EFFECTS OF FELINE PANLEUCOPAENIA ON THE POPULATION CHARACTERISTICS OF FERAL CATS ON MARION ISLAND

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SUMMARY

(1) This paper evaluates the effects of the artificial introduction of feline panleucopaenia (FPL) as a primary control measure of a feral cat population on the sub-Antarctic Marion Island (46°54′S, 37°45′E).

(2) The population decreased from an estimated 3409 cats in 1977 (introduction of control factor) to 615 (S.E. = 107) cats during 1982, suggesting an annual rate of decrease of 29%.

(3) Litter size decreased and the age structure changed significantly because of a decrease in subadult numbers. Age specific mortality rates were higher but followed the same pattern as in 1975 because there were fewer subadults but the same age structure of adults.

(4) The intrinsic rate of increase, as suggested by the survival and fecundity schedules of the population, was higher in 1975 owing to a greater proportion of adults and a higher fecundity in age class II.

(5) Antibody titres of FPL were lower in 1982 than in 1978 which illustrates that FPL did affect the cat population but is no longer spreading effectively. FPL was independent of feline herpes (FVR), an endemic disease of the cat population, and FPL was, therefore, directly responsible for the decrease in cat population density.

(6) During 1982 the cat population showed a decrease of 8% year^{-1}, which indicates stabilizing of the negative growth rate. This observation was supported by lower titres of FPL.

INTRODUCTION

The accidental and/or deliberate introduction of exotic predators to islands has severely affected indigenous bird populations. The estimated 2139 (S.E. = 290) descendants of a founder group of five feral cats (*Felis catus* Linn.), introduced to Marion Island in 1949, were killing some 450 000 petrels (Family Procellariidae) each year by 1975. The predicted annual increase of the number of birds killed was equalled by the observed population increase of cats of *c.* 23% year^{-1} (van Aarde 1978, 1980). In order to control the susceptible and isolated population of cats, feline parvo virus was introduced during 1977 in an attempt to create an epidemic of the disease feline panleucopaenia (FPL).

The properties and epidemiology of FPL in relation to the Marion cat population have been outlined by Howell (1984). FPL is a highly contagious, host-specific disease, mainly of domestic cats, where morbidity in a susceptible population often approaches 100%. High mortality rates are most prevalent amongst kittens. The virus is excreted in high concentrations in faeces, urine, saliva and vomit, is resistant to many chemicals and has a wide temperature tolerance. Transmission usually occurs through direct contact between susceptible and infected cats but can also occur indirectly through contact with contaminated objects (Fastier 1968; Gillespie & Scott 1973).

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Marion Island (46°54'S, 37°45'E) is a sub-Antarctic island of approximately 290 km² in the Southern Indian Ocean. It is of volcanic origin with a tundra biota experiencing low temperatures and strong winds (Huntley 1967; Verwoerd 1971; Schulze 1971).

In the present paper we evaluate the hypothesis that FPL is an effective control measure by comparing the population characteristics of cats in 1975, before introduction of FPL, with those in 1982 following introduction of the virus in an attempt at biological control of the cats to conserve the avifauna.

MATERIALS AND METHODS

Characteristics for the 1982 population were derived from material and information obtained between April 1981 and May 1983, these being collected and analysed as described for the 1975 population (van Aarde 1978, 1979, 1983; van Aarde & Robinson 1980). The data collected by van Aarde during 1975 were used as a control.

