

# Demographic parameters of the feral cat *Felis catus* population at Marion Island

R.J. van Aarde

Mammal Research Institute, University of Pretoria

The need to control the feral cat population inhabiting the sub-antarctic Marion Island required the definition of the characteristics of the population. The present paper reports on age determination and age-related population parameters of the population estimated at approximately 2 100 adults in 1975. The number of cementum lines counted in decalcified longitudinal sections of canines changed predictably with age. Combined eye lens mass was not regarded as a reliable indicator of age. Intrinsic rate of natural increase for the seasonally breeding population was 117,3% per year and the population's age structure represented that of an increasing population with 71% of all cats younger than 36 months of age. Age-specific changes in sex ratio are ascribed to the social organization of the species, and the steep increase in mortality rate after the age of 48 months may be owing to the relatively harsh environment in which these cats live.

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Die behoefte om die wilde huiskatbevolking wat die sub-antarktiese Marioneiland bewoon, te beheer, het die bepaling van die kenmerke van die bevolking genoodsaak. Hierdie artikel lewer verslag aangaande ouderdomsbepaling en bevolkingsparameters gebaseer op ouderdom vir die bevolking geskat op ongeveer 2100 volwasse diere in 1975. Die aantal sementumlyne getel in gedekalsifiseerde lengtesnitte van slagtande het voorspelbaar toegeneem met ouderdom. Ooglensmassa is nie beskou as 'n betroubare indikator van ouderdom nie. Die intrinsieke natuurlike groeitempo van die bevolking was 117,3% per jaar en die bevolking se ouderdomstruktuur was verteenwoordigend van 'n toenemende bevolking met 71% van alle katte jonger as 36 maande. Ouderdomspesifieke veranderinge in geslagsverhouding is toegeskryf aan die sosiale organisasie van die spesies en die skielike styging in mortaliteitstempo vir katte ouer as 48 maande, is waarskynlik aan drastiese omgewingsfaktore toe te skryf.

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## Introduction

The presence of established feral domestic cat *Felis catus* L. populations on several southern oceanic islands and the reported destruction of bird populations by exotic predators resulted in the initiation of several independent surveys of cat populations inhabiting subantarctic islands (Derenne 1976; Derenne & Mougouin 1976; Jones 1977; Pascal & Castanet 1978; van Aarde 1978). The research programme on the cats at Marion Island (46°54'S/37°45'E) was designed to investigate the influence of these cats on their prey populations (van Aarde 1980), to define the characteristics of the population, and if deemed necessary, to attempt to either exterminate or control the population (van Aarde & Skinner 1981).

The present day cat population at Marion Island represents the offspring of a founder group of five taken to the island as pets by members of the first meteorological team during 1949. The 1975 population was estimated at  $2139 \pm 290$  (S.E.) adults and ecological densities were  $13,85 \pm 1,37$  and  $4,98 \pm 0,58$  adult cats per km<sup>2</sup> for the coastal and interior regions of the island respectively (van Aarde 1979). Because the cats feed mainly on burrowing petrels (fam. Procellariidae) an estimated 450 000 petrels of seven species must have been killed to provide the minimum energy requirements of the 1975 cat population (van Aarde 1980). This, and the fact that at least three of the 12 petrel species which breed, or are thought to breed on the island, have not been recorded breeding lately, resulted in the decision to attempt either to exterminate or at least to control this exotic predator population.

The implementation of such an effort and the evaluation of its effect(s) on the target population required the definition of some of the characteristics of the population. The present paper, therefore, deals with age-specific population parameters and the estimation of some population statistics such as survival rate, mortality rate and intrinsic rate of increase.

Marion Island is situated in the subantarctic region 2 100 km south-southeast of Cape Town, is volcanic in origin and approximately 290 km<sup>2</sup> in area. The island can be described as a tundra biome and is continuously subjected to low temperatures (annual average 5,0°C), strong westerly winds and a high humidity. The mean annual rainfall is 2576 mm and precipitation is evenly distributed throughout the year

R.J. van Aarde

Mammal Research Institute, University of Pretoria, Pretoria  
0002, Republic of South Africa

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(Shulze 1971).

