPING VARIABLE IS DATE\$

GROUP	COUNT	RANK SUM
May	154	38605.500
June	45	11029.000
July	138	35518.000
Aug	94	29296.000
Sept	96	24679.500

KRUSKAL-WALLIS TEST STATISTIC = 36.877

PROBABILITY IS 0.000 ASSUMING CHI-SQUARE DISTRIBUTION WITH 4 DF

KRUSKAL-WALLIS ONE-WAY ANALYSIS OF VARIANCE FOR 527 CASES

DEPENDENT VARIABLE IS P4

GROUPING VARIABLE IS DATE\$

GROUP	COUNT	RANK SUM
May	154	40117.000
June	45	12112.000
July	138	36232.000
Aug	94	25025.500
Sept	96	25641.500

KRUSKAL-WALLIS TEST STATISTIC = 0.504

PROBABILITY IS 0.973 ASSUMING CHI-SQUARE DISTRIBUTION WITH 4 DF

KRUSKAL-WALLIS ONE-WAY ANALYSIS OF VARIANCE FOR 527 CASES

DEPENDENT VARIABLE IS P5

GROUPING VARIABLE IS DATE\$

GROUP	COUNT	RANK SUM
May	154	39412.000
June	45	11626.000
July	138	35635.500
Aug	94	25579.500
Sept	96	26875.000

KRUSKAL-WALLIS TEST STATISTIC = 16.083

PROBABILITY IS 0.003 ASSUMING CHI-SQUARE DISTRIBUTION WITH 4 DF

KRUSKAL-WALLIS ONE-WAY ANALYSIS OF VARIANCE FOR 527 CASES

DEPENDENT VARIABLE IS P6

GROUPING VARIABLE IS DATE\$

GROUP	COUNT	RANK SUM
May	154	40565.000
June	45	11700.000
July	138	35880.000
Aug	94	25762.500
Sept	96	25220.500

KRUSKAL-WALLIS TEST STATISTIC = 12.184

PROBABILITY IS 0.016 ASSUMING CHI-SQUARE DISTRIBUTION WITH 4 DF

KRUSKAL-WALLIS ONE-WAY ANALYSIS OF VARIANCE FOR 527 CASES

DEPENDENT VARIABLE IS P7

GROUPING VARIABLE IS DATES

GROUP	COUNT	RANK SUM
May	154	34417.000
June	45	9922.500
July	138	30429.000
Aug	94	26420.500
Sept	96	37939.000

KRUSKAL-WALLIS TEST STATISTIC = 235.261

PROBABILITY IS 0.000 ASSUMING CHI-SQUARE DISTRIBUTION WITH 4 DF

KRUSKAL-WALLIS ONE-WAY ANALYSIS OF VARIANCE FOR 527 CASES

DEPENDENT VARIABLE IS P8

GROUPING VARIABLE IS DATES

GROUP	COUNT	RANK SUM
May	154	35011.500
June	45	9886.500
July	138	38824.000
Aug	94	26971.500
Sept	96	28434.500

KRUSKAL-WALLIS TEST STATISTIC = 45.164

PROBABILITY IS 0.000 ASSUMING CHI-SQUARE DISTRIBUTION WITH 4 DF

KRUSKAL-WALLIS ONE-WAY ANALYSIS OF VARIANCE FOR 527 CASES

DEPENDENT VARIABLE IS P9

GROUPING VARIABLE IS DATES

GROUP	COUNT	RANK SUM
May	154	38534.000
June	45	12989.500
July	138	30980.500
Aug	94	28272.000
Sept	96	28352.000

KRUSKAL-WALLIS TEST STATISTIC = 26.234
PROBABILITY IS 0.000 ASSUMING CHI-SQUARE DISTRIBUTION WITH 4 DF

KRUSKAL-WALLIS ONE-WAY ANALYSIS OF VARIANCE FOR 527 CASES

DEPENDENT VARIABLE IS P10
GROUPING VARIABLE IS DATE\$

GROUP	COUNT	RANK SUM
May	154	44016.000
June	45	12359.500
July	138	34707.000
Aug	94	23901.500
Sept	96	24144.000

KRUSKAL-WALLIS TEST STATISTIC = 39.391
PROBABILITY IS 0.000 ASSUMING CHI-SQUARE DISTRIBUTION WITH 4 DF

KRUSKAL-WALLIS ONE-WAY ANALYSIS OF VARIANCE FOR 527 CASES

DEPENDENT VARIABLE IS P11
GROUPING VARIABLE IS DATE\$

GROUP	COUNT	RANK SUM
May	154	41988.500
June	45	11410.000
July	138	34634.500
Aug	94	23473.500
Sept	96	27621.500

KRUSKAL-WALLIS TEST STATISTIC = 20.777
PROBABILITY IS 0.000 ASSUMING CHI-SQUARE DISTRIBUTION WITH 4 DF

>

APPENDIX 5.

Radio telemetry location fixes of individual cats throughout the study.

Date	Time	Cat	Grid
31/7	2045	004	3,10
10/8	2400	004	3,14
11/8	0630	004	3,10
	1715	004	3,9
		005	5,4
	2400	004	3,14
		005	3,6
12/8	0600	004	3,14
		005	4,6
	1200	004	3,10
		005	3,7
	1800	004	3,10
	1945	004	3,12
	2400	004	3,9
13/8	1200	005	5,3
	2000	006	6,7
		004	3,6
		005	3,3
14/8	1745	004	3,10
		006	3,9
29/8	1800	004	3,9
		006	5,3
	2400	004	3,9
30/8	0600	004	3,9
		006	5,5
	1200	004	3,9
		006	5,2
		005	5,5
	1800	004	3,9
		006	4,5
	2400	004	3,9
		006	5,3

Date	Time	Cat	Grid
31/8	0600	004	3,9
		006	5,3
	1200	005	4,5
		006	3,9
	1800	006	3,14
		005	4,4
		004	3,14
29/9	1200	004	5,2
		006	5,2
		005	5,5

Cat identification

004: adult female

005: adult male

006: juvenile male

Cat den locations

Cat	Grid
004	5,2
005	5,2
006	5,5

APPENDIX 6.

Analysis of variance between North and South Rookery: spatial and temporal analysis.

Levels encountered during processing are:

DAY	138.000	158.000	208.000	213.000	223.000	227.000
	241.000	244.000	268.000	272.000		
SITE	1.000	2.000				

Dependent variable: ARCPROP N: 60 MULTIPLE R: 0.891

SQUARED MULTIPLE R: 0.7

ANALYSIS OF VARIANCE

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
DAY	0.611	9	0.068	14.610	0.000
SITE	0.020	1	0.020	4.366	0.043
DAY*SITE	0.085	9	0.009	2.044	0.059
ERROR	0.186	40	0.005		

**Determinants Of Predatory Techniques And Efficiency
In Felid Carnivores**

**A literature review submitted to the Zoology Department
University of Tasmania, in partial fulfilment to the requirements for the
degree of Bachelor of Science with Honours.**

Jay Chin Liang Beh

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Chapter 1: Literature Review

1. Introduction

Mammalian carnivores have generated considerable and persistent interest among ethologists and ecologists alike. Eisenberg (1986) noted that "trends in their evolution, including convergent and parallel development of (their) life history strategies have intrigued us all". The ordinal name Carnivora may be colloquially rendered literally as "eaters of flesh"; thus it describes an attribute or the ecological niche occupied by some, if not all of the species comprising the taxon.

The perceived importance of carnivores appears to be disproportionate when it is considered that these remarkable animals constitute only approximately 10% of all of the genera of mammals so far identified and a tiny proportion (approximately 2%) of the total biomass estimated for the class (Gittleman 1989). In ancient Egyptian culture, cats have been worshipped as gods (e.g. Bastet) or believed to be endowed with supernatural attributes. In Greek mythology, the majority of the recognised deities were depicted with their robes and headwear bearing ornaments representing felid carnivores. One of the most enduring and heroic deeds in Greek folklore was the feat of Hercules in killing the allegedly invulnerable lion of Nemea with his bare hands (Serpell, cited in Turner and Bateson 1988).

Much of our fascination with carnivores can be attributed to fear, economic concerns and even unwarranted hatred related to their role in direct competition and as predators. Many incidences involving "man-eating" African lions, Indian and South-East Asian tigers, etc., as well as the often exaggerated reputation of carnivores as indiscriminate killers of livestock and game have frequently encouraged communities and government organisations to adopt sweeping policies designed to exterminate these animals, notwithstanding the fact that extreme aversion and phobia may be unfounded or promoted primarily by folklore and emotional responses of the inhabitants of jungles and remote country areas.