Density and population estimates were extrapolated from data collected in a study area of 32·8 km², which was stratified into a coastal (0–100 m a.s.l.) and an interior zone (100–450 m a.s.l.), and divided into equal sized (0·67 km²) grid blocks (van Aarde 1979). The area was surveyed on foot at monthly intervals and individual identification was based on coat colour patterns and body size. Resightings were excluded from the data and population size ($\hat{Y}$) was estimated as

$$\hat{Y} = \sum_i N_i \bar{y}_i$$

where N_i is the total number of grid blocks in the ith zone and $\bar{y}_i$ is the average number of cats in each of the sampled grid blocks. The standard error of $\hat{Y}$ was obtained using

$$\text{var } \hat{Y} = \sum_i \frac{N_i (N_i - n_i)}{n_i} S^2_{y_i}$$

where

$$S^2_{y_i} = \frac{1}{(n_i - 1)} \sum_i (y_{ij} - \bar{y}_i)^2$$

y_{ij} is the number of cats in the jth observed grid block of the ith zone and n_i is the number of sampled grid blocks (Jolly 1969). Estimates of population growth rate (r) are based on the exponential function $N_t = N_0 e^{rt}$ where N_t is the population size at time t, N_o is the population size at time zero and e is the base of natural logarithms (Caughley 1977).

All cats were grouped into age classes, according to body size, as adult, subadult and juvenile (van Aarde 1978). Coat colour phenotypes were scored as described by van Aarde & Robinson (1980). Reproductive status was recorded and the skull and serum were collected from cats culled between January and May 1982 and between October 1982 and May 1983. Age determination of cats with a permanent dentition was based on counts of cementum lines in teeth (van Aarde 1983). Population parameters were estimated as discussed in van Aarde (1983). The Leslie type of fecundity (F_x) was used where $F_x = m_x \cdot l_1$. F_x is the number of female offspring produced per female in each age class that will survive to enter the first age class, m_x is the age specific fecundity and l_1 is the
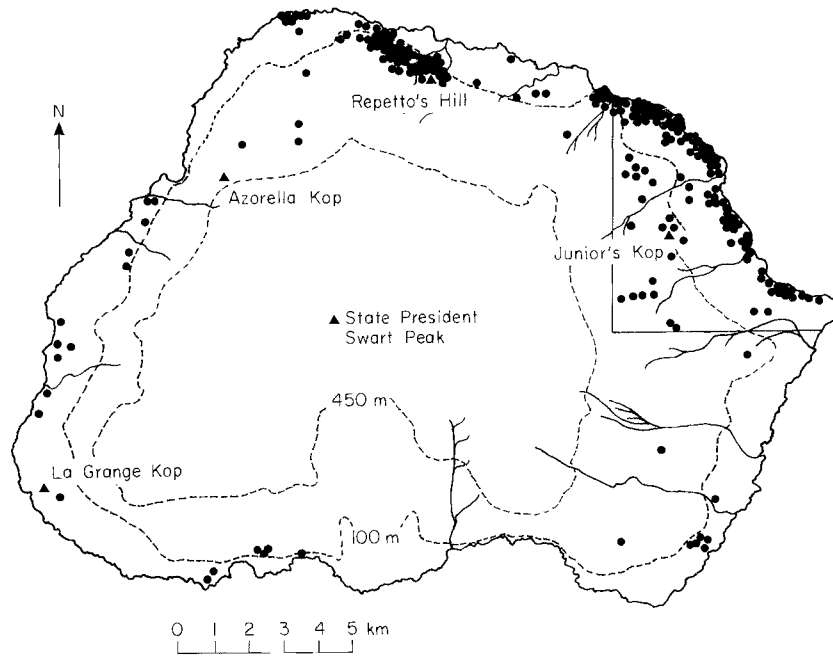
FIG. 1. Distribution of feral cats on Marion Island (46°54′S, 37°45′E) in 1982 based on 258 sightings.

probability that newborn will survive to enter the first age class (Michod & Anderson 1980), l_1 being estimated as

$$\frac{\text{prenatal litter size}}{\text{post-weaning litter size}},$$

based on the assumption that the litter size at birth = prenatal litter size. The intrinsic rate of-increase (r) was calculated from:

$$\lambda = \sum_{x=1}^{n} \frac{N_x F_x}{N_1},$$

where N_x is the number of animals in age class x, N_1 is the number of animals in age class 1 and F_x is Leslie's age specific fecundity and where $r = \ln \lambda$ (Michod & Anderson 1980). The statistics l_x, s_x, p_x and q_x were estimated according to Caughley (1977). Age frequencies were corrected by assigning cats collected during the 1982–83 season to the 1981–82 season (observed age − 1). Correction of age frequencies is based on the assumption of an equal sampling intensity during the study period. Age frequencies were smoothed using a log-polynomial function following Caughley (1977).

