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on Marion Island

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INTRODUCTION

Marion Island ($46^{\circ}52'S$, $37^{\circ}51'E$), situated in the south Indian Ocean in the sub-Antarctic region, 2,100 km SSE of Cape Town (South Africa), is 290 km^2 in area and entirely volcanic in origin. The fauna and flora are continuously subjected to low temperature (mean 5.5°C), strong westerly winds, and a high humidity. Rainfall is evenly distributed, falling on 300 days per year.

During the latter half of the nineteenth century, whaling and sealing, and the establishment of meteorological stations resulted in the introduction of domestic cats on eight sub-Antarctic islands (Holdgate, 1966). Man's increasing concern about the destructive influence of feral cats on island avifauna, previously not exposed to aggressive terrestrial predators, has resulted in several recent ecological studies on feral cat populations, for example, on Kerguelen Island (Derenne, 1976; Pascal, 1977), L'ile aux Cochons (Derenne and Mougin, 1976) and Macquarie Island (Jones, 1977). Prior to the present study (December, 1974 - April, 1976), the only other published account on the feral cats at Marion Island was that of Anderson and Condy (1974), on their distribution.

Van Aarde (in press) estimated ecological densities at 13.85 and 4.98 cats per km^2 for the coastal and interior regions, respectively. He also estimated that 635,472 burrowing petrels (family Procellariidae) were killed by cats from September, 1974, to October, 1975, illustrating the destructive influence of cats on the avifauna of this island (van Aarde, 1977).

Reproduction in the domestic cat was studied as far back as 1784 by Spanlazani (Scott and Lloyd-Jacob, 1955). A remark by Kingsbury (1938) that as early as 1908, 426 pages were devoted by Winiwarter and Sainmont (1908 in Kingsbury, 1938) to a description of the ovary of the cat, gives some indication of the extent to which this species has been studied. Since then, many more observations concerning reproduction and reproductive behaviour have been published by various authors. Most of these accounts were based on animals living under laboratory conditions, or animals obtained from urban areas. The present study provides information on feral cats in an environment virtually uninfluenced by man.

MATERIALS AND METHODS

Between December, 1974, and April, 1976, information on reproduction was obtained by direct observations and from material collected from 205 cats. One hundred fifty-three cats were shot with a 410-gauge shotgun, and 52 were trapped using traps fitted with remote signalling devices (Condy, Anderson, Heijnen and Smit, 1974). All the animals killed were

weighed and measured, and grouped into one of three age classes. The classes were based on tooth replacement; adult - dentition permanent, subadult - dentition undergoing replacement, juveniles - deciduous dentition. Observations made on captive animals indicated that replacement of the deciduous teeth commenced at approximately 16 weeks of age and was completed by 28-30 weeks of age. These findings are similar to those published by Mellen (1946 in Dawson, 1950). Animals observed in the field were grouped into one of three age classes based on body size, *viz.* large (adult), medium (subadult) and small (juvenile). In general, good agreement existed between these two age classing techniques.

Testes and epididymides were collected from 133 males and weighed when fresh. They were fixed in Bouin's fluid for 48 hours and, thereafter, stored in 70 per cent alcohol. Samples from these testes were later dehydrated, embedded in paraffin wax, sectioned at 5 to 8 μm and stained in Delafield's haematoxylin, using eosin as a counterstain. The stained sections were microscopically examined for the stage of spermatogenesis. Mean seminiferous tubule diameter for each animal was calculated from 25 round tubules measured in cross section, using a micrometer eye-piece and a 10x objective.

Reproductive tracts of 57 females were removed and examined. Ovaries were weighed when fresh, and foetuses from 17 pregnant females were weighed and their crown/rump lengths measured. Following fixation in 10 per cent formalin, ovaries were examined macroscopically. They were sliced longitudinally at about 1 mm intervals and all corpora lutea in ovaries of pregnant females counted. Foetuses were aged by the method of Huggett and Widdas (1951).

The term "sampling period" has been used throughout this paper, and is defined as a period of 30-31 days, commencing on the 22nd day of a month and ending on the 21st day of the following month.

RESULTS AND DISCUSSION

Age Structure

Seasonal changes in the age structure of the population, indicated by the percentage of individuals in each age class that were collected during each sampling period, are illustrated in Figure 1. From December through February the population consisted of adults and juveniles, from March to May, all three classes were represented, and from May to September, only adults and subadults were collected, with a definite decrease in the number of subadults collected over these months. All animals collected from 22 September to 21 December were adults. This distinct seasonal change in the age structure of the population is the result of seasonal breeding. Births occurred from September to March and, assuming that kittens spend their first two months in their subterranean lairs, they will only be collected from December to May, as illustrated in Figure 1.

According to Bodenheimer (1938, in Odum, 1971), three ecological age classes, *viz.* pre-reproductive, reproductive and post-reproductive, can be distinguished in a population. In this cat population, juveniles and

subadults represented the pre-reproductive age class, while adults represented the reproductive and post-reproductive classes. Twenty-six per cent of the cats collected from January, 1975, to January, 1976, were juveniles and sub-adults, indicating that 74 per cent of this population were either reproductive or post-reproductive. Jones (1977) found that 20 per cent of the Macquarie Island cat population were kittens and adolescents, and Derenne (1974) indicated that adults comprised 72 per cent of his sample of culled cats on Kerguelen Island. However, the age structure of the population at Marion Island changed as the year progressed (Figure 1) and, therefore, percentage composition by age class varied, rather than being static. Female cats attain puberty at an age of nine (7-12) months, and males at an age of 12 (10-14) months (Marshall, 1922; Robinson, 1977). An individual, therefore, passed through all three age classes the first year of its life.

All females collected during the breeding season were either pregnant or lactating, indicating that most of the adult age class was in the reproductive category and that the post-reproductive category is probably a minor component of the adult population. According to Robinson (1977), cessation of breeding in the female cat is a gradual process and is characterised by an increase in the number of sterile copulations and a decline in litter size. Normal reproductive life span is 8-10 years, and it is rare for a female to reproduce beyond the age of 14 years (Robinson, 1977). Pascal (1977) concluded that feral cats at Kerguelen Island attained an age of eight years. As environmental conditions are similar on Marion Island, this age can be accepted in the present study and it may be concluded that females reproduce throughout their adult lifespan.

Group Structure

Mean group size was 2.65 ± 0.95 ($N = 79$; Table 2). Group size frequency as given in Table 1 indicates that most cats observed were solitary. Rosenblat and Schneirla (1972) stated that under natural conditions cats led a solitary life, except during the breeding season, and Barron, Steward and Warren (1956) concluded that the domestic cat was asocial and individualistic. This, however, does not imply that cats are unsocial and group formation was not found to be confined to the breeding season in the present study. Groups consisting of two to five animals have been observed throughout the year (Table 2).