The dramatic impact of the skill and power or the sheer presence of carnivores may be daunting. They often move quickly, yet silently, attaining rapid bursts of speed to secure a kill; their muscles are aligned to deliver powerful and fatal attacks; their canines and powerful jaws are highly adapted to rip open carcasses and tear flesh with conspicuous efficiency. Partly because of the fear engendered by their impressive adaptations, trophy hunting of carnivores has been, and to some extent, still is viewed as a demonstration of bravery and skill.

Derivative products (fur, glands and musk) of the animals are treasured even currently, (although alternative synthetic facsimiles of these have been developed) and still regrettably featured in widespread trade, based on organs of the larger felid species in the belief that they are capable of conferring longevity, virility and other fictitious benefits. In addition, despite an enduring interest in carnivores, there is still a substantial level of ignorance of the majority of species within the order (Gittleman 1989).

Species of the Carnivora exhibit very wide morphological, ecological and behavioural variation. They inhabit numerous habitats and vegetational zones, including open plain with short grasses (meercats), sparse woodland (lynx and bobcats), dense tropical forests (some sub-species of tigers and panthers), taiga (Siberian tigers and Amur panther), deserts (caracals and feral cats) even oceanic waters (sea otters). In terms of their social organisation, they also vary considerably, from those leading solitary lives, apart from brief, episodic encounters between adults during the breeding season (lynx and ermines), to those that form monogamous pair bonds (cheetahs) and to species that associate in persistent packs (prides) such as the African lions.

Since the publication of classic investigations of comparative anatomy by R.I. Pocock and D. Davis and the pioneering studies of G.G. Simpson, the carnivores have formed the focus of many studies in comparative and evolutionary biology (Gittleman 1989). However, until recently, studies of the order that required detailed information about their behaviour have been handicapped by difficulties in locating individual subjects and monitoring their activities. The habits of most species have long remained obscure, as a consequence of their elusive, nocturnal and solitary habits, mobility and often aggressive tendencies. At present, following the development of greatly improved investigative techniques, particularly radiotelemetry and infrared photography, improved conservation and captive management programs and the impetus of resurgent interest in the ecological and ecological implications of carnivore behaviour, many species particularly those of the Felidae are better documented and understood.

The carnivores comprising the family Felidae (cats) exhibit high levels of specialisation related to active predation. They are generally considered to have originated in forested habitats (Serpell, cited in Turner and Bateson 1988) and the majority of the extant representatives of the taxon have retained the ability to climb skillfully. With the exception of the cheetah, (*Acinonyx jubatus*), a cursorial pursuit hunter over short distances, they are highly adapted for concealment and the ability to perform a rapid terminal rush to overcome their prey. A conservative tendency to live and hunt as solitary individuals is generally characteristic of the felids; however, the African lion is a notable exception, since this is a highly social species (Kleiman & Eisenberg 1973).

A prerequisite for efficient hunting is a considerable capacity for learning and a corresponding versatility with respect to other types of behaviour. It is generally recognised that predators and their prey may coevolve, the latter becoming increasingly adept at avoiding capture and the former continuously improving their technique of locating, ambushing, attacking and dispatching of the prey (Eisenberg 1989). Both of these facets of predator-prey interactions have important implications for animal communities in general, particularly for their diversity.

Felids are presumably the most highly specialized extant terrestrial carnivores and in this selective review, it is proposed to describe the characteristic and diverse techniques they employ to approach, capture and kill their prey. The varied methods of their feeding behaviour, including those directed at processing and ingesting the food so obtained will also be examined.

Whatever their accomplishments in terms of their hunting specialisations, cats are confronted with the problems common to all carnivores; of having to obtain sufficient food in order to survive. Surprisingly, their efficiency and the efforts they are required to expend in this context appear to vary considerably. For example, cheetahs resort to scavenging food only in exceptional circumstances, whereas lions, which may be less efficient as hunters, make a regular habit of supplementing their diet by such means (Kitchener 1991). The many ecological factors that interact with predator techniques and affect hunting success will also be reviewed in the present study.

The majority of felid species so far investigated are specialised for feeding on small rodents, although the largest cats have overcome the problems of utilising prey that are occasionally very much larger than themselves. Nevertheless, there is a general tendency to hunt prey of similar size to their own and for capturing only a few prey species (Rosenzweig 1966, Kruuk 1986). Thus, individual species of the Felidae prey on the average upon four prey items, whereas canids and viverrids (e.g. civets), may utilize more than six (Kruuk 1986). Some of the larger cats, e.g. the cheetah, have developed reliance on ambush followed by rapid pursuit as a very efficient strategy of hunting but others such as lions hunt cooperatively to capture large prey. However, the usual method adopted by felids involves patient and stealthy stalking with the aid of cryptic colouration, followed by explosive flurries of attacking actions to ensure fatal injuries to the prey.

In the past, predators have often been believed to impose detrimental effects on populations of the prey species they exploit (Gittleman 1989). This has led to frenzied and uncontrolled extermination campaigns directed at such carnivores in ill-conceived attempts at preserving game animals for the exclusive use of recreational hunting (Gittleman 1989). Even the former President of the United States Of America, Theodore Roosevelt, acclaimed for his enlightened policies of protecting wildlife has described a carnivore, the wolf, as "the beast of waste and desolation" (Gittleman 1989). Contrary to these emotive and prejudiced views, predators have in fact been demonstrated to exert a wide variety of different effects on prey populations including the total extermination of certain species when feral cats are introduced to islands previously lacking predators, regular or hierarchical impact on the size of herds of prey and lastly, no discernible influence; e.g. lions preying on migratory species of ungulates on the Serengeti Plains (Schaller 1972, Lever 1985).

In many of the earlier published studies of such interactions, evidence has been adduced demonstrating that the natural cycle of population regulation in the principal prey species may, in fact, exert a modifying effect on the size of predator populations. Thus, the exceptionally well documented relationship of population cycles of snowshoe hares and Canadian lynx (*Lynx rufus*), have indicated that populations of the latter species can be profoundly and directly affected by the amounts of their available prey (Haglund 1966).

The role of actively hunting carnivores, as prudent or imprudent predators, may be essential in regulating the size and diversity of prey populations and the concept of prudence has become an important consideration in addition to the other ecological factors that may determine predator-prey relationships (Dickman 1994). Accordingly, this review is intended to incorporate an evaluation of the ecological factors that are considered to be of paramount importance in understanding predator-prey biodynamics.

2. Ecological Constraints On Predation

The evolutionary fitness of all predators, whether they are spiders capturing insects or lions hunting buffalos, depends largely on the quality and quantity of their respective diets. Predatory strategies are profoundly influenced and refined by natural selection to maximise nutrient intake within the limits of a wide variety of ecological constraints (e.g. prey density, habitat) that may differ considerably for the same species at the extremes of its geographical distribution. The basic processes of locating and gathering food under such restrictions fundamentally affect the extent to which animals are able to use temporal and spatial dimensions, as well as the precise structure of their social systems.

General discussions of the ecological constraints operating on predation are inevitably complicated (and often confounded) by nuances of the relevant definitions. It is generally conceded that such factors must be biologically relevant (Clutton-Brock and Harvey 1983), as it is essential that the variables examined in the contexts should reflect the experiences of animals of their environment, rather than those of the observers (Jarman 1982). The associated problems are exacerbated when the subjects are secretive, nocturnal predators because there are many other pertinent factors that human investigators can neither perceive nor quantify. Certainly, we are a long way from being able to construct realistic optimal foraging models for felid predators (Sunquist and Sunquist 1989).

In behavioural terms, a solitary existence is incompatible with felid specialisations in predation and with the exception of the African lion, the species of this family are non-communal (non-cooperative) hunters and feeders (Kleinman and Eisenberg 1973). All felids are highly specialised carnivores and their feeding habits are influenced by several ecological constraints that are to some degree measurable.

Characteristics of the prey species such as their temporal and spatial distribution, abundance and density, body shape and size, anti-predatory defences and tactics may, to varying degrees, represent ecological constraints on predation. In addition, the distribution and abundance of cover, variable environments and habitats, climatic conditions and the presence and abundance of conspecifics and congeners, as well as their potential competitors may exert modifying effects; however, an effective ecological constraint for one species may not be a limiting factor for another (Sunquist and Sunquist 1989). This review will examine the most important ecological variables that affect foraging by felids and adduce appropriate examples from published accounts of field based investigations that illustrate their effects.

2.1. Attributes Of The Prey

2.1.1. Density

Within any given area there is, in principle, a measurable amount of energy that can be considered as potentially available to carnivores. The density of prey species can be estimated using a variety of methods, (e.g. transects, sample area counts, quadrats) and the values so obtained are commonly expressed as total biomass which is calculated by multiplying average density by the average individual weight. Prey density and biomass estimates recorded for a particular area are useful parameters because high levels of both are good indicators of the general availability of food for predators and thus can ultimately be expected to result in higher predator densities. Newsome *et al.* (1991) demonstrated this relationship in populations of feral cats (*Felis catus*) and foxes (*Vulpes vulpes*), in conjunction with an assessment of the population densities of their prey, rabbits.

