

# A case study of an alien predator (*Felis catus*) introduced on Dassen Island: selective advantages

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*Dassen Island (33°25'S, 18°06'E) is an offshore island which has suffered alteration by man through elimination and reduction of native species due to exploitation and competition for resources and through introduction of alien species. Domestic cats have become feral on the island. There were 20-25 cats in May 1979, 37-50 in June 1980, 65-85 in March 1981, 98-115 in March 1982 and 50-70 in May 1985. Between 1979 and 1982 the cats' diet contained 43,5 per cent introduced rabbits (*Oryctolagus cuniculus*) and 51,6 per cent native birds of which 88 per cent were taken as carrion. The cats were exapted to their island habitat by domestication, seasonality of breeding, early weaning of kittens and ranging behaviour. They were adapted in the occurrence of kitten fostering, communal foraging by independent juveniles and the absence of infanticide by adult males. The cats' diet and foraging behaviour were adapted to the taking of large mammal prey but not to the taking of the island's fiercely defensive birds. Thus the presence of large numbers of cats on Dassen Island depended on the effects of man's interference.*

*Dassen-eiland (33°25'S, 18°06'O) is 'n kuseiland wat verander is deur die mens se eksploitasie van en mededinging om bepaalde hulpbronne wat tot die uitkakeling en vermindering van inheemse spesies gelei het, asook deur die inbring van uitheemse spesies. Die huiskatte op die eiland het wild geword. Daar was in Mei 1979, 20-25 katte, 37-50 in Junie 1980, 65-85 in Maart 1981, 98-115 in Maart 1982 en 50-70 in Mei 1985. Tussen 1979 en 1982 het 43,5 persent van die katte se dieet uit ingevoerde konyne (*Oryctolagus cuniculus*) en 51,6 persent uit inheemse voëls bestaan waarvan 88 persent as aas gevreet is. Die katte is lank vooruit reeds deur temming, seisoenale teling, die vroeë speen van katjies en die diere se omswerwingsgedrag by die eilandhabitat aangepas. Hulle is verder deur pleegsorg vir klein katjies en die gemeenskaplike kossoekery deur onafhanklike jong katte en deurdat volgroeiende mannetjies nie die kleinjies doodgebyt het nie in hul aanpassing gehelp. Die katte se dieet en vreetgedrag is by die verkryging van groot soogdiere as prooi aangepas, maar nie by die eiland se fel verdedigende voëls nie. So het die mens se inmenging 'n uitwerking op die aanwesigheid van groot getalle katte op Dasseneiland.*

## Introduction

Aspects of the cat's biology which allow it to invade largely undisturbed island habitats such as that of Marion Island have been dealt with by Van Aarde (this volume) and Van Aarde & Skinner (1982). Here I shall consider the cat's adaptations to a grossly altered island system, including their responses to culling and their utilisation of resources generated by man's interference. The bulk of this paper is drawn from work carried out between 1979 and 1982 on feral cats living on offshore Dassen Island, South Africa.

## Study area

Dassen Island (33°25'S, 18°06'E) lies 8 km off the west coast of South Africa 65 km NNW of Cape Town. It is 224 ha in area, low-lying, and flat. Its surface consists of sandy soil, exposed rock and tumbled boulders. The island's vegetation is low-growing and its climate is Mediterranean. Dassen Island has a long history of human exploitation and interference; in 1601 it supported colonies of Cape fur seals (*Arctocephalus pusillus*) and hyrax (*Procavia capensis*) which were exploited to extinction (Skead 1972, 1980 and references therein). Birds and their eggs were collected for food from 1601 onwards. Collection of penguin eggs continued on a large scale until 1968 and on a small scale, by island residents and visitors, until at least 1980 (pers. obs.) and contributed to the decline in numbers of jackass penguins (*Spheniscus demersus*) (Frost *et al.* 1976). Eggs of the kelp gull (*Larus dominicanus*) were routinely destroyed in large numbers by Sea Fisheries staff until 1980 (pers. obs.). Dassen Island has been used for a variety of farming activities (Cooper *et al.* 1985). Of the 31 species of flowering plants recorded from the island by Brooke & Crowe (1982) at least 14 are aliens. All three of the island's terrestrial mammals are introduced; domestic rabbits (*Oryctolagus cuniculus*) were introduced between 1662 and 1668 (Skead 1980), the arrival of house mice (*Mus musculus*) is undocumented. House cats have been on the island at least 100 years (Cooper *et al.* 1985) with occasional extra introductions, the latest of which, in 1982, was an adult male, kept as one of three house pets by the Sea Fisheries head man (pers. obs.). The cats were subject to intermittent culling until 1978, to a low level of culling between 1978 and 1985 and to an intensive cull in May 1985 (Berruti, this volume).