Serum samples were analysed for antibodies of FPL with the haemagglutination inhibition test and for antibodies of feline herpes (feline viral rhinotracheitus, FVR) with the serum neutralization test (Johnson 1971).

TABLE 1. The Marion Island cat population size estimated from densities derived from the selected study area (N_i is the total number of grid blocks, n_i is the number of grid blocks surveyed, y_i is the average number of cats per grid block, $\hat{Y}$ is the population size and var $\hat{Y}$ = variance)

Zone	(N_i)	(n_i)	(y_i)	($\hat{Y}$)	(var $\hat{Y}$)
Coastal	148	29	3·00	444·00	8545·72
Interior	202	20	0·85	171·70	2955·63
Total	350	49		615·70	11501·35

$$\sqrt{11501·35} = 107.24$$

TABLE 2. Age structure of the 1975 (control) and 1982 cat populations of Marion Island based on field observations of cats

	1975		1982		χ^2
	Number	Percentage	Number	Percentage	
Juvenile	76	11·4	20	9·8	0·24
Subadults	163	24·5	15	7·4	22·72
Adults	425	64·0	168	82·7	7·90
Total	664		203		30·86

RESULTS

Between December 1981 and March 1983, 258 cat sightings were made on Marion Island (Fig 1); 134 of these represented 104 different individuals within the defined study area. The 1982 population was estimated at 615 (S.E. = 107) cats (Table 1), a decrease of 29% year^{-1} ($\bar{r}$ = −0·343) since the introduction of FPL in 1977 when the population numbered 3405 cats (van Aarde 1978). Population estimates for 1981–82 and 1982–83 for a comparable part of the study area were 577 (S.E. = 122) and 531 (S.E. = 115) respectively, a decrease of 8% year^{-1} ($\bar{r}$ = −0·083), which was not significant (t = 1·47).

The population's age structure changed significantly (χ_2^2 = 30·86; $P < 0·005$) from 1975 to 1982 (Table 2), with subadult numbers decreasing (χ_1^2 = 22·72; $P < 0·005$) and adult numbers increasing (χ_1^2 = 7·90; $P < 0·005$).

The age distribution of the 1981–82 and 1982–83 samples did not differ (χ_7^2 = 13·39) and it was assumed that the population's age distribution was stable. These age frequencies were, therefore, grouped together (observed), corrected and smoothed (Table 3). Sex specific age distribution for the observed and corrected frequencies did not differ significantly (χ_7^2 = 10·26 and 4·64 for males and females, respectively). Similarly, there were no differences between the age distributions of the sexes of the corrected frequencies (χ_7^2 = 10·99). The smoothed and corrected frequencies also did not differ significantly (χ_7^2 = 3·49). The age distributions of the 1975 and 1982 populations did not differ significantly (χ_7^2 = 10·87) from each other (Fig. 2). However, the ratio of subadults (age class I) to adults (age classes II–IX) differed significantly (χ_1^2 = 5·02; $P < 0·05$, Fig. 2).

Litter size at birth was unknown but mean prenatal litter size was 4·50 (S.E. = 1·7; n = 8) and did not differ from the 1975 (control) value of 4·59 (S.E. = 1·12). The mean 4·56 (S.E. = 1·29) of the two subsamples was, therefore, used in all computations. Litter size at