An analysis of the age structure of groups indicated that 33.0 per cent of all groups consisted of adults only, 17.7 per cent consisted of juveniles only, and 7.6 per cent consisted of subadults only. Seventy-five per cent of all groups had an adult component and juveniles were present in 45.6 percent of all groups observed.

As has been mentioned previously, an individual will pass through all three age classes in its first year of life and, therefore, this will influence age structure of groups at any given time of the year. Groups with juveniles only were observed between December and June. Since these juveniles may remain in their subterranean lairs until two or three months of age, groups with a juvenile component were seen beginning two to three months after the onset of the birth season (September-October) and ending two to three months after the birth season (February-March). Groups with a subadult component were observed from February through to the onset of the next breeding season in September when subadults became adults.

Information on the sex composition of only three adult groups was obtained. Three males were collected in a group of five; one male and one female in a group of three; and a male and female in a group of two. Both females were pregnant, illustrating that group formation is not necessarily related to mating. Data on the permanency of adult groups are limited. Two adult males were observed at the same site over a period of two months. However, an identifiable individual was observed in company with different animals on different occasions during a period of seven months. On a few occasions "family units", consisting of an adult female and her kittens of two consecutive litters, were observed at the same lair site in which both litters were probably born.

Sex Ratio

Data on age specific sex ratios are given in Table 3. Prenatal sex ratio was obtained from foetuses older than 37 days (crown/rump lengths >7 mm, Figure 7). Since the observed prenatal sex ratio, as well as the sex ratio of juveniles, did not deviate significantly from unity, it may be assumed that at birth the sex ratio is 1:1. In both the subadult and adult age classes, a significant deviation in favour of males was observed. In the case of the subadults, this may be due to the small sample size. With the exception of the March-April and April-May sampling periods, sex ratios favoured males (Figure 2). The existence of a seasonal breeding pattern is believed to be the reason for this apparent seasonal deviation in sex ratio. During the breeding season lactating females spend about 80.0 per cent of their time in their subterranean lairs (Pascal, 1977). The chance of encountering and collecting females during this period are thus considerably lower than for males. After the breeding season, when female activity was not confined below ground, there is a much greater chance of collecting them. During this period (March-May), sex ratios are in favour of females. This may be due to a combination of two factors; the artificially created greater proportion of females following the heavier hunting pressure on males during the breeding season; and a difference in behaviour patterns and foraging areas, with a greater foraging activity on the part of females attempting to regain body condition following pregnancy and lactation.

During July-August mating occurs and, by August-September, all adult females are pregnant. The sex ratios collected during these periods returns to favouring males. This probably results from greater male activity during the breeding season. However, a sex ratio in favour of males may also be the result of sex specific mortality factors. To establish if the observed deviation was due to such a cause, the sex of 104 adult skulls that had been collected in the field was determined by employing a principal component and discriminant function analysis (Du Toit, van Aarde and Steyn, in prep.). The sex ratio of these animals (that had presumably died of natural causes) did not deviate significantly from the expected 1:1 ratio ($\chi^2 = 2.46$, $P > 0.05$). The observed ratio in favour of males appears, therefore, to be the result of an inequality in the sampling technique employed. It is noteworthy that a similar pattern was observed in samples collected from Kerguelen Island (Pascal, 1977).

Male Reproduction

(a) Age differences and sexual maturity

Mean body mass, mean combined testes mass and seminiferous tubule diameter for different age classes are given in Table 4, and all indicate an increase with age. Statistical analysis (Student's paired t test) showed that left and right testis mass did not differ significantly from each other ($t = 0.73$, $P < 0.01$, $N = 91$) and, therefore, testes mass is combined mass of left and right testes. Six cases in which cryptorchidism occurred were excluded from these results.

Spermatogenesis had not commenced in the juveniles but had started in 16.0 per cent of the subadults, and was present in all stages in all adults. The smallest subadult male undergoing spermatogenesis had a mass of 2.2 kg, testes mass of 0.77 g, and seminiferous tubule diameter of 116.3 μm . The mean body mass (2.43 ± 0.17 kg) of subadults showing spermatogenesis indicated that they were seven months old, according to the mass for age data of Scott and Scott (1967). At this age, mean testes mass was 0.54 ± 0.20 g, and mean seminiferous tubule diameter 145.32 ± 25.8 μm . The information indicated that for the Marion Island population, males younger than eight months of age were not sexually mature.

According to Robinson (1977), sexual maturity in the male domestic cat is attained at an average age of 12 months, ranging from 10-14 months. The period of puberty is regarded as the interval of time when reproduction is possible, terminating when full reproductive capacity is reached (Emmers, 1969). Thus, the pubertal interval in males at Marion Island extended over a minimum period of three to five months, commencing at approximately seven months of age and being completed at 10-14 months of age. However, according to Robinson (1977), factors such as month of birth, body growth, and body mass also influence the age of sexual maturity with males usually starting to take part in sexual activities when a body mass of approximately 3.5 kg has been attained.

The relationship between body mass and testes mass followed an exponential function described by the formula $y = 0.11e^{0.78x}$, where y = mean combined testes mass (g), and x = mean body mass (kg), with a coefficient of determination (r^2) of 0.84, indicating that the largest cats had the largest testes mass.

(b) Reproductive Senescence

Spermatogenesis was found in all adult testes examined, indicating that sterility due to old age did not occur in the sampled population. The only gross reproductive abnormalities that were recorded were for six (4.5 per cent) cases of unilateral cryptorchidism. Unilateral cryptorchidism occurs spontaneously in practically all mammalian species (Nalbadov, 1976), usually resulting in a reduced sperm count, but normal fertility (Roberts, 1958). This abnormality would not, therefore, necessarily impair reproduction in the population.

(c) Seasonal Reproductive Activity

Seasonal changes (on a monthly basis) in mean testes mass, mean seminiferous tubule diameter and mean combined epididymides mass for adult males are given in Figures 3 and 4. There are definite seasonal changes for all these parameters, with a trough for testes mass, tubule diameter and epididymides mass during the March to June sampling periods. Peaks for these measurements occurred from October to December sampling periods. Although spermatogenesis took place continuously all year in adult males, mean tubule diameter increased by 30.3 per cent from the April-May to the October-November sampling periods. This measurement, furthermore, increased by 15.5 per cent from the end of the non-reproductive to the onset of the reproductive period.

Statistical analysis (Student's t-test) indicated a highly significant ($P < 0.001$) seasonal difference in mean testes mass, mean tubule diameter and mean epididymides mass, where the non-reproductive period for males was considered as the period 22 January-21 June and the reproductive period 22 June-21 January (Table 5). For the austral summer reproductive period mean combined testes mass, mean combined epididymides mass and mean tubule diameter were 3.10 ± 0.7 g ($N = 44$), 0.65 ± 0.11 g ($N = 44$) and 213.4 ± 15.7 μm ($N = 44$) following 2.33 ± 0.68 g ($N = 31$), 0.51 ± 0.17 g ($N = 31$) and 184 ± 20 μm ($N = 31$) for the austral winter non-reproductive period (Table 5). With the exception of mean testes mass, the range of these measurements, as reflected by the standard deviation of the mean, were considerably bigger during the non-reproductive than the reproductive period.