### Material and Methods

The information and material used in this study were obtained from cats killed between January 1975 and April 1976. Date, sex, relative age based on body size (van Aarde 1978), and standard morphometric data were recorded for all killed cats. Reproductive tracts and skulls of both sexes were collected for later examination and reproductive status was recorded for all females. Age determination was based on tooth eruption for animals younger than eight months (van Aarde 1978), and for cats with a permanent dentition on the number of cementum lines in decalcified longitudinal sections of canines cut at 25  $\mu\text{m}$  using a cryostat and stained with Carrazzi's haemotoxylin. The validity of these lines as an indication of age was based on three known-age individuals that were respectively 10, 18 and 31 months old. All cats with a deciduous or partly deciduous dentition, or completely open-rooted permanent canines with no cementum lines were assigned to age class I (0–12 months). Adult cats (>12 months) were assigned to eight age classes from II to IX where those with one cementum line represented age class II (13–24 months); those with two cementum lines, age class III (25–36 months); those with three cementum lines age class IV (37–48 months) etc. Eye lenses were removed from eyeballs after preservation in 10 percent formalin, dried in an oven at 80°C for eight weeks to a constant mass, and weighed.

Statistical analysis of data related to age determination followed Dapson (1980) and population parameters and statistics were estimated according to Caughley (1977) and Michod & Anderson (1980). The calculation of the intrinsic rate of population increase ( $r$ ) was based on the calculation of  $\lambda$  where

$$\lambda = \sum_{x=1}^n \frac{N_x l_1 m_x}{N_1} \quad (1)$$

and  $N_x$  = number of animals in age class  $x$ ,  $N_1$  = number of animals in age class 1,  $l_1$  = the probability that newborn survive to begin the first interval,  $m_x$  = age-specific fecundity (Michod & Anderson 1980), and where  $r = \ln \lambda$  (2)

Since it has been established that the method of Michod & Anderson (1980), when applied to the present data set, results in an increase of the probability of survival ( $l_x$ ) with age,  $l_x$ ,  $d_x$ ,  $p_x$  and  $q_x$  were estimated according to the methods of Caughley (1977), with  $\bar{r} = 0,233$  (van Aarde 1978).

In requiring the aged sample to be time specific and by assuming that sampling intensity was approximately constant throughout the sampling period, cats collected after the onset of the 1975/76 birth season (September to March), were assigned to the age class in which they would have been during the 1974/75 birth season (therefore observed age class – 1). Cats born during the 1975/76 birth season were excluded from analyses related to age-specific schedules. The age structure derived in this manner is referred to as the 'corrected' age structure. The assumption of stable age distribution was based on a comparison of the observed age structures of the population reflected by the samples col-

lected within a month after the two breeding seasons. Smoothing of age frequencies followed the log-polynomial model suggested by Caughley (1977).

### Results

#### Age determination

Eighty-three per cent of the 205 cats collected were assigned to a specific age class based on tooth eruption and counts of cementum lines. Variation in the counts of cementum lines per individual for 28 cats, and over-decalcification of canines of seven cats resulted in 35 individuals being excluded from the analyses. An analysis of the material obtained from known-age individuals suggested that the number of cementum lines in canines increased predictably with time, where each additional line represented an additional year in the life of the animal.

The relationship between age class and combined eye lens mass when cats in age class I were grouped into two separate classes (0 and I), where class 0 represented animals with a deciduous or partly deciduous dentition (0–8 months; van Aarde 1978), and class I the remainder of the class (9–12 months), was best described by a logarithmic function for both sexes. Age-specific mean eye lens mass for males and females did not differ significantly ( $F = 0,0027$ ,  $P < 0,001$ ) and data for the sexes could therefore be combined. A logarithmic transformation of age-specific eye lens mass regressed against age class resulted in a significant linear fit ( $r^2 = 0,75$ ;  $t_9 = 19,76$ ;  $P < 0,001$ ). Heteroscedasticity, even when both variables were transformed to  $\log_{10}$  precluded the calculation of valid confidence limits and prohibited the use of the relationship between age and combined eye lens mass for predictive purposes.

#### Age structure

The age structure of a subsample of the population collected after the 1974/75 birth season did not differ significantly from that collected after the 1975/76 birth season ( $\chi^2_8 = 3,38$ ;  $P < 0,01$ ). It has therefore been assumed that the age distribution of the population did not change during the study period (except for the seasonal effect) and that this age distribution remained.