TABLE 3. Age distribution of the 1982 population on Marion Island

Age class	Observed Males	Observed Females	Corrected Males	Corrected Females	Total	Smoothed
I (4–12 months)	11	11	22	11	33	27·3
II (1 year)	21	11	11	4	15	20·5
III (2 years)	7	5	7	7	14	16·7
IV (3 years)	9	8	10	10	20	14·2
V (4 years)	8	12	6	10	16	12·2
VI (5 years)	7	11	2	6	8	10·0
VII (6 years)	1	5	2	4	6	7·6
VIII (7 years)	2	1	2	4	6	5·1
IX (8 years)	1	3				2·9*

* Based on extrapolation from the log-polynominal function, $N_x = 1·439 - 0·151x^1 + 0·028x^2 - 0·003x^3$ ($r = 0·900$), used to smooth age distribution.
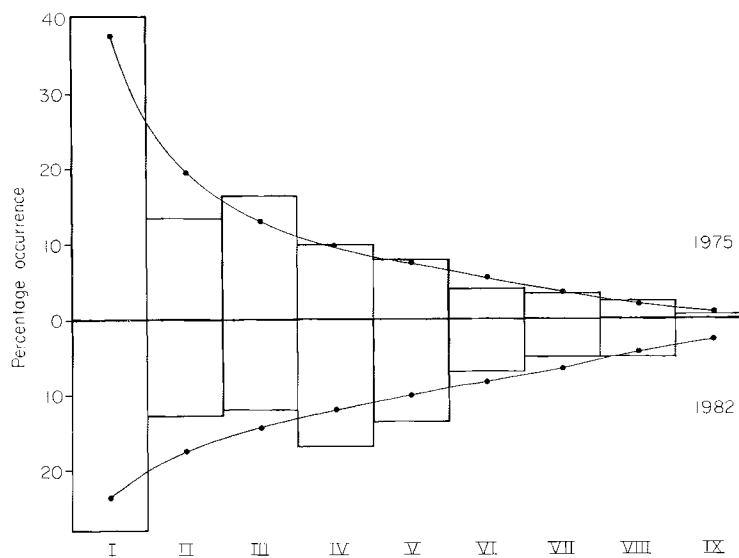

FIG. 2. Age structure of the 1975 (control) and 1982 cat populations of Marion Island.

weaning decreased from 2·66 (S.E. = 0·76) in 1975 to 1·65 (S.E. = 0·71) in 1982 ($t_{70} = 5·80$; $P < 0·005$). The birth season lasted from mid-September to mid-March (mean date of birth = 30 December (S.E. = 80 days)) with adult females producing two litters per season.

The age specific fecundity (F_x) schedules based on litter size and the frequency of pregnant and lactating females in each age class during the breeding season are provided in Table 4. This indicates that 93·6% of all females collected during the breeding season were reproductively active, and mean age specific fecundity (F_x) was estimated as 1·54 surviving female births per female per season for all reproductive age classes. Age specific fecundity was lower during 1975 for age classes II, VIII and IX and higher for age classes

TABLE 4. Observed age-specific reproductively active females during the breeding season of the cat population on Marion Island

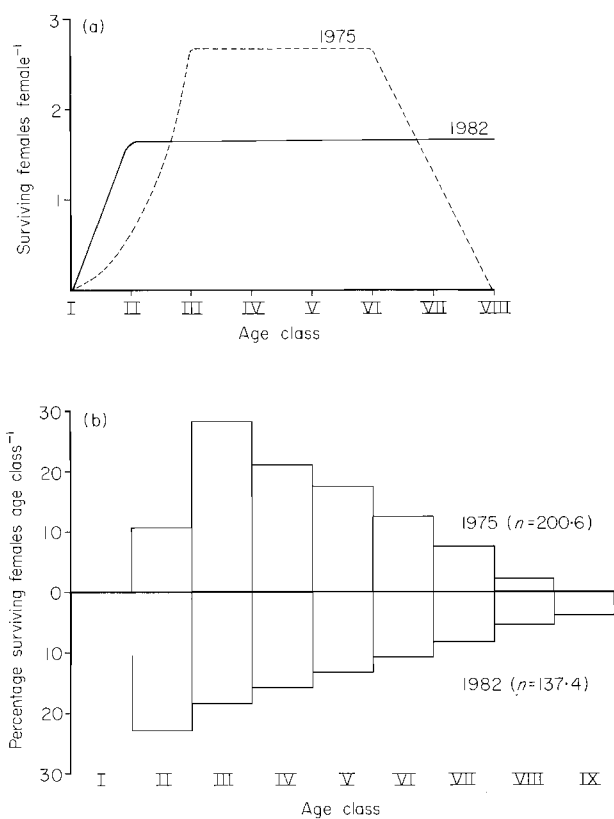| Age class	Percentage	n
I	0	
II	100·0	5
III	100·0	5
IV	100·0	4
V	80·0	5
VI	85·7	7
VII	100·0	4
VIII	—	0
IX	100·0	1
Total		31