Eighteen species of bird nest on Dassen Island (Brooke & Crowe 1982) but data on their numbers are incomplete. In 1978 the number of jackass penguins varied seasonally from 11 220 to 16 049 (Shelton *et al.* 1984). In 1982, 10 000 nesting pairs and 100 000 courting or non-breeding Cape cormorants (*Phalacrocorax capensis*) were on the island (Duffy *et al.* 1984). In 1979, 5 784 kelp gulls nested (Crawford *et al.* 1982). Thus during the period considered here Dassen Island was used by at least 140 000 birds.

## Methods

Work on the island was carried out for 14 months between March 1979 and June 1980, between 3 and 26 March 1981 and between 23 February and 11 March 1982. Cats were counted by a modification of Boguslavsky's (1956) method (Apps 1983). A minimum value for the number of cats dying each year was calculated from the number of cats present in year  $t$  less the number of adults present in year  $t+1$  since if mortality had been zero all cats present in year  $t$  would still have been present in year  $t+1$ . The specific natality rate

(according to Odum 1971, p. 169) was calculated as the number of kittens surviving long enough to be sighted (6-8 weeks, at which age they emerged from their dens) divided by the number of adults present. All calculations employ median values for cat numbers.

Cat scats ( $n = 605$ ) were collected and examined for food remains. Representation indices and kill frequencies were based on examination of 282 prey and carrion carcasses (Apps 1983) and were used to calculate the cats' diet and the numbers of prey killed (Apps 1981, 1983). The cats' behaviour was observed directly, and indirectly by radio tracking, with a total of 1 780 cat sightings for the three field work sessions. In March 1982 the number of rabbits on the island was estimated by counting on a transect 1.6 km long and 100 m wide running through an approximately representative subset of the island habitat. The transect was walked on 4 successive days.

## Results

Between May 1979 and March 1982 the number of feral cats on Dassen Island (excluding household pets) increased from

20-25 to 98-115 (Fig. 1). The annual rate of increase in cat numbers declined from 91 per cent to 41 per cent, the mortality rate (deaths per year per hundred cats) increased from at least 14 per cent to at least 52 per cent and the specific natality decreased from 105 per cent to 93 per cent (Fig. 2). Between March 1982 and May 1985 the number of cats decreased by approximately 50 per cent to slightly below its March 1981 level (Berruti, this volume). In 1979-1980 all adult female cats ( $n = 7-10$ ) produced at least one litter and 2-3 of them produced two litters (Apps 1983). The peak of births coincided with a seasonal increase in food availability (Apps 1981). Mean litter size at age 8 weeks was 2.7 ( $n = 7$  litters, range 2-4). From 1980 to 1982 there was a decline in the proportion of the cat population made up by subadults and an increase in the proportion made up by juveniles (<14 weeks old) (Fig. 3). Kitten survival to June 1980 was 80 per cent.