In a study of one of the larger felids Dunham (1992) described the responses of lion populations in Central Africa to changes in the abundance of their principal prey, the Cape buffalo (*Syncerus cafer*). After the drought periods of 1983 and 1984, the number of buffalo using the riverine woodlands during the dry season exhibited a statistically significant decline. Following their reduction in numbers, the utilisation of this species as prey also decreased; lions increasingly hunted and fed upon other large herbivores, particularly impala (*Aepyceros melampus*) and zebras (*Equus burchelli*).

Prey density may also exert direct and pronounced effects on habitat utilisation by vertebrate carnivores. The former parameter has been reported to be inversely correlated with home range size (Holmes 1970, Smith 1978, Mares *et al.* 1976). Litvaitis *et al.* (1986) studied the diet, habitat use and home range size of bobcats (*Felis rufus*) in relation to the density of snowshoe hares (*Lepus americanus*) in two areas of Maine during the inclusive period of 1979-1984. Observations conducted in their study indicated that bobcats avoided some localities within their home range, possibly because they supported lower densities of their prey. The investigators concluded that habitat utilisation by the predators was influenced by the distribution of snowshoe hares, although the relationship was not linear (Litvaitis *et al.* 1986). Similar conclusions were formulated by Brand *et al.* (1976) in a study of the responses of lynx to variations in the density of the same species of prey in Central Alberta.

However, prey densities do not necessarily represent precise estimates of the amount of food available to predators (Bertram, 1973). To suggest an extreme example, the total herbivore biomass assessed within a particular area may be high but if it comprises predominantly elephants and rhinoceros, then the adult prey are expected to be essentially inaccessible to larger felids because in terms of individual size, they are too large to kill. Similarly, humid, tropical, wet rainforests often support a very high mammalian biomass but a large proportion of the constituent species may be arboreal (Eisenberg *et al.* 1972, Eisenberg 1980) and again, are generally unavailable as prey to large felids, notwithstanding the ability of the latter to climb with varying degrees of skill.

2.1.2. Spatial and Temporal Distribution of Prey

The amount of energy available in a specified area is often determined primarily by the corresponding density of prey but an additional consideration is how the former is distributed in relation to space. Whether the dispersion of prey is random, uniform or clumped is also important, since such features influence the search time associated with predation and this usually has substantial energetic, spatial and social consequences for the predators themselves (Davies and Houston 1984). Again, if prey are arboreal or fossorial, they are less likely to be vulnerable to predation by large felids. African lions occasionally excavate warthogs (*Phacochoerus aethiopicus*) from their burrows but this method is probably not often effective (Van Orsdol 1984). Similarly, both young and adult female leopards may be more successful than males at hunting in trees (Muckenhirn and Eisenberg 1973) but the frequency of successful captures achieved by them are probably very much lower.

Other attributes, e.g. whether prey are migratory, sedentary or renewed at some interval rates, may have important consequences for predators. If the prey engage in extensive seasonal movements or migratory activities in response to variations in environmental factors such as those well documented for the Serengeti (Maddock 1979), Idaho (Seidensticker *et al.* 1973) and the Kalahari (Owen and Owen 1984), then predators need to abandon or to expand their home ranges and follow the migratory prey; otherwise they need to utilise alternative prey species (Schaller 1972, Seidensticker *et al.* 1973, Matjushkin *et al.* 1977, Hanby and Bygott 1979, Owens and Owens 1984, Van Orsdol *et al.* 1985, Litraitis *et al.* 1986, Dunham 1992). For example, in Idaho, mule deer (*Odocoileus hemionus*) and elk (*Cervus canadensis*) have been reported to be relatively concentrated during the winter but are widely dispersed in the summer. Correspondingly, the ranges of several radio-tagged resident female mountain lions in the same area were almost twice as large in summer as in winter (Seidensticker *et al.* 1973). During a period of drought in the Kalahari desert, large prey species were widely dispersed and the range of a resident pride of African lions increased from 702km² to more than 3900km² (Owens and Owens 1984).

In Eastern Siberia, tigers prey mainly on red deer *C. elaphus*, wild pig *Sus scrofa* and moose *Alces alces* (Matjushkin *et al.* 1977). Some of these prey species exhibit high levels of seasonal mobility and the ranges of tigers are also large; adult females roam over areas of 200-400km², whereas adult males cover 800-1000km² (Matjushkin *et al.*, Bragin 1986). In contrast, sedentary, predictable prey resources are often associated with small, exclusive predator ranges or territories (Brown 1964, Gill and Wolf 1975, 1977, Davies and Houston 1984).

In the Himalayas, snow leopards (*Panthera uncia*) typically occur above the timberline in the dry, rocky, alpine steppe (Jackson and Ahlborn 1984). Given the nature of the terrain, the size of their individual ranges may be expected to be large. However, a study by Jackson and Hillard (1986) of this species, based on radio-tracking, indicated that the ranges of several adults were relatively small (approximately 30km²) and overlapped extensively. Leopards (*Panthera pardus*), in Sri Lanka, maintain small (8-10km²) exclusive ranges that are related to an abundant but localised prey base (Eisenberg and Lockhart 1972, Muckenhirn and Eisenberg 1973). Similarly, the presence of an abundant and seasonally stable, nonmigratory prey base on the flood plain of the Royal Chitwan National Park, Nepal, has been inferred to be related to the development of small (10-51km²), exclusive ranges of tigresses (Sunquist 1981, Smith *et al.* 1987).

Beh *et al.* (1994), obtained indications that scat analysis studies of feral cats (*Felis catus*), in the Simpson Desert, South-Western Queensland, reflected effective switching of prey in response to prey availability, prey migration and seasonality. When heavy rains broke the droughts of 1991 and 1992, this culminated in migratory plagues of spinifex hopping mice (*Notomys alexis*) and long-haired rats (*Rattus villosissimus*) invading certain areas of the desert. These small rodents were then hunted and preyed upon almost exclusively by cats. The latter also demonstrated the ability to track the rodents as they followed the rains. When the rodent populations finally stabilised and eventually declined to negligible sizes, feral cats expanded their dietary spectrum and reverted back to other available prey that were present in abundance, such as skinks, snakes and other reptiles, as well as birds.

The distribution of prey in space and time presents critical factors for parturient and lactating female predators because they may be initially confined to an area in the immediate vicinity of den sites and this often effectively restricts their foraging radius. Data obtained in field studies of leopards, tigers, mountain lions and ocelots (*Felis pardalis*) have demonstrated a dramatic reduction in the size of maternal home range immediately following the birth of cubs. Under these conditions, the adult females need to locate and kill prey, feed and return to the den every 24-36 hours (Seidensticker *et al.* 1973, Seidensticker 1977).

Thus, prey distribution and "catchability" (Bertram 1973) are vital to females in the first two months of maternal dependency when the young are largely sedentary. The offspring of large felids are nutritionally dependent on their mother for one to two years (Sunquist and Sunquist 1989). Temporal or spatial separation of predators may also be related to the rates or intervals at which prey are renewed. Waser (1990) suggested that a high rate of renewal of insect prey is related to high population densities, complete overlap of ranges and low levels of competition in small nocturnal carnivores inhabiting the Serengeti Plain. With respect to predators feeding on large ungulates, the renewal rate may also be affected by other conspecifics and competitors foraging in the same area, as prey are less likely to be vulnerable in localities that have recently been intensively hunted (Hornocker 1970, Charnov *et al.* 1976).

2.1.3. Quality and Size Considerations

Optimal foraging theory predicts that predators ought to select the most "profitable" prey (MacArthur and Pianka 1966, Schoener 1971, Pulliam 1974, Werner and Hall 1974, Charnov 1976). Classic experiments on shore crabs *Carcinus maenas* (Elner and Hughes 1978), sticklebacks *Spinachis spinachis* (Kislaliogu and Gibson 1976), pied wagtails *Motacilla alba* (Davies 1977), bluegill sunfish *Lepomis macrochirus* (Werner and Hall 1974), great tits *Parus major* (Krebs *et al.* 1972) and redshanks *Tringa totanus* (Goss-Custard 1977) demonstrated that these predators did indeed select the most profitable prey.

Considering the requirements of large felids, their most profitable dietary items may, on preliminary assessment of the relevant criteria, appear to be the largest available prey that can safely be killed. However, the importance of search time, encounter rates and the energetic costs of capture for various prey types also need to be taken into account. Furthermore, if large prey are uncommon, search times may be prolonged to levels at which they become energetically too costly. Smaller but more abundant prey might then become more profitable alternative.

Although differences in the digestibility and the nutrient qualities of prey may be selected for in some predators, their importance to large felids is not likely to be significant because the large felids possess efficient digestive systems (Ewer, 1973).