Chapman (1972) indicated that definite seasonal changes do exist in the size, histology and secretions of male reproductive glands of a number of mammalian species. Even in animals that are fertile throughout the year, the quality of sperm (mobility and longevity) tends towards a seasonal pattern (Ortavant, Mauleun and Thibault, 1964, in Chapman, 1972). Due to the changes in climatic factors, seasonal changes in fertility of male domestic animals is influenced by the geographical distribution pattern of the species. In areas away from the equator, with an increase in latitude, seasonal changes in day length have an increasing influence on seasonal changes in fertility in some animals (Lodge and Salisbury, 1970). Although seasonal change in day length is one of the most important factors controlling the seasonal reproductive pattern in males (Assenmacher and Benoit, 1969 in Chapman, 1972), the influence of other environmental factors such as temperature (VanDemark and Free, 1970) and feeding (Moustgaerd, 1969; Leathem, 1970) also have an important effect on changes in fertility.

The population under discussion is not exposed to severe annual changes in air temperature, February being the warmest month with a mean of 7.5°C and August the coldest with a mean of 3.2°C . Rainfall and wind are also evenly distributed throughout the year (Schulze, 1971). Nonetheless, van Aarde (1977) noted definite seasonal changes in fat deposition that can be related to a seasonal pattern in food abundance, and these may have a considerable influence on seasonal breeding.

Day length varies appreciably, from a minimum daily mean of 8.82 ± 0.16 hours during the May-June sampling period to a maximum of 15.58 ± 0.16 hours per day during the November-December sampling period. Although the relationship between mean day length and mean combined testes mass, as well as the relationship between mean day length and mean seminiferous tubule diameter is not highly significant (correlation coefficient of 0.40 and 0.67; $P < 0.01$, respectively), these parameters follow the same basic trend, viz. a decrease from January to June and an increase from July to December. It can thus be said that although changes in day length may not be the only factor controlling seasonal changes in male reproductive parameters, they must be an important factor influencing this regular pattern.

Female Reproduction

(a) Age difference and sexual maturity

Mean body mass and mean combined ovary mass for the different age classes are given in Table 6, and these indicate an increase in these parameters with age. Mean combined ovarian mass for juveniles was 0.24 ± 0.7 g, for subadults 0.31 ± 0.22 g and for adults 0.34 ± 0.15 g.

In the house cat, corpora lutea are formed only after successful mating or artificial ovulation (Dawson, 1946). For feral cats, it is, therefore, expected that corpora lutea will only occur in animals that have mated. Macroscopical examination of ovaries indicated the presence of follicles, but the absence of corpora lutea, in subadults, suggesting that none of these individuals had mated. Corpora lutea in different stages of development and regression were recognisable in the ovaries of 89.0 per cent of adult females collected throughout the year. Corpora lutea in an advanced stage of regression are identifiable up to eight months after the time of mating (Dawson, 1946), explaining the presence of these bodies even in adult females collected during the non-breeding season. Mean body mass of females classified as adults with no corpora lutea was 2.64 ± 0.29 kg, and lower than the mean for the total adult sample. These females were collected during the non-breeding season and during the onset of the breeding season and were, most probably, young adults (transitional between subadults and adults).

During this study adult animals were defined as those older than eight months. It can, therefore, be concluded that sexual maturity is attained at an age of approximately eight months. In the Kerguelen population sexual maturity is attained at the age of approximately seven months (Pascal, 1977). Similar to the situation at Kerguelen (Pascal, 1977), females on Marion Island produced their first litter during the first season following their birth. It is of interest to note that the two captive females conceived at the age of nine and ten months, respectively.

According to Marshall (1922), the female cat will breed when 10 months old. Robinson (1977) stated that sexual maturity in the female normally occurs between the ages of 7 to 12 months and that rapidly growing females may reach maturity as early as six months. However, size is apparently the governing factor since females commence breeding when weighing 2.5 kg, approximately. Pascal (1977) stated that 30.0 per cent of the pregnant females collected at Kerguelen were 7 to 15 months old.

(b) Seasonality

The percentage of adult females found to be pregnant or lactating, during all the sampling periods from January, 1975, to January, 1976, are shown in Figure 5. This information indicates a sharply defined breeding season for females. All females collected from August to March were either pregnant or lactating, and no pregnant females were collected from March to June.

At Kerguelen Island ($49^{\circ}15'S$, $69^{\circ}30'E$) kittens were born during all months from August to April (Derenne, 1976), with a peak period from October to January (Pascal, 1977). At L'ile aux Cochons ($46^{\circ}06'S$, $50^{\circ}14'E$) births occurred from October to May with two definite peaks, the first during November and the second during April (Derenne and Mougin, 1976). At Macquarie Island ($54^{\circ}30'S$, $158^{\circ}57'E$), kittens were born between November and March, although some have been born in other months (Jones, 1977).

(c) Breeding interval

Information on this aspect is limited to observations made on two primiparous females in captivity. One produced her first litter on 14 November, 1974, and a second litter on 28 February, 1975. The other female produced her first litter on 17 September, 1977, and a second on 7 January, 1978, giving breeding intervals of 116 and 112 days for the two females, respectively. With a mean 65 days gestation period (Scott and Lloyd-Jacob, 1955; Robinson, 1977), ranging from 64 to 68 days (Dawson, 1950; Scott, 1955) this information indicates that these females conceived 57-61 days postpartum. Considering that the lactation period may extend to 60 days (Dawson, 1950), ranging from 50-60 days (Robinson, 1977), it appeared that a post-parturition anoestrus period occurred in these cats. However, two culled females were found to be both pregnant and lactating, indicating that oestrus is not necessarily post-lactational. The ages of the foetuses from these females were estimated at 20 and 33 days, and Scott (1955) and Scott and Lloyd-Jacob (1955) proved that fertile matings can occur during lactation, four to six weeks post partum. It seems that the wild cats on Marion do not undergo full lactational anoestrus, and are dioestrous as stated by Liche (1939). For the cats studied by Liche (1939), the first cycle usually occurred in spring and the second in autumn. However, under laboratory conditions, females may maintain a regular two week cycle for several months (Dawson, 1950).

(d) Reproductive senescence

All females collected during the breeding season were either pregnant or lactating, indicating that none of them represented post reproductive individuals. Similar to the situation in males, sterility due to age is not of any consequence to this population. According to Mellen (1946, in Dawson, 1950) females are at their sexual prime when from 2 to 8 years old and Marshall (1922) indicated that females rarely produced kittens after 14 years of age. The oldest females identified by Pascal (1977) in the cat population at Kerguelen were seven years of age and pregnant. For the Marion Island population, which is exposed to similar environmental conditions, this pattern might be the same.