FIG. 3. Age-specific fecundity of the control and 1982 cat populations of Marion Island.

III–VII than in 1982 (Fig. 3a). Age class II had the highest reproductive output of all age classes in 1982, whereas in 1975, age class III was the highest (Fig. 3b).

Intrinsic rate of increase (r) for 1982 was 1·608, and probabilities of surviving (l_x), or dying (d_x), and survival (p_x) and mortality rates (q_x) based on $\bar{r} = -0.083$ and an assumed stable age distribution are presented in Table 5.

Table 5. Life table statistics for the 1982 cat population on Marion Island ($\bar{r} = 0.083$) (x is the age class, f_x is the smoothed age frequency, l_x is the probability of surviving, d_x is the probability of dying, p_x is the survival rate and q_x is the mortality rate)

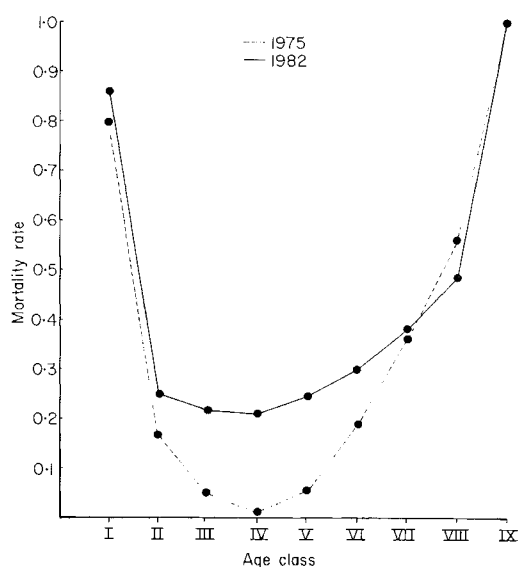| x	f_x	l_x	d_x	p_x	q_x
I	137·4*	1·0000	0·8627	0·1373	0·8627
II	20·5	0·1373	0·0343	0·7502	0·2498
III	16·7	0·1030	0·0224	0·7825	0·2175
IV	14·2	0·0806	0·0169	0·7903	0·2097
V	12·2	0·0637	0·0156	0·7551	0·2449
VI	10·0	0·0481	0·0145	0·6985	0·3015
VII	7·6	0·0336	0·0128	0·6190	0·3810
VIII	5·1	0·0208	0·0099	0·5240	0·4760
IX	2·9	0·0109	—	0·0000	1·0000

* Estimated from fecundity rates.

Fig. 4. Mortality rates of the cat populations on Marion Island in 1975 and 1982.

Mortality rates decreased after the first year, remaining relatively constant until age class V when they started to increase to attain a value of 1·0 in age class IX (Fig. 4).