Between 1979 and 1982 the bulk of the cats' diet consisted of rabbits and bird carrion (Table 1). In 1985 rabbits were, at least seasonally, less important (Table 1) (Berruti, this volume). In 1979-1980, 22 per cent of the rabbits and 88 per cent of the birds eaten by the cats were obtained by scavenging rather than hunting (Table 2). The cats depended for 43

Table 1

Annual food intake of feral cats on Dassen Island calculated from occurrence of food remains in scats by applying representation indices and mean carcass weights (Apps 1983). Stomach contents are from 45 cats shot by the Sea Fisheries Institute in May 1985 (Berruti, this volume).

Food type	Mean number of carcasses eaten annually by each cat			Mean mass of meat (kg) eaten annually by each cat			No. of stomachs with food type
	1979-80	1980-81	1981-82	1979-80	1980-81	1981-82	
Rabbit, adult	35	26	24	41.6	30.8	29.3	
Rabbit, young	45	27	14	12.1	7.4	3.8	7
Rabbit, unaged	55	59	56	40.5	43.5	41.1	
Rabbit, total				94.1	81.7	74.2	
Mouse	24	37	44	0.6	0.9	1.1	8
Penguin, adult	26	26	12	37.1	36.5	17.5	
Penguin, chick (fledged)	5	3	4	3.1	2.3	3.5	24
Penguin, hatchling	6	0	6	0.4	0.0	0.4	
Penguin, total				40.6	38.8	21.4	
Cormorant, adult	5	19	9	3.3	13.4	6.8	
Cormorant, chick	20	47	76	14.5	34.0	55.1	
Cormorant, total				17.8	47.4	61.9	
Gulls/Terns	23	18	34	27.6	22.1	41.2	
Downy chicks	4	7	2	1.1	2.2	0.4	
Unidentified birds	6	7	3				3

Table 2

Feral cat predation pressure on vertebrate prey on Dassen Island each year 1979-1982. Calculated by applying kill frequencies (Apps 1983) to annual intake of carcasses (Table 1). Figures have been rounded to the nearest whole number.

Prey type	Mean number of prey killed by each cat			Total number of prey killed		
	1979-1980	1980-1981	1981-1982	1979-1980	1980-1981	1981-1982
Rabbit, adult	23	17	16			
Rabbit, young	39	24	12	2 231	3 217	3 979
Rabbit, unaged	43	46	43			
Mouse	24	37	44	510	1 361	2 423
Penguin, adult	0	0	0			
Penguin, chick (fledged)	0	0	0	64	0	135
Penguin, hatchling	3	0	2			
Cormorant, adult	1	2	1			
Cormorant, chick	3	6	10	85	316	620
Gulls/Terns	3	2	4	64	88	248
Downy chicks	5	3	1	106	105	32
Unidentified birds	1	1	1	21	34	26