The large felids are known to take very large prey occasionally but the modal prey size is usually less than their body weight (Packer 1986). However, the latter measure can vary considerably between different geographic areas for the same species. The two interrelated factors considered to influence modal prey size of large felids to the largest extent appear to be availability and vulnerability. Mountain lions in Idaho have been reported to kill equal numbers of elk (body weight: 175kg) and mule deer (64kg), although the latter were more abundant. Elk were apparently more vulnerable in the winter when they were forced to occupy terrain offering ideal hunting conditions for the predator (Hornocker, 1970). Mountain lions also took small prey, in addition to the two species of deer. One female with young subsisted throughout a summer feeding primarily on ground squirrels (*Spermophilus columbianus*), supplemented by an occasional elk or deer (Seidensticker *et al.* 1973).

Belden and Maehr (1986) stated that in South Florida, mountain lions prey mainly on feral hogs (body weight: 25kg), white tailed deer *Odocoileus virginianus* (40kg) and raccoons *Procyon lotor* (5kg). Small prey within the range of 1-10kg are also important in the diet of mountain lions in Southeastern Peru (Emmons 1987). But, as this study indicated, the sample sizes obtained were too small for establishing confident inferences (Sunquist and Sunquist 1989).

In Southeastern Peru, jaguars have been observed to prey mainly on larger animals, including deer, capybara (*Hydrochoerus hydrochaeris*) and collared peccary (*Tayassu tajacu*) (Emmons 1987). Although they took agouti (*Dasyprocta variegata*), paca (*Agouti paca*), deer and capybara in proportion to their estimated abundance, they killed peccaries more often than was predicted by the basis of availability, probably because the latter were more vulnerable (Emmons 1987).

In Belize, jaguars have been reported to prey primarily on the small but abundant and particularly susceptible armadillo (*Dasypus novemcinctus*); relative densities of larger prey such as the paca, collared anteater (*Tamandua mexicana*), brocket deer (*Mazama americana*) and peccary appeared to be much less than that of the armadillo and larger prey items occurred much less frequently in scats (Rabinowitz & Nottingham, 1986).

Sunquist (1981), stated that tigers in Chitwan killed sambar (*Cervus naicolor*) more often than expected on the basis of availability, this suggests that these larger deer (150-250kg) was selected for or that they were easier to capture than the smaller but more abundant chital (*Axis axis*) and hog deer (*A. porcinus*) (Sunquist 1981). The gaur (*Bos gauris*), an extremely large bodied animal (450-900kg) was also present in the area but it was not common and its habitat was mainly confined to the hills. There was no evidence either from carcasses or faeces that tigers killed gaur at Chitwan and it was assumed that this species was invulnerable to predation largely by virtue of its size (Sunquist 1981).

However, Schaller (1967), reported that tigers at Kanha National Park, India, occasionally killed adult male gaur. In Nagarahole National Park, in South India, gaur densities are high and this species comprises a substantial portion of the tiger's diet (Ullas Karanth, K. pers. comm.; cited in Sunquist and Sunquist, 1989). Thus, the low density of gaur at Chitwan was probably the reason tigers did not prey on this challenging prey species.

In most areas of the Serengeti Plain, African lions prey mainly on wildebeest (*Connochaetes taurinus*) and zebras (*Equus burchelli*) when they are abundant during the annual migration; at other times, buffalo and topi (*Damaliscus karrigum*) are the principal source of food for the predators (Schaller 1972). Detailed records of the annual migrations of one of the Serengeti Plain's most numerous ungulates, Thompson's gazelle (*Gazella thompsonii*), revealed that the movements of female cheetahs and non-resident male cheetahs (*Acinonyx jubatus*) mirrored the movements of Thompson's gazelles but those of resident male cheetahs remained relatively independent of the migratory activities of such prey (Durant *et al.* 1988). All of these prey species are relatively large, the modal prey size being approximately 150kg (Packer 1986). The lions of several other African National Parks, including Kafue, Kruger, Nairobi and Albert also prey mainly on the more numerically abundant large prey (Schaller 1972).

In Ruwenzori National Park, Uganda, the modal prey size of lions in the area was 40-50kg, whereas in an adjoining area of the park where prey densities were five times higher, the corresponding measure was 65-100kg (Van Orsdol 1982). In both areas, lions preyed primarily on relatively common species of prey, further characterised by larger individual sizes.

Eloff (1973), reported that in areas where large prey were relatively scarce, as in the Kalahari Desert, small mammals and juveniles constituted more than 50% of the diet of lions and porcupines (*Hystrix africaeaustralis*) alone accounted for almost 26% of the recorded kills. Gemsbok (*Oryx gazella*), particularly calves, represented a major dietary constituent. Under these circumstances, small mammals of less than 50kg may provide the most profitable prey.

The leopard of the Kalahari desert, being considerably smaller than the lion, appears to be able to coexist with the lion by taking more small prey (Bothma & LeRiche, 1986). A small sample of identified kills by both male and female leopards in the Kalahari indicated that most of the animals killed by these predators weighed less than 30kg and many captures were of animals weighing not much above 5kg (Bothma and LeRiche 1986). Hoppe (1984), reported similar observations for leopards in the Ivory Coast; 39% of the scats of these leopards contained small prey (< 5kg), 58% contained medium sized prey (5-45kg) and only 3% contained large prey (>45kg). Small bovids, principally duikers (*Cephalopus spp.*), were the most common prey. Interestingly, almost 45% of the prey were arboreal, including at least seven species of primates.

To date, this is the only documented account that has provided evidence of significant levels of predation by leopards on arboreal primates (Cheney and Wrangham 1986). Studies of the food habits of leopards in Chitwan (Seidensticker 1976, Sunquist 1987), Rhodesia (Smith 1978), Kenya (Hamilton 1976) and the Northern Serengeti (Bertram 1982) also indicated that small animals (2-40kg) may be the principal prey of adult leopards.

In all of these investigations, leopards have been noted to prey mainly on prey species that were relatively abundant. However, studies of the same species in other areas (Kruger, Serengeti, Willpattu and Kafue parks), suggested that they regularly take larger prey (Mitchell *et al.* 1965, Kruuk and Turner 1967, Pienear 1969, Schaller 1972, Muckenhirn and Eisenberg 1973). However, this predator has a very extensive geographical range and its diet appears to be more varied than those of any other large felid species.

At Lake Manyara National Park, Tanzania, Cape buffalo (*Syncerus caffer*) were reported to be the most abundant of the large mammals and constituted 62% of kills by African lions (Makacha and Schaller 1969, Schaller 1972). 81% of all the buffalo killed were adult males; these were often separated from the herds and thereby apparently rendered more vulnerable to predation. Increased male mortality relative to that of females has been observed in many other studies of ungulate populations, including male deer *Odocoileus hemionus* (Robinette *et al.* 1957; Klein and Olson 1960), wildebeest *Connochaetes taurinus* (Talbot and Talbot 1963), tsessebe, *Damaliscus lunatus* (Child *et al.* 1972) and hartebeest *Alcelaphus buselaphus* (Rudnai 1974). Several reasons for the differential survival of the two sexes have been suggested (Clutton-Brock *et al.* 1982), one of which is that males experience higher predation rates than females as a result of their reproductive activities. While there is evidence that males are more likely to succumb to predators than females (Robinette *et al.* 1957, Estes and Goddard 1967, Hornocker 1970, Krunk 1972, Schaller 1972), the factors relating to such a bias have not been thoroughly investigated.

Hornocker (1970) suggested that male mule deer are more vulnerable to predators than females because they are often on their own and tend to be in poor conditions, particularly after the rut. Robinette (1957) concluded that they are more vulnerable because they are less cautious than females and tend to occupy positions around the periphery of herds. It is often assumed that territorial males are most at risk (Bradley 1979, Estes and Goddard 1967), although non-territorial bachelor males may, in fact, be more vulnerable since they tend to occupy high vegetation, usually in an unfamiliar habitat and are frequently injured during fights (Walther 1969, Gosling 1986).

Fitzgibbon (1990) observed cheetah (*Aciononyx jubatus*) hunting groups of Thompson's gazelle (*Gazella thompsonii*) in the Serengeti National Park, preferentially selecting individuals that were situated at the periphery of social groups. Although even the largest felids can subsist and rear young on a diet of small (5-10kg) abundant prey (Seidensticker 1973, Owens and Owens 1984, Rabinowitz and Nottingham 1986), they are morphologically specialised to kill prey as large or larger than themselves and readily do so when the opportunity arises. In this sense, felid predators forage optimally and variations in the food habits characteristic of a given species appears largely to reflect primarily differences in the availability and vulnerability of various prey species.