The ratio of susceptible to immune cats (for FPL) did not change from 1978 to 1982 ($\chi_1^2 = 0.53$). However, antibody titres did change significantly ($\chi_6^2 = 28.59$; $P < 0.005$), with a decrease in the frequency of the high antibody titres (1 : 512) to lower titres (1 : 32) from 1978 to 1982 (Table 6). During 1982 most (65%) adult females had titre values of 1 : 128 to 1 : 1024, with c. 21% having titres from 1 : 16 to 1 : 64, and 14% being susceptible (Table 7). FVR antibody titres changed significantly from 1976 (before the introduction of FPL) to 1978 ($\chi_2^2 = 8.09$; $P < 0.025$). This was due to an increase in the frequency of higher antibody titres, although it decreased again from 1978 to 1982 (Table 6). However, this

TABLE 6. The frequency of FPL and FVR antibody titres of the cat population on Marion Island

Year	FPL antibody titres									
	0	16	32	64	128	256	512	1024	2048	4096
1978	12	0	1	7	9	9	10	5	2	2
1982	19	5	22	23	17	13	15	1	0	0

Year	FVR antibody titres													
	0	2	5	10	15	20	25	30	40	60	75	80	125	375
1976*	14	1	—	2	—	4	—	1	3	1	—	3	—	—
1978	22	—	1	—	6	—	8	—	—	—	10	—	6	8
1982	35	—	11	—	—	—	29	—	—	—	—	—	13	—

* Before the introduction of FPL.

TABLE 7. Percentage of FPL antibody titres of the adult female cats on Marion Island in 1982 ($n = 43$)

Titres	0	16	32	64	128	256	512	1024
Percentage	14·0	2·3	7·0	11·6	18·6	25·6	18·6	2·3

TABLE 8. The frequency of phenotypes of the 1975 and 1982 cat populations on Marion Island

Year	Non-agouti a	Agouti a$^+$	Tabby t^b	t$^+$	Dilution d	d$^+$	Piebald S	s$^+$
1975*	530	113	37	76	11	645	192	464
1982	217	41	16	31	1	257	70	188
χ^2	0·37		0·03		2·38		0·41	

* van Aarde & Robinson (1980).

decrease was not significant ($\chi^2_2 = 5\cdot96$). There was also no significant change in the immune and susceptible cats between 1976 and 1978 ($\chi^2_1 = 1\cdot22$) and between 1978 and 1982 ($\chi^2_1 = 0\cdot39$); FPL and FVR were independent of each other in the proportion of immune and susceptible cats in 1982 ($\chi^2_1 = 2\cdot00$). The frequency of occurrence of the different phenotypes also did not change significantly from 1975 to 1982 (Table 8).

DISCUSSION

Control of pest species can be achieved only when the rate of control is higher than the population's rate of increase. Conditions prevailing on the sub-Antarctic Marion Island rendered mechanical control methods (i.e. hunting and trapping) ineffective as control measures in the short term with such a large population of cats (van Aarde & Skinner 1981). The successful deliberate introduction of a virulent strain of feline parvo virus to the island in an attempt to create an epidemic disease (Howell 1984) provided an

opportunity to evaluate the effect of such a biological control measure on the demography of a susceptible and isolated feline population.

Earlier analyses on the effect of FPL on the population include the reported reduction in density indices based on information obtained from line transect surveys (van Aarde 1984), and a decrease in postweaning litter size (Howell 1984). The most conspicuous change that has taken place in the population was a drastic decrease in density as estimated from intensive surveys of selected stratified grids sampled before and after the introduction of FPL. Criteria for the reliability of the method and applicability to the Marion Island situation have been discussed by van Aarde (1979). The distribution pattern of cats around the island was not affected by the viral disease, confirming earlier speculation that the clumped distribution of cats is not a factor of density, but rather of food availability (van Aarde 1980).

Observed changes in the relative (Table 2) and year class (Table 3) age structures of the population resulted from a decrease in subadult numbers. The hypothesis that these changes are due to FPL infection is supported by the fact that morbidity and mortality ɔccur mainly amongst cats < 1 year old (Fastier 1968; Reif 1976).