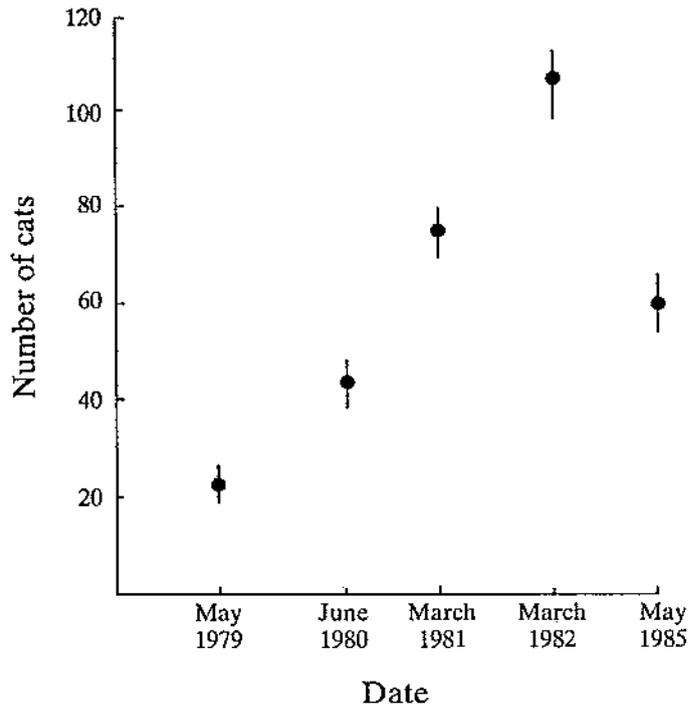


Fig. 1. Numbers of cats on Dassen Island (excluding house pets). From 1979-1982 numbers were estimated by Boguslavsky's method, vertical bars are limits of errors due to uncertain recognition of cats. Numbers for 1985 are from shooting and estimate of number remaining (Berruti, this volume).

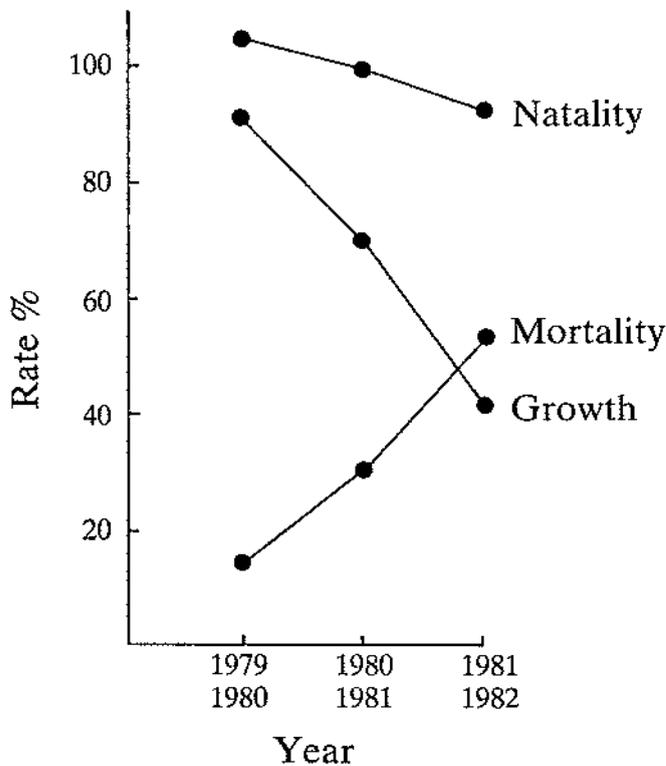


Fig. 2. Rates of; growth in numbers, mortality (deaths per year per hundred cats) and specific natality (births per year per hundred cats) of feral cats on Dassen Island between 1979 and 1982 calculated from median values of numbers of cats present.

per cent of their diet on rabbits and for 49 per cent on bird carrion.

The adult cats on Dassen Island were solitary; 93 per cent of sightings of adults were of lone cats. Subadults (14 weeks to 10 months old) formed temporary groups of variable size (2-6 cats) (Apps 1981). Cats of all ages occupied home ranges with areas between 11 and 63 ha, any given area was shared by approximately 12 cats and no territorial behaviour was observed (Apps 1986 in press).

Kittens accompanied their mothers (or 'aunts') on foraging trips from an age of eight weeks. Kittens which became separated from their families temporarily joined other family groups. Half (4/8) of the kittens and all (5/5) of the families studied intensively took part in such fostering relationships (Apps 1981). Kittens became independent at 14-16 weeks of age. Independent subadults foraged for carrion communally in groups of up to six and shared large carcasses such as those of adult penguins. Groups were short lived and unstable in size and membership (Apps 1981). Except for disputes over food all interactions between adult, male cats and kittens or subadults less than 6 months old were either neutral or friendly (Apps 1981). No evidence was found for infanticide by adult males.

The number of rabbits above ground in March 1982 was  $799 \pm 160$  (Fig. 3) ( $n = 4$  counts).