Cats and feral cats in Australia tend to hunt and prey exclusively on animals of adult body weights which fall within the Critical Weight Range (CWR) of 35-3500 grams. This is consistent with the theory that felid predators concentrate on prey which are generally smaller and lighter than themselves. Catling and Burt (1994) reported a complete absence of small (potoroid-sized) marsupials and a low abundance of other medium-sized mammals such as bandicoots where these species were known to have occurred previously in the coastal forests of southeast New South Wales. Such areas are now moderately high in numbers of cats, including feral animals. In Tasmania, the orange-bellied parrot, swift parrot, forty spotted pardalote, ground parrot, eastern barred bandicoot, long nosed potoroo, Tasmanian bettong and New Holland mouse are believed to be potentially threatened by cat predation. On the islands, sooty shearwaters, little penguins and some populations of reptiles are locally vulnerable (Copson 1994).

Long-nosed bandicoots (*Perameles nasuta*) and common ringtail possums (*Pseudocheirus peregrinus*), comprise over 50% of the diet of feral cats at South Head Reserve, New South Wales, during the spring. In the Simpson Desert, after seasonal rains when small mammal populations increase, species such as the long-haired rat (*Rattus villosissimus*), spinifex hopping mouse (*Notomys alexis*) and sandy inland mouse (*Pseudomys hermannsburgensis*) are taken almost exclusively (Dickman, 1993).

In radically altered habitats, such as farms, feral cats may not regularly prey on native species, preferring to concentrate on the more abundant introduced mammals such as rats, mice and rabbits (Moodie 1994). However, when the latter become scarce for reasons such as drought, the remaining native species of comparable size and body weight become very vulnerable to predation by cats, particularly at watering sites, in small remnants of bushland and other refuges which effectively become resource-based islands at times of drought (Harris *et al.* 1990, Boughey 1993, Newsome, cited in Potter 1991).

3. Hunting Cover.

All felids rely extensively on physical (structural / vegetational), features of their habitat, using almost any type of cover to approach as close as possible to prey before initiating the final attack. Despite the importance of this manoeuvre, few studies have quantitatively analysed its effects on the hunting success of felid predators. The investigations that have addressed the potential effects of this variable indicated that the minimum distance covered in the final charge is strongly correlated with accomplishing a successful capture (Gittleman 1989).

Using data from recorded bouts of stalking and computer simulations of associated parameters, Elliot *et al.* (1977) demonstrated that African lions in Ngorongoro Crater achieved a high probability (0.8) of catching Thompson's gazelles (*Gazella thompsonii*) when attacks were launched at distances of 7.6 meters or less but at 15.2 metres, the probability was zero. The author calculated that lions hunting the larger wildebeest and zebras achieved a 50% level of success at distances of 15.2 metres. Similarly, in the Queen Elizabeth National Park, Uganda, lions that were able to approach to within about 20 metres of their prey were much more likely to succeed in securing a kill (Van Orsdol 1984).

Using indirect methods of assessment (interpreting tracks in the snow), Matjustkin *et al.* (1977) inferred that Siberian tigers occasionally launched their attacks from as far away as 30 metres but more commonly from 10-15 metres; they estimated that the predators were successful only once every 3 to 5 attempts but did not provide data of success rates related to varying distances.

The availability of stalking cover directly influences the distance traversed during the final charge. Elliot *et al.* (1977), suggested that 0.4 metres of grass cover is necessary for successful daytime hunting by lions. Van Orsdol (1984) reported that hunting success in this species increased with grass height up to 0.8 metres, and Schaller (1972) noted that lions hunting in grass of 0.3-0.6 metres in height were twice as successful as those hunting in grass that was less than 0.3 metres high.

As the majority of felids are nocturnal (Gittleman 1985) and practice much of their hunting under the cover of darkness, it appears to be reasonable to assume that lunar phases might also affect hunting success. Logistic problems have often impeded field investigations from obtaining such information. However, Emmons *et al.* (unpublished data), reported that ocelots in southeastern Peru spent equal amounts of time foraging on moonlit and dark nights, although on moonlit nights they confined their hunting to dense cover (Sunquist and Sunquist 1989). Van Orsdol (1984) also stated that lunar phases influenced the hunting success of lions, the animals were almost twice as successful in capturing prey during moonless hours than during moonlit nights. At one of the study sites investigated (Ishasha), no successful bouts of hunting were recorded on moonlit nights, compared with 30.4% success rate on moonless nights at the same locality.

4. Climatic Conditions and Variable Environments.

Climatic factors may impose limitations on the time and space available for foraging and even affect the susceptibility of prey, enhancing or reducing the effectiveness of predation. Large predatory felids often encounter periods of intense heat, cold, flooding and storms. Many field-based studies suggested that climatic conditions affect predatory strategies and occasionally hunting success. Hornocker (1970) reported that mountain lions are able to kill more elk in the winter when the depth of the snow compelled the elk to occupy steep terrain where they are apparently more vulnerable. In Nepal, tigers have been noted to hunt less during the daytime in the hot season and during periods of flooding they shift their activities to higher, drier ground (Sunquist 1981). Van Orsdol (1984), noted that African lions tend to initiate hunts more often when storms are imminent; he hypothesised that this strategy is related to the reduced ability of prey to detect the predator. Matjushkin *et al.* (1970), reported that Siberian tigers have difficulty in travelling during a two to four month period in winter when snow cover is deep and soft (35-50centimetres).

Feral cats (*Felis catus*) in Australia exhibit the classic traits associated with successful invaders; they are highly adaptable to extremes of climate and other environmental features and they possess the potential for long distance dispersal over a short period of time (Newsome, cited in Potter 1991, Pettigrew 1993). The ability to survive without access to free water is an important factor in their successful colonisation of most of the semi-arid and arid zones of Australia (Jones, cited in Walton *et al.* 1989).

Cats are now found living independently throughout Australia in all habitats from arid desert to tropical rainforest and on at least 45 offshore islands. They are most abundant in urban areas. Feral populations appear to be more abundant in arid and semi-arid areas, particularly where there are large numbers of rabbits. They are less abundant in dense forest. This may be a consequence of their preference for open areas to hunt, rather than utilising dense vegetation cover in which their movements may be impeded. They are secretive animals and leave little sign of their presence, consequently they are extremely difficult to census (Jones and Coman 1980, Dickman 1993).

In a recent study of the distribution and abundance of ground dwelling mammals in 5000 hectares of coastal eucalypt forest in southeastern New South Wales, feral cats were found to be widespread and abundant. They were recorded in all forests, generally in medium to high abundance and occurred in 78.6% of the identified community types (Catling and Burt 1994).

5. Anti-Predator Strategies

It is often difficult to assess the extent to which prey characteristics influence predatory behaviour; in open habitats, many ungulate species form large herds, a social organisation which may reduce their vulnerability to predators (Sunquist and Sunquist 1989). Taylor (1976) constructed a model of predation predicting that prey clumping almost invariably benefits the prey and impedes the predator. However, increase in group size is not necessarily conducive to more effective predator detection. Van Orsdol (1984) reported that African lions hunting at night were detected significantly more often by kob (*Adenota kob*) than by topi, even though the mean group size of kob was half that of the latter. However, Schaller (1972) stated that topi are the most vigilant and least vulnerable prey species in the Serengeti. Prey species may also employ other defensive tactics. Primates may climb, warthogs and armadillos frequently take refuge in burrows, whereas others may defend themselves with horns, antlers, tusks and spines (Sunquist and Sunquist 1989). Serious injuries and fatalities associated with attempts at prey capture have been noted in lions, mountain lions and tigers (Corbett 1944, Hornocker 1970, Packer 1986).

Prey may also alter their distribution in response to the presence of predators. Temporary refuges can provide protection for prey at certain times of the day, year or season. For example, chital deer in many national parks and reserves in India exhibit a nightly yarding behaviour (Johnsingh 1983). At dusk, hundreds of chital gather over open grounds of the park headquarters near staff quarters; they spend the night on lawns close to buildings and return to the forest at dawn. These nightly aggregations obviously do not serve the purpose of grazing, as very little foliage is available in the localities where they occur. Tiger and leopard, two of the most important predators of chital, are primarily nocturnal, whereas dhole (*Cuon alpinus*) are predominantly diurnal, suggesting that these chital aggregations are primarily useful in avoiding predation by felids. However, Johnsingh (1983) estimated that 23% of dhole kills, which included a few chital were achieved before sunrise or after sunset, so it is possible that the yarding behaviour of the chital also confers some protection against predation by dholes. By spending the night in a relatively open area close to human activities and habitation, the chital reduce their chances of being captured by all three of their most common predators. The fact that this yarding activity does not occur throughout the distribution range of the chital may well reflect possible differences in predation pressures and a "cultural" transmission of the behaviour itself (Sunquist and Sunquist 1989). Mech (1977) also hypothesized that the yarding behaviour of deer provides important anti-predator benefits. In a study conducted in northern Minnesota, Nelson and Mech (1981) noted that deer increased their prospects of survival over winter by migrating to large yards, especially those near human habitation or in buffer zones between the home ranges of wolves (*Canis lupus*).