(e) Ovulation rate and litter size

Examination of the ovaries of 17 pregnant females indicated a mean ovulation rate per female of 5.88 ± 1.17 (range = 4-8). Mean prenatal litter size was 4.59 ± 1.12 (range = 2-7). For five (29.4 per cent) of these females, the total number of corpora lutea and foetuses for each was similar. For all the females combined, the mean difference between ovulation rate and litter size was 1.29 ± 1.16 (range = 0-4), indicating a foetal wastage of approximately 28.0 per cent. On the other hand, mean litter size obtained during field counts gave an average of 2.66 ± 0.76 (range = 2-5, N = 41), the mean body mass of the kittens collected being 1.001 ± 0.32 kg, indicating an average age of ten weeks (Scott and Scott, 1967). This may be interpreted as resulting from a further mortality of about 42 per cent during the first ten weeks of life.

Pascal (1977) concluded that at Kerguelen the mean litter size for primiparous females was 3.85 and for mature females 4.26. Derenne (1976), for the same population, indicated a mean litter size of 3.3 ± 0.23 (range = 1-6), calculated for 39 litters collected over a period of four years, from 1970 to 1974. He furthermore indicated an increase in mean litter size for each year (from 2.5 in 1970 to 3.7 in 1974). Mean prenatal litter size at L'ile aux Cochons was calculated at 4.0 ± 1.1 (range = 2-7, N = 5), while the mean at the age of approximately four months was 2.9 ± 0.26 , illustrating a mortality of 27.5 per cent during the first four months (Derenne and Mougin, 1976).

According to Dawson (1950) litter size tended to be smaller in very young and very old females. Litter size is, furthermore, influence by the weight of the mother. Large females tended to produce bigger litters than smaller females (Hall and Pierce, 1934; Robinson, 1977). A survey by Hall and Pierce (1934) produced a mean of 3.88 for litter size and that of Robinson (1977) revealed a mean of 3.9 kittens at birth. The differences in mean litter size of cat populations living on sub-Antarctic islands under similar climatic conditions might be a reflection of differences in the age structures of these populations or due simply to sampling error.

(f) Foetal age determination and growth

Foetal ages for 64 conceptuses (14 litters) were derived from the expression of Huggett and Widdas (1951):

$$W^{\frac{1}{3}} = a(t - t_0)$$

where $W^{\frac{1}{3}}$ was the cube root of foetus mass (mean for each litter) in grams; the specific growth velocity was calculated at 0.104, using a gestation period (t_g) of 65 days (Scott and Lloyd-Jacob, 1959; Robinson, 1977) and a birth weight of 106.4 g (Hall and Pierce, 1934); t_0 was the numerical estimate derived from the expression $t_0 = 0.3 \times t_g$ for animals with a gestation time between 50 and 100 days (Huggett and Widdas, 1951). The conception age (t) of a cat foetus can thus be determined using the regression equation:

$$W^{\frac{1}{3}} = 0.104 (t - 19.5)$$

or, alternatively, by using the graph in Figure 6, where t_0 of 19.5 days

is the first fixed point and t_g of 65 days and its ordinate $W^{\frac{1}{3}}$ of 4.71 fixes the second point. By calculating $W^{\frac{1}{3}}$ for each foetus (mean for each litter) the conception age for each of these could be derived. It is of interest to note that a specific growth velocity (a) of 0.11 for the cat, living under urban conditions, was calculated by Frazer and Huggett (1974). This value was not very different from that (0.104) calculated for feral cats living under rather extreme climatic conditions at Marion Island.

Mean crown/rump length (mm), mean body mass (g) and age as determined from the above equations are graphically illustrated in Figure 7. The increase in crown/rump length with age followed a straight line with an equation $y = 2.432x - 40.62$ (where y = mean crown/rump length for a litter in mm, and x = age in days). The correlation coefficient is 0.88 and highly significant ($P < 0.001$). This expression can be used, therefore, to determine foetal age. Increase in body mass fitted an exponential curve, $y = 0.058e^{0.1236t}$ (y = mean body weight of foetuses in grams and t = age in days), with the exponential phase during the last third of pregnancy. This is also implicit in the Huggett and Widdas formula. Also, information on foetal growth and development of the domestic cat have been compiled by various authorities, notably Windle and Griffin (1931), Windle and Fish (1932) and Dawson (1950). Data on crown/rump length increasing with age were given by Dawson (1950) and were used by Boyd (1976) during a survey on the development of the foetal skull.

A comparison of the data in Figure 7 on increase in crown/rump lengths with that published by Dawson (1950), indicates a remarkable similarity up to the length of 38 mm (33 days). From the thirty-sixth day to birth, the measurements given by Dawson were considerably larger than those obtained in this study. These differences might be ascribed to different physiological and morphological factors influencing the mass and size of foetuses, such as litter size and body size of the mother (Hall and Pierce, 1934). Latimer (1931) indicated that limitations in space in the uterus, as the foetuses increase in size, may induce variation in the crown/rump lengths of older foetuses. He therefore used nose/anal length, a parameter that would not be influenced by the curves of the vertebral column due to changes in the position of foetuses. However, the linear relationship between nose/anus and crown/rump lengths were statistically significant (Latimer, 1931).

Projection of Breeding Season

Month of conception and month of birth for 14 pregnant females was estimated by back-dating and extrapolating the information obtained through age determination of their foetuses. With the information it was possible to separate the breeding season from the birth season (Figures 8 and 9). According to information in Figure 8, the breeding season extended over a period of six months, from July-August to the December-January sampling periods, with a definite peak for the August-September sampling period.

Assuming a gestation period of 65 days, births would occur from the September-October to the February-March sampling periods, with most (37 per cent) occurring during the October-November sampling period (Figure 9). Dawson (1950) defined the breeding season for this species as the

total period in "which females may exhibit sexual receptivity". According to this definition, the breeding season for the Marion Island cat population will thus be the period of the year from 22 July to 21 January. This pattern of seasonality in females coincides very closely with that observed for males. As males are fertile throughout the year, seasonality in breeding will thus be the result of a female seasonal sexual cycle. According to Foster and Hisaw (1935) and Dawson (1941), the seasonal cycle of the female cat is characterized by a definite anoestrous period, influenced by various factors such as feeding, climate and changes in day length (Dawson, 1941, Scott and Lloyd-Jacob, 1959). Dawson (1950) stated that "in the northern United States cats may be found in heat at any time of the year from January to July inclusive, with varying dioestrous intervals, and that the breeding cycle is characterized by a single definite anoestrous period lasting about five months". Dawson (1941), furthermore, indicated that many investigators have succeeded in inducing oestrous by treating females with the appropriate hormones. However, during the anoestrous period, only limited success was obtained.