## Discussion

Of the interacting effects on the ecology of Dassen Island resulting from man's interference those which most directly affect the feral cats are: the introduction and reintroduction of the cats themselves; heavy cat mortality from culling and rapid growth in numbers when it was temporarily discontinued; introduction and reintroduction of rabbits and mice; and heavy mortality of birds due to depletion of fish stocks (Shelton *et al.* 1984) leading to the presence on the island of large quantities of carrion.

That the widespread dispersal of the domestic cat by man depends on the cat's domestic status can be seen by comparing the cat's record of introduction to islands with that of wild felids; none of which have been introduced to any island. Domestication is thus an exaptation (Gould & Vrba 1982) to dispersal to islands with human residents or visitors.

Domestic cats are seasonally polyoestrous which leads to peaks of births in spring and early summer (Van Aarde 1978, Liberg 1980). Thus their seasonality of breeding on Dassen Island was an exaptation.

Where a wide range of potential food is available e.g. in temperate areas, free ranging cats select a diet of small rodents, lagomorphs, birds, insects and carrion (McMurry & Sperry 1941, Toner 1956, Pearson 1964, Liberg 1980). Approximately 80-90 per cent of this diet is made up of items smaller than 100 g and 70-90 per cent of it is mammals. The Dassen Island cats' diet was biased towards large items; 99 per cent weighed more than 100 g. While the cats had successfully altered their diet to include large mammal prey and bird carrion they showed only partial adaptation to the abundance of live birds on the island. Live birds outnumbered rabbits by approximately 140:1 but hunted birds contributed only 20 per cent as much to the cats' diet as hunted rabbits - a bias of 700:1 in favour of rabbits as prey. Plainly the Dassen Island cats had not altered their hunting behaviour to the taking of the fiercely defensive birds which make up the majority of the island's avifauna. This may be because such an alteration was rendered unprofitable by the occurrence of rabbits, because of phylogenetic inertia (Wil-

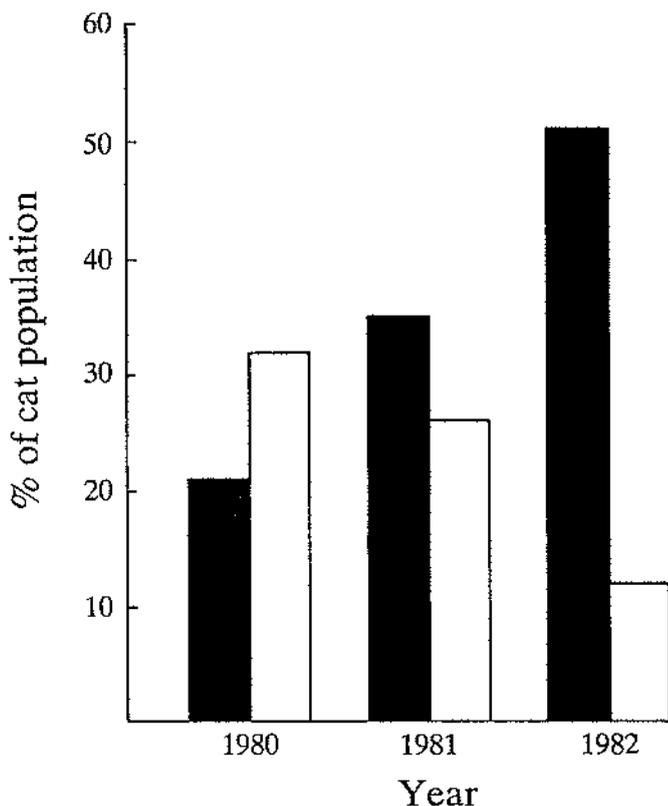


Fig. 3. Proportion of cat population on Dassen Island made up by juveniles (<14 weeks old) (black) and subadults (14 weeks - 10 months old) (white) in March each year.

son 1975, p. 33) or because of conservative cultural transmission of behavioural traits (Mainardi 1980). Where live birds are almost the only available prey cats do not prey on the more aggressive species (Van Aarde 1980). Not surprisingly large, fiercely defensive birds are not a favoured or readily available prey of feral cats.