Ungulates are most vulnerable to predation during their first few weeks of life (Geist 1971, Lent 1974). Not only are the newborn handicapped by not possessing the agility of adults but they are additionally vulnerable to a greater range of predators by consequence of their smaller size. In natural populations of ungulates predation is frequently the major source of mortality for infants (Cook *et al.* 1971, Huegel *et al.* 1985, Smith 1986, Borner *et al.* 1987). The anti-predator strategies of ungulates are broadly assignable to two categories based on the responses of hiding and following (Walther 1965, Lent 1974, Leuthold, 1977). In "follower" species, the young accompany the mother soon after birth, whereas in "hider" species the young lie hidden at some distance away from the mother for the first few days of life, relying primarily on cryptic colouration and minimal activity to avoid detection by predators. The mother and infant are in contact for only brief periods when the offspring suckle and the mother ingests the faeces (Walther 1965, 1968).

Thomson's gazelles (*Gazella thomsonii*), similarly to the majority of gazelles, the cervids and many antelopes are hidiers (Lent 1974, Ralls *et al.* 1986). In such species, hiding behaviour generally begins to decline by the third week but there is much interspecific variation (Ralls *et al.* 1987).

Once predators detect the young in the open, the latter may crouch out of sight, adopting a prone position which may make them less visible and more difficult for the predator to locate (Lent 1974). This posture differs from the normal hiding position in which the head is kept low on the ground and the animal remains almost motionless. Although this response is common among hidiers, it also occurs in several "follower" species like the caribou *Rangifer tarandus* (Lent 1966).

Fitzgibbon (1990) investigated the use of hiding and the adoption of the prone response as anti-predator strategies by immature Thomson's gazelles in the grass plains of the Serengeti National Park, Tanzania. Young individuals of this species are vulnerable to a wide range of predator species, including cheetahs (*Acinonyx jubatus*), lions (*Panthera leo*), wild dogs (*Lycaon pictus*) and spotted hyaenas (*Crocuta crocuta*). Schaller (1972) estimated that predators kill over 27000 fawns per year. Immature gazelles, particularly fawns, form a large component of the diet of cheetahs (Borner *et al.* 1987, Schaller 1968, Fitzgibbon and Fanshawe 1989). Hiding, a behaviour restricted almost entirely to fawns, decreased the probability of infants being located by cheetahs at a time when their ability to outrun predators was poor. However, the period of transition from hiding to active attempts at decamping appeared to coincide with high mortality (Fitzgibbon 1990).

Another widespread anti-predatory defense is based on associations with conspecifics or mixed species grouping; individuals in groups are frequently considered to benefit from a reduced risk of predation (Neill and Cullen 1974, Kenward 1978, Foster and Treherne 1981, Morgan and Godin 1985). Such anti-predator advantages are believed to arise in two ways. Firstly, predators hunting grouped prey tend to have lower success rates than those hunting individuals (Kenward 1978, Morgan and Godin 1985). This results from the superior ability of groups to detect (Powell 1974, Siegfried and Underhill 1975, Kenward 1978, Lazarus 1979), confuse (Neill and Cullen 1974, Milinski 1977, Pitcher 1986) and mob (Hoogland and Sherman 1976, Curio 1978, Shedd 1982, Buitron 1983) predators. Secondly, as members of groups, individuals have a lower probability of being selected by the predator in consequence of dilution effects (Hamilton 1971, Bertram 1978a, Foster and Treherne 1981, Fitzgibbon 1988).

In addition, individuals in groups may also spend less time being vigilant than isolate individuals (Powell 1974, Berger 1978, Caraco 1979, Lazarus 1979, Lipetz and Bekoff 1982) and as a result, have more time available for feeding (Caraco 1979, Elgar *et al.* 1986).

However, individuals can benefit from the early warning advantage of associations in mixed groups only if the information that a predator has been detected is effectively transmitted to participants and if all group members are alert to the same predator species (Leuthold 1977, Metcalfe 1984). An additional possible benefit of mixed species grouping may arise if predators show evidence of a preference for a particular prey species. Sinclair (1985) suggested that the zebra *Equus burchelli* in the Serengeti are able to reduce their vulnerability to predation by remaining in close proximity to wildebeest (*Connochaetes taurinus*), the preferred prey of large carnivores in the area.

Andersson and Erlinge (1977) noted that felid predators can be assigned to several categories on the basis of their degree of specialisation (specialists or generalists) and mobility (resident or nomadic). A review of quantitative studies of the diet of house and feral cats (*Felis catus*) indicates that they are versatile generalist predators, exploiting a wide range of prey and are able to switch readily from one type of prey to another (Fitzgerald 1988). Andersson and Erlinge (1977) described them as partially migrating generalists because they switch from small rodents and marsupials to domestic subsistence at certain times but they are probably better considered as resident generalists.

Cats existing in continental populations are chiefly predators of small mammals, particularly of young lagomorphs and of microtine or murid rodents; birds comprise only a small part of their diet and reptiles are even less important except at low latitudes, where they may be exposed to predation to a greater extent than is usually acknowledged (Fitzgerald, cited in Turner and Bateson 1988). These animals are introduced predators of the Australian continent. To date, studies aimed at elucidating many of the ecological aspects of their biology have strongly supported the view that cats pose a serious threat to populations of small to medium sized Australian fauna (Dickman 1993). For any animal to develop efficient anti-predatory strategies and related responses, a sufficient period of time is essential for the process of coevolution between predator and prey to occur.

Many Australian animals, particularly rodents, reptiles and marsupials falling within the spectrum of the Critical Weight Range / CWR of 35 - 5500 grams represent "virgin" fauna which have had very limited or negligible exposure to such efficient predators. Hence, these vulnerable indigenous animals may be expected to experience relentless predation from introduced cats without effective techniques of anti-predator defense to ensure self preservation.

6. Hunting Strategies

The majority of small felids employ two main hunting strategies (Corbett 1979, Geertsema 1985, Kruuk 1986). The mobile (M) strategy involves movement in the direction of the prey and includes patrolling the home range until a potential prey animal is encountered. The stationary (S) strategy relies on prey moving towards the predator and includes waiting in ambush until the former approaches. For domestic cats hunting rabbits on Hosta, North Uist, in Scotland, the M strategy was reported to be more successful than the S strategy: 4.2 rabbits per hour compared with 1.1 rabbits per hour (Corbett 1979). Cats that used the M strategy were usually socially dominant subjects, whereas subordinate individuals generally employed the S strategy. Furthermore, male cats used the M strategy more than females and adult animals practised the M strategy more than juveniles (Corbett 1979). It is generally believed that subordinate cats have no alternative but to use the less successful S strategy more often because the M strategy is associated with increased conspicuousness, hence it may increase the probability of attack from dominant conspecifics; this would probably result in disruption of hunting activities and consequently result in an even lower hunting success than for the S strategy (Kruuk 1986).

In Canada, lynxes often hunt snowshoe hares using the S strategy by lying in wait on a "hunting bed" in the snow. Saunders (1963a) reported that in Newfoundland, 61% of hares that were preyed upon were captured by ambush; however, Nellis and Keith (1968) noted that only 12% of the hares were caught this way in Alberta. Difference in the use of the S strategy appears to be related to densities of the hares. When prey populations are low, lynx are compelled to search out their prey actively, rather than to adopt a passive ambush method of strategy (Nellis and Keith 1968).

Elliott *et al.* (1977) defined three types of hunting strategy for lions in the Ngorongoro Crater in Tanzania. Type 1 hunting involves killing prey that the predator happens to encounter; Type 2 hunting involves stalking and killing prey and Type 3 hunting involves actively searching out animals before stalking and killing them. The authors proposed that Type 3 hunting is driven by hunger, whereas the other two strategies are more opportunistic and would be used more frequently at high densities of prey. Bothma and LeRiche (1990) argued that increasing levels of hunger affect the various hunting activities of Southern Kalahari leopards (*Panthera pardus*); these cats are unable to increase the rate of hunting per kilometre travelled as hunger increases, because of a limited prey base which is already fully utilized. However, by moving increasingly longer distances, the leopards do effectively increase the actual number of their hunting actions per 24 hour period.

7. Methods of Prey Capture

The acts directly associated with the capture of prey are very similar in all species of wild felids. Sources of descriptive accounts of such behaviour and the slight variations between species are listed in Table 1.

The majority of felid species locate their prey primarily by sight and secondarily rely on hearing. However, some members of the family specialise in detecting and capturing prey by other methods. For example servals specialise in hunting rodents in tall grass, having perfected hunting by hearing alone (Geertsema 1985). Their widely spaced, large ears assist in establishing the exact source of the slightest rustle in the grass. They hunt various species of mole rats in different ways according to the burrowing habits of the latter. Servals are able to detect the activities, hence positions of *Tachyoryctes* spp. in their shallow burrows and simply dig them out. These cats use a different ploy for catching the mole rat *Cryptomys* which resides in deep burrows; the serval damages the burrow's entrance and simply waits for the rodent to investigate (Ewer 1973, Kingdon 1977).