Kittens from cats with low (1:10 to 1:100) and moderate titres (1:100 to 1:1000) possess maternally derived antibodies for 4–8 and 8–12 weeks, respectively (Scott, Csiza & Gillespie 1970). Since the majority of the 1982 adult females possessed moderate titres (Table 7), it is expected that most of the juveniles that died of FPL were older than three months, resulting in a decrease in subadult numbers. The decrease in postweaning litter size from 1975 to 1982 could, therefore, be the result of kittens losing their maternally derived resistance between 4–8 weeks of age as a result of females having low titres.

Reif (1976) found FPL peaking in occurrence from July to September in Pennsylvania, U.S.A., and concluded that this seasonality and seasonal breeding of cats must be incorporated when constructing an epidemiological model to illustrate the phenomenon of herd immunity. Fox et al. (1971) illustrated that the number of susceptibles and the probability of contact between them determine epidemic potentials in random mixing populations, and that population size does not influence the probability of spread. (Contact rate is the probability that any two animals in a population will make contact which will result in the transmission of an agent from an infectious to a susceptible individual (Fox et al. 1971) or, simply stated by Reif (1976), when the number of susceptibles increases and contact rates remain constant, the number of new cases will increase). This happens 2–3 months after birth when kittens become susceptible, which results in an epidemic of FPL, mainly amongst kittens (Reif 1976). Because of the high juvenile mortality rate and seasonal breeding (van Aarde 1978), a seasonal epidemic of FPL has probably occurred annually on Marion Island since the introduction of the virus.

Since the age distributions of the 1975 and 1982 populations did not differ, the patterns of mortality were similar, but the higher mortality rates in 1982 are due to the lower frequency of cats in age class I. The greater proportion of adults and a higher fecundity of age class II in 1982 resulted in a higher intrinsic rate of population increase than in 1975 ($r_{1975} = 1 \cdot 117$; $r_{1982} = 1 \cdot 608$). The higher fecundity in age classes II, VIII and IX is probably a reaction of the population to the lowered density. Longevity of the Marion Island cats has been estimated at 8 years and it is therefore possible that the lowered fecundity of age classes VIII and IX in 1975 was not age specific but rather due to smaller samples taken in these age classes (e.g. van Aarde (1983) did not collect any females in age class IX). On the other hand, since cats (even females with kittens) changed shelters regularly on Marion Island, breeding shelters could be a limiting factor for age class II females at high densities (e.g. before the introduction of FPL), because of the overlapping home ranges of females.

Fresh carcasses of cats could not be collected and none of the cats shot, caught or sighted, showed clinical symptoms of FPL. The clinical features of FPL (Carpenter 1971) are of such a nature that cats would die in their subterranean shelters. Corpses lying in the open on Marion Island are, furthermore, rapidly scavenged by skuas *Catharacta antarctica* (Mathews), gulls *Larus dominicanus* (Lichtenstein), sheathbills *Chionis minor* (Hartlaub) or giant petrels *Macronectes* spp. Therefore, mortality could not be ascribed directly to FPL. However, the shift from moderate to low titres of FPL illustrates that FPL did affect the cat population but that it no longer spreads as efficiently. Serum samples collected from cats taken from around the island also illustrated that FPL has spread successfully throughout the population. Since FPL and FVR were independent of each other, the increase of antibody titres of FVR after the introduction of FPL could not be ascribed to FPL. As FVR is an endemic disease of the Marion Island cats (Howell 1984), the increase in FVR titres may have been part of a natural fluctuating cycle of the disease. FPL was, therefore, directly responsible for the decrease in cat numbers, but had no selective effect on the cat population's phenotypic profile.

The decrease of 29% year^{-1} over 5 years (1977–82) as compared to 8% year^{-1} over the fieldwork period (1981–82 to 1982–83) suggests that the population may be stabilizing. The shift in antibody titres of FPL supports this conclusion.

Lowered fecundity, a drastic decrease in density, a change in the age structure and a decrease in growth rate illustrated by our analyses indicate that FPL can be used effectively as a biological control measure to reduce the density of susceptible cat populations as part of an effort either to control or to eliminate such populations.

ACKNOWLEDGMENTS

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