Where food is freely available cats are able to reach very high densities (100-2 350 cats km<sup>-2</sup>) despite heavy kitten mortality from infectious disease (Dards 1978, Oppenheimer 1980, Izawa *et al.* 1982). That the number of cats on Dassen Island halved between 1982 and 1985 despite the presence of 140 000 birds is a further indication that those birds were not available as food. It would appear that large numbers of feral cats could exist on Dassen Island only because man's interference resulted in the availability of rabbits and large quantities of bird carrion.

Free ranging or feral cats typically occupy home ranges whose size is dependent on both food availability and cat density (Dards 1978, Macdonald & Apps 1978, Corbett 1979, Izawa *et al.* 1982). The ranging behaviour of the cats on Dassen Island fits this pattern and is appropriate to the local resource distribution (Emlen 1980).

Nomadism of young kittens, kitten fostering by solitary females and communal foraging by subadults have not been recorded for feral cats other than those on Dassen Island and appear to be adaptations to conditions on the island. It was easier for a female to bring kittens to food than to carry a large carcass back to them. Separation of kittens from their mothers was, at least partly, due to this practice. Three days isolation was sufficient to kill a kitten (Apps 1981) and although its selective basis was uncertain (Apps 1981) fostering presumably enhanced kitten survival. Group foraging is

more effective than a solitary strategy when food patches are rich, scattered and distributed unpredictably in space and time (Emlen 1980) as were the carcasses exploited by the subadult cats. The loose structure of the foraging groups compared to that of groups of cats around predictable food sources (Macdonald & Apps 1978) and their members' ready reversion to the more typical solitary foraging indicate an incomplete adaptation to the resource distribution on Dassen Island.

Fast rearing and early weaning of offspring are expected to be the result of a high, unpredictable adult mortality rate (Warner 1980) such as would arise from intermittent culling. Such a breeding pattern would contribute to fostering and communal foraging (Apps 1981). Rapid population turnover or growth rate will have increased the percentage of primiparous females and the resultant delay in the time of breeding (Apps 1981) may account for at least part of the observed alteration to the age distribution among juveniles and subadults (Fig. 3) and for the slight drop in specific natality (Fig. 2). The effects of cat culling, the presence of rabbits and the abundance of bird carrion have had interacting effects; e.g. weaning of kittens before they were old enough to hunt rabbits was viable only because bird carrion was available.