Breeden (1989) observed a female fishing cat (*Felis viverrina*) hunt in Bharatpur, India. The animal positioned itself on a log overhanging the water and held its nose a short distance from the surface, thereby presumably reducing refraction; then it launched itself head first into the water grasping a fish in its mouth. This method of hunting is quite different from that employed by domestic cats (*Felis catus*) which capture fish by dipping their claws into the water.

Table 1. Descriptive studies of prey capture behaviour of cats. (After Kitchener, 1991).

Species	Source
Ocelot	Emmons (1988)
Feral/domestic cat	Corbett (1979), Leyhausen (1979)
Fishing cat	Breeden (1989)
Flat-headed cat	Muul and Lim (1970)
Iriomote cat	Yasuma (1981)
Serval	Geertsema (1976, 1985)
Caracal	Pringle and Pringle (1979), Grobler (1981)
Puma	Hornocker (1970), Wilson (1984)
Cheetah	Kruuk and Turner (1967), Schaller (1972), Eaton (1974) Wrogemann (1975)
Eurasian lynx	Haglund (1966)
Canadian lynx	Saunders (1963a), Barash (1971), Parker <i>et al.</i> (1983)
Snow leopard	Schaller (1977), Fox and Chundawat (1988)
Leopard	Kruuk and Turner (1967), Schaller (1972) Bothma and LeRiche (1986)
Jaguar	Schaller and Vasconcelos (1978), Mondolfi and Hoogestein (1986)
Lion	Kruuk and Turner (1967), Schaller (1972), Elliott <i>et al.</i> 1977
Tiger	Schaller (1967), Sunquist (1981)

Cats seldom use their sense of smell to locate prey, although prey tracking by odour detection has been observed in servals and leopards (Geertsema 1985, Bothma and LeRiche 1986). It is often stated that felids take account of wind direction when hunting, always approaching from down wind and so avoiding detection (Tehsin 1979). However, Schaller (1972) observed that lions hunt randomly with regard to wind direction. Elliott *et al.* (1977) attempted to ascertain if this variable affected the hunting success of lions in the Ngorongoro Crater; the study concluded that it had no bearing on hunting success and was ignored by the animals. Feral cats and servals also appear to be unaffected by wind direction when hunting (Corbett 1979, Geertsema 1985). Although prey animals may be alerted by the scent of a predator, they only take flight when they sight the direction of its approach. (Schaller 1972); since otherwise if they panicked after detecting predator odours, they might run towards a predator in blind confusion, instead of away from it (Kitchener 1991).

After locating their prey, cats (*Felis catus*) normally approach rapidly in a crouching posture, the typical "stalking or slinking run", relying on the use of cover where available (Bradshaw 1992, Ewer 1973, Leyhausen 1979). On arriving within a few metres, cats often lower themselves into a watching posture in which the body is pressed flat to the ground. The forelimbs are retracted so that the forefeet are positioned under the shoulders; the head is extended forward and the pinnae of the ears are flexed erect and pointing forwards. This may be followed by a second stalking run, presumably as a consequence of the prey being assessed as not being sufficiently close for effective pouncing. While preparing for the latter action, cats withdraw the hind limbs gradually by alternately treading with each foot (Bradshaw 1988, Kitchener 1991). The final approach to the prey is usually a brief sprint and whenever possible the final spring is maintained short so that both the hind feet are on the ground when the forefeet strike the prey. During the strike, the whiskers (mystacial) are directed anteriorly, presumably supplying precise information about the position of the prey and compensating for the poor vision of the cat at this close range. Prey that escape into nearby cover such as crevices too small for the cat to introduce its head may be "fished" for with an extended paw; this hunting behaviour is typical of the majority of the smaller cats and is adapted for capturing small rodents and other terrestrial mammals which retreat into a nearby burrow (Ewer, 1973; Kitchener, 1991).

Although the stalk and capture method is regarded as the classic felid hunting technique, Bothma and LeRiche (1986) ascertained that Kalahari leopards killed less than 5% of their prey by using such strategies. It is possible that prey densities are so low in the Kalahari that virtually all kills are opportunistic. Many other felids similarly kill much of their prey opportunistically. Stalking is not usually the optimal method for hunting birds; cats do not normally adopt a waiting posture before attacking them but rush directly at such prey, grasping with both forefeet. This pattern has been recorded in jaguars, caracal, tiger cats and ocelots (Ewer 1973, Schaller and Vasconcelos 1978, Leyhausen 1979, Emmons 1988). Lions tend to run straight at gazelles on sight from only a short distance away but they prefer to stalk zebra and wildebeest. Gazelles are able to accelerate much faster and to a higher maximum velocity than lions, hence the lions' recourse to a sudden and "surprise" strategy (Elliott *et al.* 1977).

The precise method whereby prey are killed by feral cats (*Felis catus*) depends on the type of animal sought for capture. Insects are normally pounced upon with both forefeet, as are small birds. Murid rodents are usually struck with one paw on the back or shoulder and are then immediately bitten on the nape of the neck (occiput). If the prey is slightly larger like a young rabbit or if the initial bite is not fatal, cats often hold the prey with their teeth and repeatedly strike with their forefeet. If the prey continues to offer resistance, the cat may fall on its side and rake at the body of the prey with the claws of its hind feet while restraining the animal with its teeth and forefeet (Kitchener 1991).

The killing bite is ideally delivered to the neck, so directed that one of the canine teeth slides between two vertebrae and severs the spinal cord. These teeth are surrounded by proprioceptors which probably assist in locating the precise target during the bite. Long-necked prey such as birds are usually bitten in the shoulder or the lower neck region initially but the second bite is always occipital in orientation (Leyhausen 1979). Grasping with the mouth is an ancient behavioural element, exhibited by many carnivorous mammals (Eisenberg and Leyhausen 1973). Grasping and restraining their prey with the forefeet is an advanced predatory technique which is particularly associated with cats. Occasionally domestic cats "slap" at small prey with the forefeet, as do the servals (Leyhausen 1979), particularly if the prey is dangerous or actively defending itself. The blows raining down on the prey may be sufficient to disorient, subdue, stun or even kill it.

Cheetahs have evolved a direct active pursuit hunting technique in contrast with that of many other felids. Victims are normally selected from a distance of about 50-500 metres away; the cheetah then dashes after them with no hint of stalking at all. When they draw alongside the prey, they attempt to knock them over with their forefeet using their well developed dew claws to rake along the side of the prey's body, both to injure and to pull down the fleeing animal. The pursuit distance of these animals is limited by their ability to store heat within the body. Taylor and Rowntree (1973) ascertained that cheetahs store metabolic heat produced by body muscles until a chase has ended, rather than dissipating the heat away during the actual chase. It was estimated that at their rate of heat production and storage, cheetahs could only pursue their prey for up to 500 metres before their body temperatures reached a lethal limit. Schaller (1972) seldom recorded pursuit distances by cheetahs of greater than 300-400 metres, well below the lethal distance. However, the distance at which cheetahs initiate their pursuit and the effort they expend during the activity depends on the vulnerability of the prey. Adult gazelles are chased from as little as 80 metres away while a vulnerable gazelle fawn may be pursued from up to 500 metres away (Bertram 1979). Schaller (1972) observed that on average, young gazelles are chased over 190 metres while adults and older juveniles are pursued over 290 metres until captured.

Small prey are killed by an occipital bite, using the canines to dislocate the cervical vertebrae. The rapid contraction time associated with deploying the jaw muscles and the abundance of mechanoreceptors in the vicinity of the canines suggests that these killing teeth can "feel" their way to the cervical vertebrae in a fraction of a second (Ewer 1973). The occipital bite may also crush the rear of the skull; jaguars kill capybara in this manner (Schaller and Vasconcelos 1978).

If prey do not die instantly, felids often rake at them with the hind feet. Large prey are usually killed by bites directed at the throat which occludes the trachea, leading to suffocation. An occipital bite would be ineffective in such contexts, since the canines would not be long enough or the jaw gape wide enough to kill by this method. Suffocation may also be achieved by clamping the jaws over the mouth and nose of the prey. The very short

canines of the cheetah make the throat bite essential for despatching medium sized prey. It has been suggested that the throat bite employed by this species may result in crippling damage to the central nervous system (Ewer, 1973).