The onset of the anoestrous period in the domestic cat is closely related to decreasing day length. Cats usually cease their breeding activities 3 to 5 weeks after the longest day of the year. Correspondingly, the onset of the breeding period occurs 3 to 5 weeks after the shortest day of the year (Dawson, 1941). Scott and Lloyd-Jacob (1959) indicated that increased illumination is a simple method of improving breeding performance of cats, by spreading the supply of kittens more evenly throughout the year. Experimental work indicated that the anoestrous period in the domestic cat can be decreased by an artificial increase in day length during the period of natural decrease in day length (Dawson, 1941; Scott and Lloyd-Jacob, 1959).

Determination of the day of conception through age determination of foetuses indicated that this first occurred on 23 July, 30 days after the shortest day of the year (21 June, 08h38) and the last on 1 January, 11 days after the longest day of the year (21 December, 15h45). Since the change in day length is one of the principal varying environmental factors to which the Marion Island population is exposed, it is reasonable to suppose that lengthening daylight plays an important part in determining the onset of breeding activities in this population, and that decreasing daylight is responsible for the onset of the anoestrous period. However, seasonality in prey abundance may also play an important role, as indicated previously.

Season reproduction on L'ile aux Cochons was ascribed to the rarity of prey during the winter months (Derenne and Mougin, 1976) and Derenne (1976) stated that the pattern at Kerguelen Island is the result of seasonal changes in prey availability, as well as seasonal changes in temperature.

Population Trend

Van Aarde (1978) estimated the population size, at the beginning of the 1975 birth season, at 2,137 individuals. The absence of terrestrial mammalian competitors and cat predators, unlimited space, and the abundance of food at the time of establishment should have enabled unlimited growth

of the cat population. Since no immigration or emigration has taken place since the original cats were introduced in 1949, population growth for the past 26 years (1949-1975) has been the result of the difference between natural natality and mortality.

Under non-limiting environmental conditions, the specific growth rate of a population becomes constant and a maximum for the existing conditions, and will be characterized by the particular population age structure (Odum, 1971). The growth of such a population is by definition exponential (Birch, 1948) and is designated by the symbol r , defined as the instantaneous coefficient of population growth (Odum, 1971).

By using the expression:

$$N_t = N_0 e^{rt}$$

where r = instantaneous rate of population growth, N_0 = the number of individuals in the population at the start of the observations, N_t = the number of individuals in the population at time t , and e = the base of natural logarithms, r was calculated at 0.233 ($N_0 = 5$; $N_t = 2,137$; $t = 26$), which indicates an estimated mean increase of 23.3 per cent per year. Theoretical population size, computed by using this value of r , for each year from 1949 to 1980 is illustrated in Table 7. For the population at Kerguelen, r was calculated at 0.43 (increase of 43 per cent per year) over a period of 12 years (Derenne, 1976). Since the overall population growth rate under unlimited environmental conditions depends on the age composition as well as specific growth rates due to age specific reproductive characteristics, the difference between the two populations, living under similar environmental conditions, may reflect different age structures.

SUMMARY

The population and reproductive ecology of the feral house cat population inhabiting sub-Antarctic Marion Island was studied utilizing information obtained from direct observations, and from material sampled from animals collected over 18 months.

Although primarily asocial, groups consisting of 2-5 (mean 2.65 ± 0.95 , $N = 79$) individuals were observed. The age composition of these groups showed a definite seasonal pattern as a result of seasonal breeding.

Age specific sex ratio deviated significantly from unity (in favour of males) in the adult ($\chi^2 = 11.59$) and subadult ($\chi^2 = 5.54$) age classes ($P < 0.05$), but in juvenile and prenatal groups the sex ratio did not deviate significantly from the expected ratio. The sex ratio of animals that died from natural causes did not deviate significantly from unity ($\chi^2 = 2.46$).

Seasonal differences in daylight length and prey abundance are probably the major factors causing a seasonal pattern in breeding. Extrapolation in foetal age from foetal mass indicated that mating occurred mainly from July to January, and parturition from September to March. Pregnant and/or lactating females were only collected from July to April. The adult male seasonal reproductive pattern, indicated by highly significant seasonal changes in mean testes mass (g) and

tubuli seminiferi diameter (μm), coincided with that observed for adult females.

Sexual maturity was attained during the first breeding season following birth by females. Adult females produced an average of two litters per season, with an average prenatal litter size of 4.63 ± 1.07 ($N = 14$) and at weaning 2.66 ± 0.76 ($N = 41$) indicating a neonatal and postnatal mortality of 42 per cent. Intrinsic rate of natural increase was calculated at 23.3 per cent per year over a period of 26 years.

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TABLE 1

Group sizes of feral house cats on Marion Island

Number of cats per group	Observed frequency	Percentage of total
1	747	90,54
2	47	5,69
3	17	2,06
4	8	0,97
5	6	0,73
	825	99,99

TABLE 2

The number of groups and mean group size for each month from January 1975 to April 1976.

Month	* Number of Observation	Number of groups	Number of groups (percentage)	Mean group size
January 1975	84	9	10,71	2,33
February	106	4	3,77	4,00
March	78	5	6,41	2,80
April	31	3	9,68	2,00
May	63	8	12,70	2,87
June	35	5	14,28	2,20
July	36	3	8,33	2,00
August	44	3	6,82	2,00
September	48	10	20,83	2,40
October	53	1	1,89	3,00
November	31	4	12,90	2,00
December	23	2	8,69	2,00
January 1976	102	14	13,72	2,86
February	45	4	8,88	3,50
March	36	3	8,33	3,00
April	10	1	0,00	2,00
Total	825	79	9,58	2,65 + 0,95

* Number of occasions when cats were observed

TABLE 3

Age specific sex ratios for feral cats collected on Marion Island

Age class	Sample			Ratio ↑↑ oo : ♀♀	Chi-square value	P-value
	↑↑ oo	♀♀	Total			
Prenatal	21	14	35	1 : 0,66	1,40	P>0,05
Juveniles	25	16	41	1 : 0,64	1,98	P>0,05
Subadults	19	7	26	1 : 0,37	5,54	P<0,05
Adults	89	49	138	1 : 0,55	11,59	P>0,005
Total (postnatal)	133	72	205	1 : 0,54	18,15	P>0,005

TABLE 4

Mean body mass (kg), mean combined testes mass (g), and mean tubuli seminiferi diameter (μm) of feral cats collected at Marion Island

Age class	Sample size	Body mass (kg)	Combined testes mass (g)	Tubuli seminiferi diameter (μm)
Adults	75	4,05 \pm 0,46	2,78 \pm 0,79	201,19 \pm 22,49
Subadults	25	2,16 \pm 0,46	0,59 \pm 0,46	120,16 \pm 41,45
Juveniles	7	1,21 \pm 0,18	0,25 \pm 0,05	76,66 \pm 15,67

TABLE 5

The level of significance in seasonal changes in mean body mass, mean combined testes mass, mean seminiferous tubule diameter and mean combined epididymides mass of adult feral cats.
 $(H_0 : \mu_1 = \mu_2)$