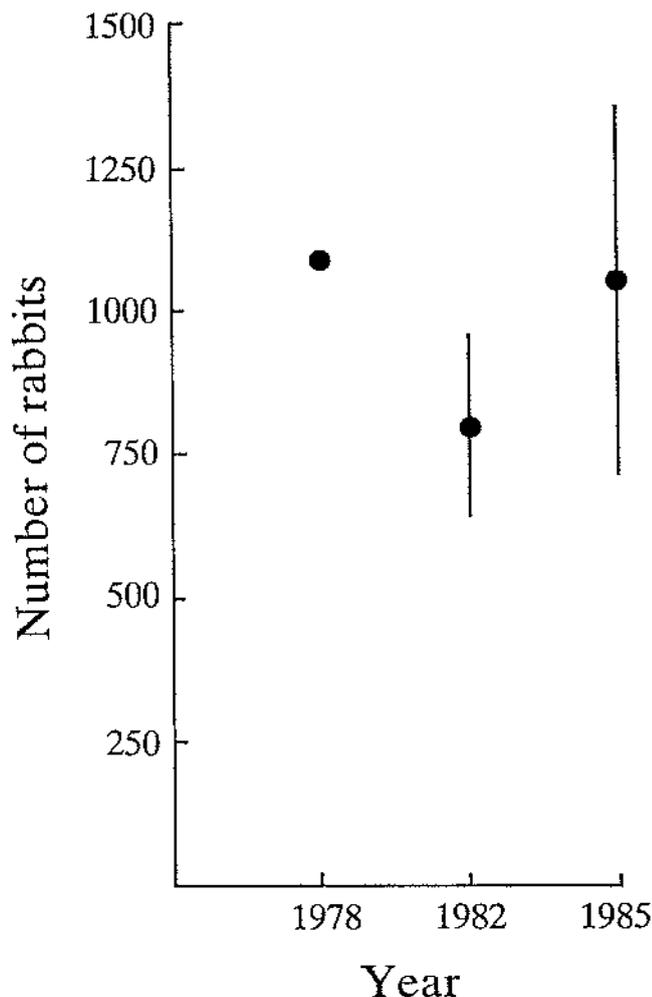


Fig. 4. Number of rabbits (*Oryctolagus cuniculus*) above ground on Dassen Island. Figure for 1978 from transect of indefinite width (R. van Aarde, pers. comm.), for 1982 from 1.6 km × 100 m transect ( $\pm$  S.D.) and for 1985 from ratio of rabbit sightings to cat sightings (Berruti, this volume).

The selective basis of the relationship between adult males and kittens or subadults was unclear (Apps 1981). Nevertheless the absence of infanticide will have enhanced kitten survival, especially since the population was dense, leading to frequent adult-kitten encounters, and the adult females were solitary, precluding group defence against infanticidal males (Macdonald *et al.* in prep.).

## Conclusions

Domestic cats were exapted to the severely disturbed habitat on Dassen Island by their domestic status, the seasonality of their breeding and their rapid rearing of offspring. As carnivores they were exapted to the exploitation of feral rabbits and birds and in their diet, foraging behaviour and social behaviour they were adapted to the hunting of large mammal prey and to scavenging the carcasses of birds. The cats were ill-adapted to hunting the fiercely defensive birds which make up most of the island's avifauna and the number of cats suffered a decline despite live birds being present in large numbers. Because they were unable to exploit live birds effectively the presence of large numbers of cats on Dassen Island depended on the presence, as a result of man's interference, of feral rabbits and bird carrion.

## Acknowledgements

The Sea Fisheries Research Institute, the Department of Transport, the Council for Scientific and Industrial Research and the Department of National Education are thanked for their support of various aspects of this work, which was carried out under the auspices of the Mammal Research Institute, University of Pretoria.