The observed and corrected frequency distribution of sex-specific age classes did not differ significantly ( $\chi^2_8 = 3,33$  and 3,52 for males and females respectively). Furthermore, the corrected frequencies for males did not differ from those of females ( $\chi^2_8 = 6,34$ ;  $P < 0,01$ ) and these could therefore be lumped to ensure a sample size which would facilitate further analysis (Table 1). Correction of the frequency distribution of ages was based on the assumption of equal sampling intensity throughout the study period. This resulted in the given age distribution being regarded as resulting from a time-specific sample which reflected the population's age distribution at the onset of the birth season. The corrected frequency of each age class  $x$  was nevertheless not always greater than that of age class  $x - 1$  and frequencies were therefore smoothed according to a log-polynomial model (Table 1).

#### Fecundity

Based on an extrapolation of information obtained by deter-

**Table 1** Observed, corrected and smoothed frequency distribution of ages of feral cats collected at Marion Island between January 1975 and April 1976

Age class	Age in months	Number of animals					
		Males		Females		Total (corrected)	Total (smoothed <sup>d</sup> )
		Observed <sup>b</sup>	Corrected <sup>c</sup>	Observed <sup>b</sup>	Corrected <sup>c</sup>		
I	4–12 <sup>a</sup>	38	45	18	24	69	62,1
II	13–24	18	15	11	8	23	32,4
III	25–36	12	15	11	13	28	21,3
IV	37–48	12	8	12	9	17	16,1
V	49–60	11	11	5	3	14	12,7
VI	61–72	6	3	2	4	7	9,5
VII	73–84	4	4	3	2	6	6,1
VIII	85–96	2	2	3	2	4	3,1
IX	97–108	2	1	0	0	1	1,1
Total		105	104	65	65	169	164,4

<sup>a</sup>Body mass for age data suggested that the minimum age for animals collected was four months (van Aarde 1978). <sup>b</sup>Frequency distribution of ages as reflected by the age of animals at date of collection. <sup>c</sup>Frequency distribution of ages as reflected by the age of animals at the end of the 1974/75 birth season. <sup>d</sup>Frequency distribution of ages based on a log-polynomial model of the third degree where  $N_x = 2,22 - 0,51x + 0,99x^2 - 0,001x^3$  ( $r^2 = 0,97$ ).

mining foetal age (van Aarde 1978), the birth season was defined as the six-month period from mid-September to mid-March with most births (37%) occurring during October–November. Mean date of birth (Caughley 1977) was calculated as 30 December with a standard error of 80 days. Litter size at birth was unknown but prenatal litter size was  $4,59 \pm 1,12$  (S.D.) and litter size at weaning  $2,66 \pm 0,76$  kittens per litter. Prenatal (for foetuses older than 37 days) and juvenile sex ratio did not deviate significantly from the expected 1:1 ratio and sex ratio at birth was therefore assumed to be at unity. Adult females commonly produce two litters per season. The age-specific fecundity schedule ( $m_x$ ), based on the information given and the frequency of occurrence of pregnant and/or lactating females in each age

**Table 2** Age-specific fecundity schedules for the cat population at Marion Island with the assumption that litter size at birth = observed prenatal litter size and

$$l_1 = \frac{\text{prenatal litter size}}{\text{postweaning litter size}}$$

Age class	Percentage pregnant during breeding season	Female births per female per season ( $m_x$ )	Surviving female births per female per season ( $F_x$ )
I	0	0,00	0,000
II	25	1,15	0,667
III	100	4,59	2,662
IV	100	4,59	2,662
V	100	4,59	2,662
VI	100	4,59	2,662
VII	100	4,59	2,662
VIII	50	2,30	1,334
IX	0	0,00	0,000

$$F_x = m_x l_1$$

class during the breeding season could therefore be calculated (Table 2). As it is based on prenatal litter size this procedure necessarily resulted in an over-estimate of  $m_x$ , which was estimated at 0 for age class I; 1,15 for age class II; 4,59 for age class III to VII and 2,32 for age class VIII.

The discrete nature of age classes used in the present analysis necessitated the use of fecundity defined as the number of female offspring produced by females in each age class that will survive to enter the first age class (Michod & Anderson 1980). This type of fecundity ( $F_x$ ) can therefore be divided into a reproductive ( $m_x$ ) and a survivorship component ( $l_1$ ) where

$$F_x = m_x l_1 \quad (3)$$

In the discrete model newborn appear before the initial age interval and  $l_1$  is thus the probability that newborn survive to begin the first interval. The estimation of  $l_1$  can be based on 'biological judgement' (Michod & Anderson 1980) and based on the observed differences between prenatal and post-weaning litter sizes, ( $l_1$ ) was estimated at 0,58 for the cat population at Marion Island. Age-specific  $m_x$  and  $F_x$  values calculated as described above are presented in Table 2.