- 307 -

Parameter	Mean for season		t value	Degree's of freedom	Level of significance
	22 June - 21 January (non-reprod.)	22 January - 21 June (reprod.)			
Body mass (kg)	3,94 ± 0,44	4,14 ± 0,44	-2,10	73	N.S.
Mean combined testes mass (g)	3,10 ± 0,70	2,33 ± 0,68	-4,70	73	**
Mean seminiferous tubule diameter (μm)	213,4 ± 15,7	184,5 ± 20,02	-6,76	73	**
Mean combined epididymides mass (g)	0,65 ± 0,11	0,51 ± 0,17	-4,29	73	**

N.S. Difference not significant

** Difference highly significant ($P < 0,001$)

TABLE 6

Age specific mean body mass (kg) and mean combined ovarian mass of feral cats collected at Marion Island

Age class	Sample size	Body mass (kg)	Combined ovarian mass (g)
Adults	48	3,11 ± 0,37	0,34 ± 0,16
Subadults	6	1,67 ± 0,35	0,31 ± 0,22
Juveniles	3	1,07 ± 0,12	0,24 ± 0,07

TABLE 7

Simulation of population size at the onset of birth seasons from 1949 to 1985, ($N_t = 5e^{0,233t}$).

Year	Population size	Year	Population size
1949 N_0	5	1969 N_{20}	528
1951 N_2	8	1971 N_{22}	842
1953 N_4	13	1973 N_{24}	1 341
1955 N_6	20	1975 N_{26}	2 137
1957 N_8	32	1977 N_{28}	3 405
1959 N_{10}	51	1979 N_{30}	5 426
1961 N_{12}	82	1980 N_{31}	6 850
1963 N_{14}	131	1985 N_{36}	21 962
1965 N_{16}	208		
1967 N_{18}	331		

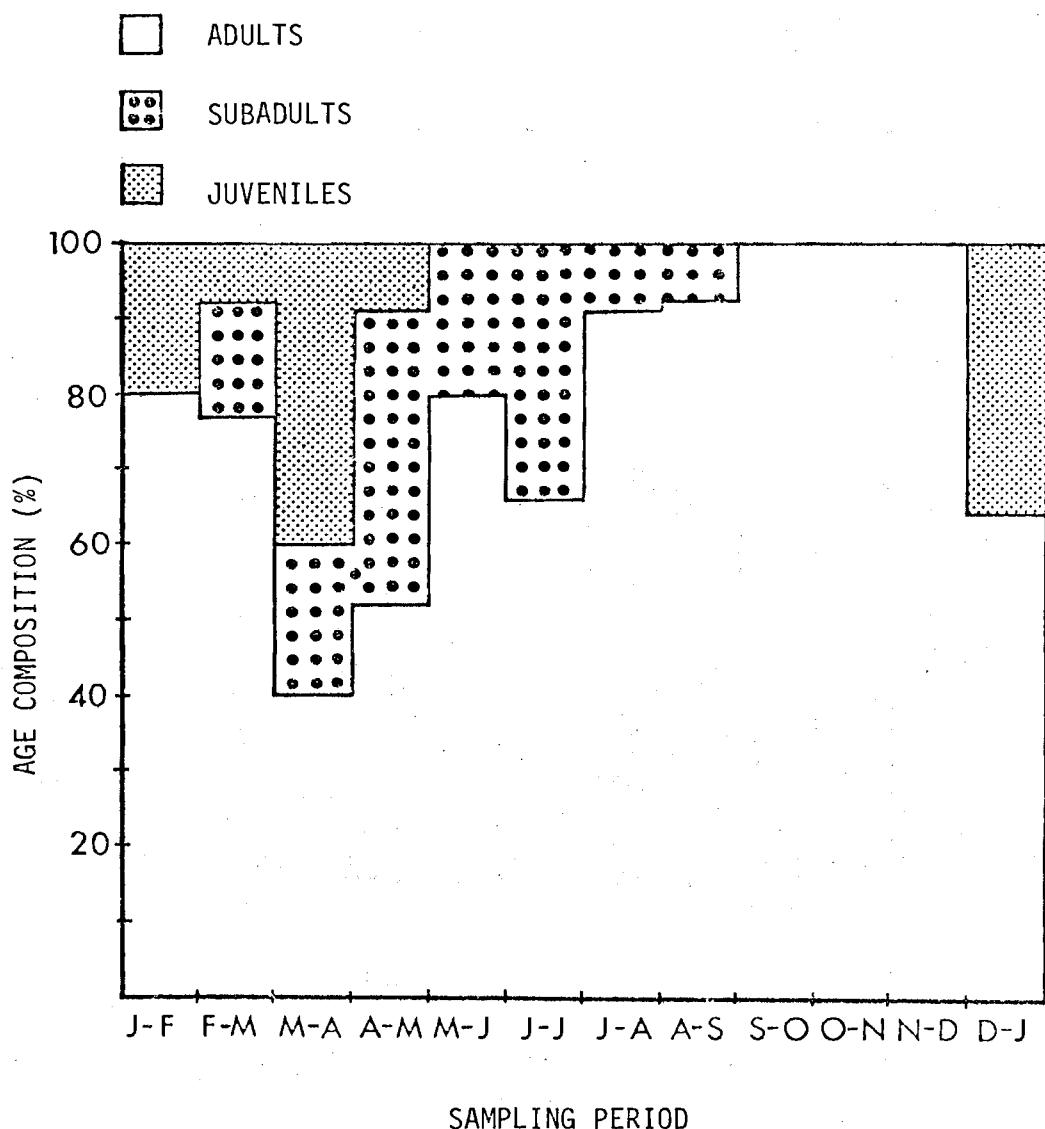


Figure 1: Seasonal changes in the age structure of the feral cat population, indicated by the number of individuals (expressed as a percentage) of each age class that were collected during each sampling period.