Since the smaller felids tend to hunt prey smaller than themselves and within the Critical Weight Range (CWR), throat bites are normally restricted exclusively to the larger cats. However, caracal kill mountain reedbuck by such methods and Eurasian lynx employ them upon reindeer as well as roe deer (Haglund 1966, Grobler 1981). Sunquist (1981) observed that tigers use the throat bite when the prey is heavier than just over half of their own weight. The killing bite ultimately used by felids to subdue prey may vary according to individual preferences or it may depend in response to the animal being attacked. Fox and Chundawat (1988) described a snow leopard attacking a goat with an occipital bite but altering this to a throat bite as the prey struggled. Kalahari lions commonly prey on gemsbok (*Oryx gazella*), killing them by breaking their lower vertebral column at the sacro-lumbar joint (Eloff 1973). This behaviour is unique and peculiar only to some areas of the Kalahari, being unknown in prides in the Etosha National Park which use the conventional throat bite.

After a kill has been accomplished, there is often an interval before the prey is actually consumed. Cats often carry or drag their prey into cover, thereby avoiding the attention of other predators and scavengers. Schaller and Vasconcelos (1978) observed that jaguars drag their prey over an average distance of 87 metres into cover before they commence feeding.

8. Sensory Modalities Employed In Prey Killing

A substantial poportion of the activities of kittens and juveniles is directed at learning how to hunt. The relevant techniques are very loosely based on the postulated model of innate releasing mechanisms (McFarland 1985). The relative importance of various senses varies as the hunting sequence progresses from the initial sighting and location of prey to its ultimate ingestion (Table 2). The primary sense used in locating prey is most probably hearing; cats appear to exhibit an innate curiosity for high pitched sounds such as rustling, scratching and ultrasonic calls, discriminating between the latter. They may even be able, with experience, to distinguish between mice and shrews.

Visually guided search for prey presumably involves reliance upon the appetent of the predator. This action may be triggered or stimulated by the appearance of holes and crevices, which are investigated carefully. Olfaction plays a minor role, although some cats are apparently able to follow recently established trails of mouse urine (*Mus domesticus*) back to occupied burrows (Bradshaw 1992).

Table 2. The principal senses used in hunting by felids, in the order in which they are used,commencing with the initial detection of the prey and culminating in eating.
(After Bradshaw 1992).

Sense	Typical Stimuli	Activity Elicited
Hearing	rustling, scratching, high frequency call notes	prey seeking
Vision	moving objects of appropriate size	stalking run, watching, springing
Touch (Vibrissae)	Contact with prey	grasping,killing bite
Touch (Mouth)	fur / feather like surface	killing bite / hold
Sight	head / neck / body shape	grasping, killing, picking up to carry around
Olfaction	?	cutting open
Flavour / Texture	?	ingestion
Touch (sinus hairs)	direction of hair on prey	direction of cutting and cutting actions

Vision is used to a much greater extent during the next phase of hunting; this occurs once a visual image has been matched to its source of sound. The image is considerably more powerful if it is moving and cats generally require more experience before they can attain associative recognition and attack stationary prey.

Of all mammals apart from primates, felids have the most highly developed binocular vision, particularly within the carnivores (Vakkur and Bishop 1963, Hughes 1976). However, they possess poor visual acuity in comparison to humans; this attribute may have been sacrificed for selection of greater visual sensitivity by the summation of the input from many more receptor cells to stimulate fewer optic neurons at very low light levels (Ewer 1973).

The killing bite is only released by furry or feathered objects and this reaction is initially directed by the visual image of the head of the prey. This action is further guided by signals obtained from the vibrissae (which are more heavily relied upon in the dark). The bite itself comprises a series of reflexes directed by trigger points located around the mouth. The anteroposterior orientation of ingestive responses directed at mammalian prey is mainly directed by the pile of the fur (Kitchener 1991, Bradshaw 1992).

9. Motivational Aspects Of Predation

9.1 Hunger and Hunting

There is no doubt that domestic cats frequently embark on hunting expeditions immediately after consuming a meal provided by their owners (Kitchener 1991). It is possible that these activities are at least partly motivated by their predilection for variety within their diet but there are no published studies of the effects of diet quality (as opposed to diet quantity) on the frequency of hunting. Farmers who keep cats for rodent control often provide minimal supplementary food, in the belief that a hungry cat is a more efficient hunter and there is some evidence from field studies that support this notion, although efficient pest control requires killing without an obligatory association with eating. There are at least three stages at which hunger may affect hunting behaviour: the stage of looking for prey, the kill itself and the consumption of prey. Thus, well fed cats might not spend as much time hunting as hungry individuals may be expected to do or they may hunt less "seriously", resulting in fewer kills. It is also possible that they kill as frequently but consume little or none of the prey (Bradshaw 1992).

There is a paucity of comparative information regarding the amounts of time spent hunting by cats with different lifestyles but well fed house cats may typically hunt for up to a quarter of each day, while feral / unfed cats can possibly spend twelve out of every twentyfour hours searching for food (Turner and Meister 1988). Adamec (1976) clearly demonstrated that feeding and killing pertain to two independently controlled motivational systems; this was achieved by introducing a live rat to cats that were already feeding; almost without exception the animals interrupted their ingestive activities and dispatched the introduced prey, dragged it alongside their feeding bowl and resumed the original meal.

Captured rats were rarely consumed but this was predictable because in separate taste preference tests it was demonstrated that rat meat was less palatable than any of the alternate foods offered. However, the most palatable food (salmon) occasionally appeared to suppress hunting, suggesting the existence of a degree of interaction between predatory behaviour and appetite. Such a relationship is also predicted from structural connections that have been discovered between the areas of the lateral hypothalamus that are concerned with eating and killing activities. However, it is clear that predatory behaviour can immediately inhibit feeding actions when prey is detected, presumably because the potential benefit from obtaining an additional food item outweighs the risk of having the first item stolen while the cat is occupied with capturing a second.

In an independent study Biben (1979) demonstrated that while cats readily engage in predatory behaviour regardless of their level of hunger; their tendency to kill increases with the intensity of the latter (and also decreases for larger prey that are more difficult to capture). Prey are not often consumed immediately; they may be killed in the proximity of an uneaten carcass. Thus, hunger principally effects the initial stages of the hunt and the probability of accomplishing a kill but visual and auditory stimuli generated by the prey itself can override any considerations of appetite and initiate predatory approaches. The actual consumption of the prey depends on the palatability of any available alternative foods as well as on hunger *per se*.

9.12 "Play" In Predation

Cats are often perceived as "cruel" because they are regularly observed to toy with their prey, both when the latter are weakened by the initial attacks but are still alive and also after they are clearly dead. Such activities might be excusable (anthromorphically) in kittens which may play in almost any situation but is also exhibited by adults which engage in them in almost no other context. It is currently hypothesized that much of this play behaviour constitutes a displacement activity, resulting from motivational conflict between the need to kill and the corresponding fear of being injured by the prey (Bradshaw 1992).

Biben (1979) reported that the frequency of play is highest in two situations; first, when fear reduces the tendency to kill the prey to a minimum; small and medium sized prey may be played with (hunger=fear), although this is less evident when the largest prey are tested (e.g. young rats) which are often avoided completely when the cats had just been fed (fear>>hunger). If a cat has not been fed for 48 hours, it kills young mice immediately (hunger>fear) but engages in play during and after attacks directed at adult mice or young rats.

10. Conclusion

The above survey of the literature relating to the predatory activities of felids clearly demonstrates that a substantial bias exists in research, favouring the ecology and general biology of these animals. The larger cats have been studied and observed in considerably greater detail than smaller species of the family; no doubt this selective attention is due in no small part to the classic megafauna syndrome or the "big game hunter" mentality which has focussed on the large, conspicuous, dramatic felines.

Large felids of the genus *Panthera* such as tigers, lions and jaguars are clearly economically important predators which are often considered to endanger livestock and even human subjects, hence intensive research directed at their biology and ecology is usually considered to be justified. Studies on the less spectacular, equally economically destructive but relatively inconspicuous smaller species, e.g. of the genus *Felis* including the domestic and feral cats (*Felis catus*) are of no less potential importance and because of their relative neglect, are urgently required. Information about these smaller felines has been obtained primarily in studies of their biology, whereas the behavioural (particularly motivational) processes related to the latter have been largely neglected. The difficulties that have handicapped research efforts directed at these features have resulted principally from the cryptic, nocturnal and secretive habits of the animals themselves. The ecobehavioural responses of feral cats which have been long disregarded include activity rhythms; the qualitative aspects of these are poorly understood and not even the daily activity cycles of common species have been adequately documented. Although prey killing in *Felis catus* has been extensively investigated, the majority of the factors related to prey killing efficiency and motivation including the effects of cover and the numbers of potential prey species on the relevant strategies and techniques are virtually unknown. In addition (and surprisingly), no formal studies have been undertaken so far to attempt a comparative investigation of feral and domestic non-feral cats. Accordingly, it is proposed to examine these poorly understood aspects of the behaviour and ecology of these animals, using a combination of field observations (expected to yield data from radio telemetry) and controlled laboratory tests based on the selective manipulation of variables in attempts to identify aspects of the general biology of the species which have been overlooked and that may be opportunistically exploited during control or eradication procedures.

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