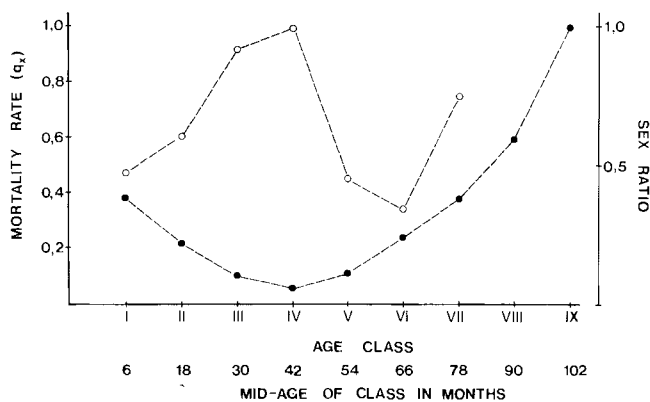
### Survival and mortality schedules

By using the relevant equations (1 and 2) the intrinsic rate of increase ( $r$ ) was calculated as 1,173 or an exponential population growth rate of 117,3%. By assuming a stable age distribution and in realizing that  $\bar{F} = 0,233$  (van Aarde 1978), age-specific probability of dying ( $d_x$ ), survival rates ( $p_x$ ) and mortality rates ( $q_x$ ) could be calculated (Table 3).

Mortality rate ( $q_x$ ) decreased rapidly during the juvenile and subadult phases (0–12 months) followed by an initial low (age class I to V) rate of mortality. Mortality rate, however, increased rapidly from age class V to IX (Figure 1). Sex ratio in terms of number of females per male decreas-

**Table 3** Age-specific probability of surviving, probability of dying, survival rates and mortality rates for the cat population with a stable age distribution increasing at  $r = 0,233$ 

Age $x$	Smoothed age frequency $N_x$	Probability of surviving $l_x$	Probability of dying $d_x$	Survival rates $p_x$	Mortality rates $q_x$
I	200,1 <sup>a</sup>	1,000	0,796	0,204	0,796
II	32,4	0,204	0,034	0,833	0,167
III	21,3	0,170	0,008	0,953	0,047
IV	16,1	0,162	0,001	0,994	0,006
V	12,7	0,161	0,009	0,944	0,056
VI	9,5	0,152	0,029	0,809	0,191
VII	6,1	0,123	0,044	0,642	0,358
VIII	3,1	0,079	0,044	0,443	0,557
IX	1,1	0,035	—	0,000	1,000

<sup>a</sup>Estimated from fecundity rates**Figure 1** Age-specific mortality rates ( $q_x$ ) (●) and sex ratios (○) for the feral cat population at Marion Island.

ed rapidly from birth to the age of 12 months but increased again from age class I to IV, thereby suggesting differential mortality in favour of females from 0–12 months of age followed by a period of increasing mortality of males during the ages of 13 to 48 months. It is suggested that the decrease in sex ratio from age class IV to VI is owing to an increase in female mortality rate after the age of 48 months has been attained (Figure 1).

## Discussion

Improper statistical treatment of data used in age estimation resulted in many papers dealing with this subject being of questionable value to future workers (Dapson 1980). The present analysis suggests that, although changes in combined eye-lens mass with age followed the logarithmic trend described for several species, it could not be used to predict age in feral cats reliably. The reason for this is the lack of homoscedasticity which would invalidate the calculation of the standard error of the estimate and confidence limits to be used in prediction. Combined eye-lens mass may, however, in this case be used as a 'first' estimator of age in an attempt to separate young adults from 'old' adults. Juveniles (< 4 months) and subadults (4–8 months) can be distinguished from each other and from adults on the basis of tooth replacement as described by van Aarde (1978).