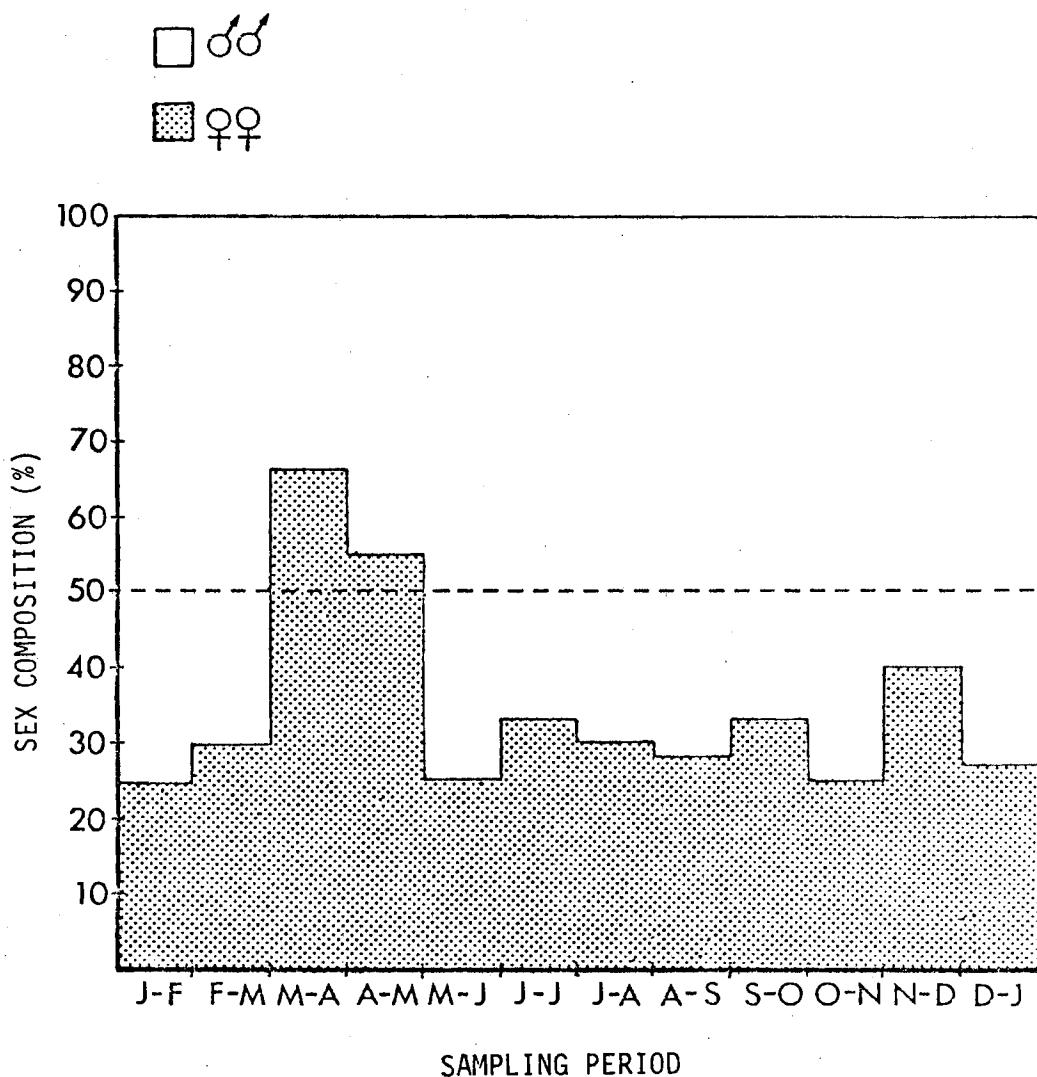


Figure 2: Seasonal changes in the sex ratio of adult cats ($n = 138$) collected on Marion Island. The expected ratio is indicated by the broken line.

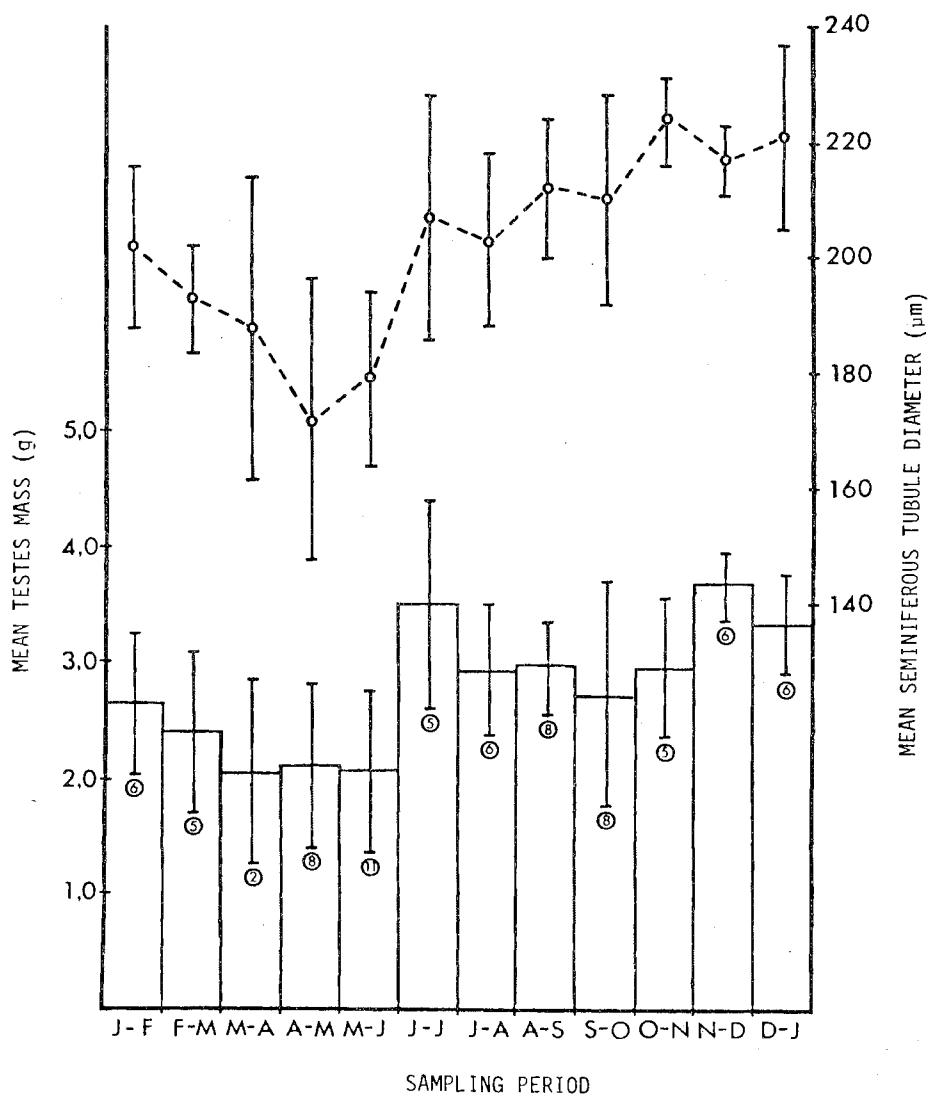


Figure 3: Seasonal variation in combined testes mass (histogram) and seminiferous tubule diameter (graph) for adult cats collected from January 1975 to January 1976. (Numbers in circles indicate sample size). Standard deviations of the means are indicated by the vertical lines