## References

- APPS, P.J. 1981. Behavioural ecology of the feral house cat (*Felis catus* Linnaeus) on Dassen Island. M.Sc. thesis, Univ. of Pretoria.
- APPS, P.J. 1983. Aspects of the ecology of feral cats on Dassen Island, South Africa. *S. Afr. J. Zool.* 18: 393-399.
- BOGUSLAVSKY, G.W. 1956. Statistical estimation of the size of a small population. *Science* 124: 317-318.
- BROOKE, R.K. & CROWE, T.M. 1982. Variation in species richness among offshore islands of the southwestern Cape. *S. Afr. J. Zool.* 17: 49-58.
- COOPER, J., HOCKEY, P.A.R. & BROOKE, R.K. 1985. Introduced mammals on South and South West African islands: history, effects on birds and control. In: Proceedings of the symposium on birds and man, Johannesburg 1983. Ed. L.J. Bunning, Witwatersrand Bird Club, Johannesburg, pp. 179-203.
- CORBETT, L.K. 1979. Feeding, ecology and social organisation of wild cats (*Felis silvestris*) and domestic cats (*Felis catus*) in Scotland. Ph.D. thesis, Univ. of Aberdeen.
- CRAWFORD, R.J.M., COOPER, J. & SHELTON, P.A. 1982. Distribution, population size, breeding and conservation of the kelp gull in southern Africa. *Ostrich* 53: 164-177.
- DARDS, J.L. 1978. Home ranges of feral cats in Portsmouth Dockyard. *Carniv. Genet. Newsl.* 3: 242-255.
- DUFFY, D.C., BERRUTI, A., RANDALL, R.M. & COOPER, J. 1984. Effects of the 1982-3 warm water event on the breeding of South African seabirds. *S. Afr. J. Sci.* 80: 65-69.
- EMLEN, S.T. 1980. Ecological determinism and sociobiology. In: Sociobiology: beyond Nature/Nurture? Eds G.W. Barlow & J. Silverberg. Westview Press, Boulder, Colorado, pp. 125-150.
- FROST, P.G.H., SIEGFRIED, W.R. & COOPER, J. 1976. Conservation of the jackass penguin (*Spheniscus demersus*). *Biol. Conserv.* 9: 79-99.
- GOULD, S.J. & VRBA, E.S. 1982. Exaptation - a missing term in the science of form. *Paleobiology* 8: 4-15.
- IZAWA, M., DOI, T. & ONO, Y. 1982. Grouping patterns of feral cats (*Felis catus*) living on a small island in Japan. *Jap. J. Ecol.* 32: 373-382.
- LIBERG, O. 1980. Predation and social behaviour in a population of domestic cat. An evolutionary perspective. Ph.D. thesis, Univ. of Lund.
- MACDONALD, D.W. & APPS, P.J. 1978. The social behaviour of a group of semi-dependent farm cats *Felis catus*, a progress report. *Carniv. Genet. Newsl.* 3: 256-268.
- MAINARDI, D. 1980. Tradition and the social transmission of behaviour in animals. In: Sociobiology: beyond Nature/Nurture? Eds G.W. Barlow & J. Silverberg. Westview Press, Boulder, Colorado, pp. 227-256.
- MCMURRY, F.B. & SPERRY, G.C. 1941. Food of feral house cats in Oklahoma. *J. Mammal.* 22: 185-190.
- ODUM, E.P. 1971. Fundamentals of Ecology. IIIrd edition. W.B. Saunders co., Philadelphia.
- OPPENHEIMER, E.C. 1980. *Felis catus* population densities in an urban area. *Carniv. Genet. Newsl.* 4: 72-80.
- PEARSON, O.P. 1964. Carnivore-mouse predation. An example of its intensity and bioenergetics. *J. Mammal.* 45: 177-188.
- SHELTON, P.A., CRAWFORD, R.J.M., COOPER, J. & BROOKE, R.K. 1984. Distribution, population size and conservation of the jackass penguin *Spheniscus demersus*. *S. Afr. J. Mar. Sci.* 2: 217-257.
- SKEAD, C.J. 1972. Van Riebeeck started game ranching with daisies at Robben Island. *Afr. Wildl.* 26 (2): 54-57.
- SKEAD, C.J. 1980. Historical Mammal Incidence in the Cape Province, vol. I. Cape Provincial Department of Nature and Environmental Conservation, Cape Town.
- TONER, G.C. 1956. House cat predation on small mammals. *J. Mammal.* 37: 119.
- VAN AARDE, R.J. 1978. Reproduction and population ecology in the feral house cat *Felis catus* on Marion Island. *Carniv. Genet. Newsl.* 3: 288-316.
- VAN AARDE, R.J. 1980. The diet and feeding behaviour of feral cats, *Felis catus* at Marion Island. *S. Afr. J. Wildl. Res.* 10: 123-128.
- VAN AARDE, R.J. & SKINNER, J.D. 1982. The feral cat population on Marion Island: characteristics, colonisation and control. Colloque sur les Ecosystemes Subantarctique 1981. Paimpont. *C.N.F.R.A.* 51: 281-288.
- WARNER, R.R. 1980. The co-evolution of behavioural and life history characteristics. In: Sociobiology: beyond Nature/Nurture? Eds G.W. Barlow & J. Silverberg. Westview Press, Boulder, Colorado, pp. 151-188.
- WILSON, E.O. 1975. Sociobiology, the New Synthesis. Belknap Harvard Press, Cambridge, Mass.