The predictive interpretation of an increase in age with an increase in the number of cementum lines depended on the availability of known-age material. The known-age material available suggested that real age could be inferred from the number of cementum lines. An 18-month-old individual had only one cementum line, suggesting that the first line was formed during the first winter after tooth replacement (therefore the second winter after birth). The 31-month-old cat had two cementum lines suggesting that three periods of 'harshness' had passed since its birth. Both these animals were, however, kept in captivity with a constant food supply, but no obvious differences in the basic pattern of cementum deposition was evident between the captive and free-ranging feral cats. The occurrence of definite cementum lines would therefore appear not to be related to seasonal restriction in food availability, but rather to other factors (i.e. physiological).

Cementum lines were previously used in age estimation of feral cats (Pascal & Castanet 1978). The lack of known-age material, however, resulted in their interpretation being different from that presented here. Based on the finding of Pascal & Castanet (1978), Pascal (1980) assigned cats with no cementum lines to the age class 0–4 months, cats with one cementum line to age class 6–12 months, cats with two lines to age class 18–24 months etc. His classification is apparently incorrect, as cats of 0–4 months old still have a deciduous dentition, while cats of 4–8 months still undergo tooth replacement.

The age structure of this population as determined by the ageing technique described, can be regarded as being relatively unbiased. Errors resulting from variation in the number of cementum lines counted were limited by excluding animals showing any variation. These animals also appeared to be equally distributed over the life span of cats at Marion. A weakness in this approach was, however, the correction of assigned ages based on the assumption of equal sampling intensity throughout the year in as far as that sampling intensity could have been influenced by seasonal patterns of abundance. Limited sex-specific sample sizes furthermore resulted in the lumping of subsamples which may have resulted in possible differential mortality by sex, not being fully accounted for.

The observed adult sex ratio (> 12 months) differed significantly from unity (van Aarde 1978) but this is apparently due to sampling bias rather than differential mortality rates (du Toit, van Aarde & Steyn 1980). Males were nevertheless observed to reach an older age than females (Table 1). Sex ratio furthermore increased from age I to age IV, decreased from IV to VI and increased again from age VI to VII. The 36-month-period following the attainment of adulthood for a specific cohort would therefore appear to be characterized by an increasing male mortality rate — this probably being the period following their independence from social groups to the time of establishment as 'competitive' males, which could conceivably cause higher mortality rates in single males.

The steep increase in mortality rate from age IV to IX may be owing to the relatively harsh environment under which these cats live. This is supported by the fact that longevity in these cats (8 and 9 years for males and females respectively) is considerably lower than that reported for pets (21 years; Robinson 1977).

The intrinsic rate of natural increase based on the survival and fecundity schedules of this population differs from that reported by van Aarde (1978) (117,1% *cf.* 23,3%) where the latter was based on population estimates only. The intrinsic rate of natural increase should, however, not be regarded as constant, especially in the case of seasonally breeding populations. Furthermore, these estimates differ from the estimate for the cat population at the subantarctic Kerguelen Island (43% per year; Derenne 1976). The Marion and Kerguelen Island populations were both founded during 1949, therefore these differences may be interpreted as resulting from differences in environmental resistance experienced by the population, or from different reactions of the populations to their environments. The coat colour genetic profile of these two populations differs considerably which is probably the result of the founder effect (Dreux 1974; van Aarde & Robinson 1980). The Kerguelen population is characterized by the near absence of the wild-type phenotypes (Dreux 1974; personal observations), while these do occur in the Marion Island population (van Aarde & Robinson 1980). Mutant genomes do have an adaptive advantage (van Aarde & Blumenberg 1979), therefore the observed difference in the annual rates of increase may be the result of the differences in the genetic constitution of the two populations. Differences in the diets of these populations (Derenne 1976, van Aarde 1980) with a more constant supply in the form of introduced rabbits (*Oryctolagus cuniculus*) for the Kerguelen population, may, however, be the principal factor responsible for these differences.

The age structure of the population at Marion represents that of an increasing population with approximately 54% of the population  $\leq$  24 months of age and 71%  $\leq$  36 months of age. When considering this as well as the relatively high intrinsic rate of increase it should be obvious that control of this population would only be feasible if more

animals can be removed from the population than are produced. Following Caughley (1977) the estimated rate of increase suggests that at least 340 to 450 cats should have been killed annually from 1975 onwards to ensure a stable population size. Control techniques such as limited hunting, trapping, the use of poisons and anti-fertility drugs were considered and some of these tested. All proved ineffective in reducing the size of the population.

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