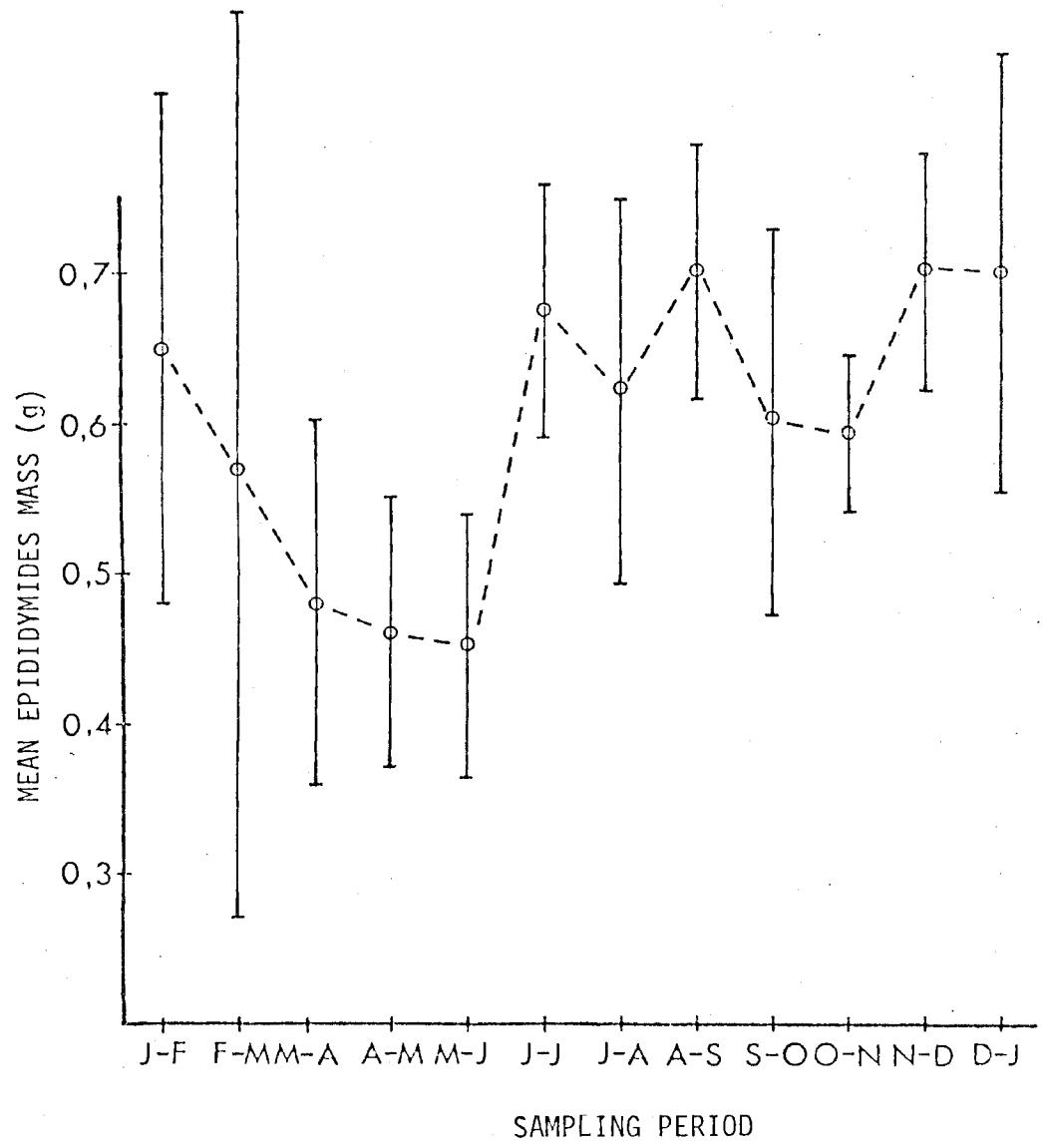


Figure 4: Seasonal changes in combined epididymides mass for adult cats.

Standard deviations of the means are indicated by the vertical lines.

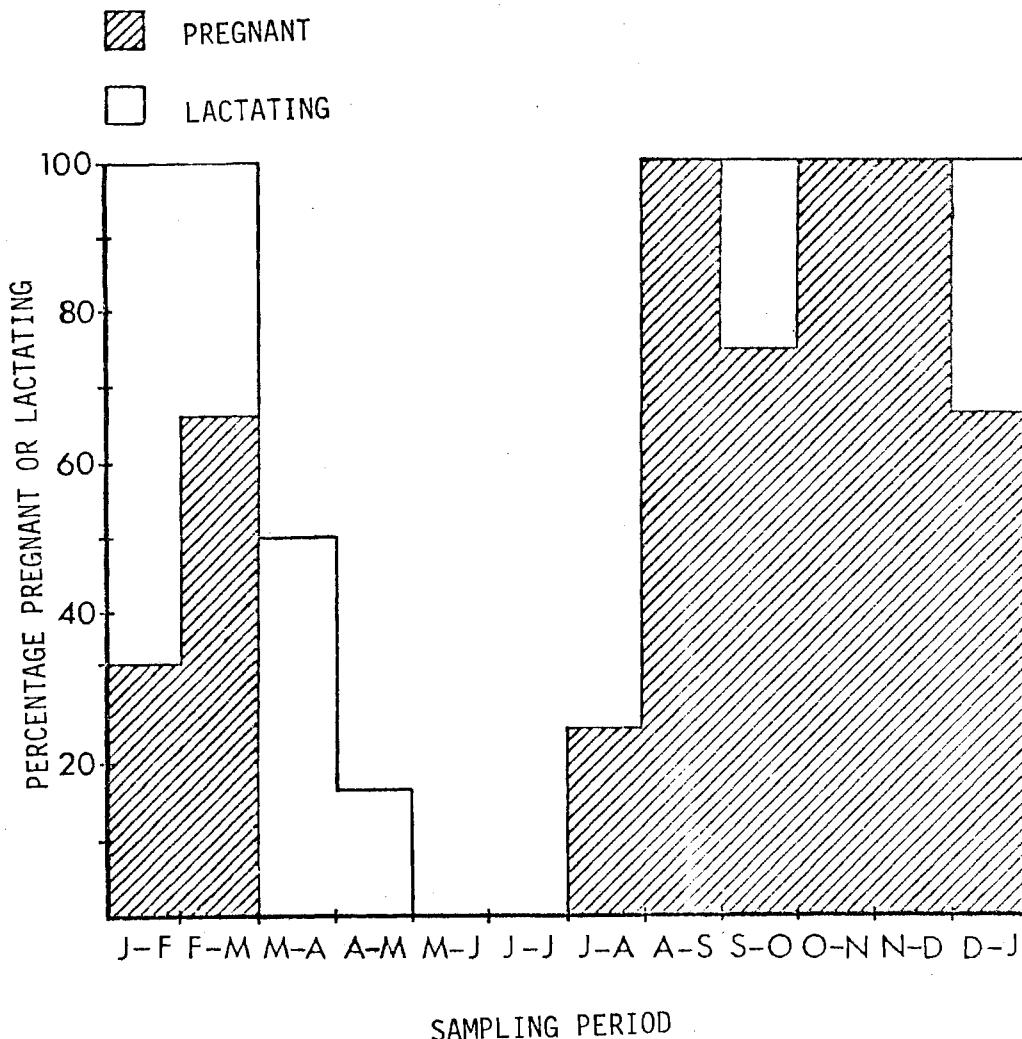


Figure 5: Number (percentage) of adult females pregnant or lactating during each sampling period from January 1975 to January 1976.
 $(n = 48)$.

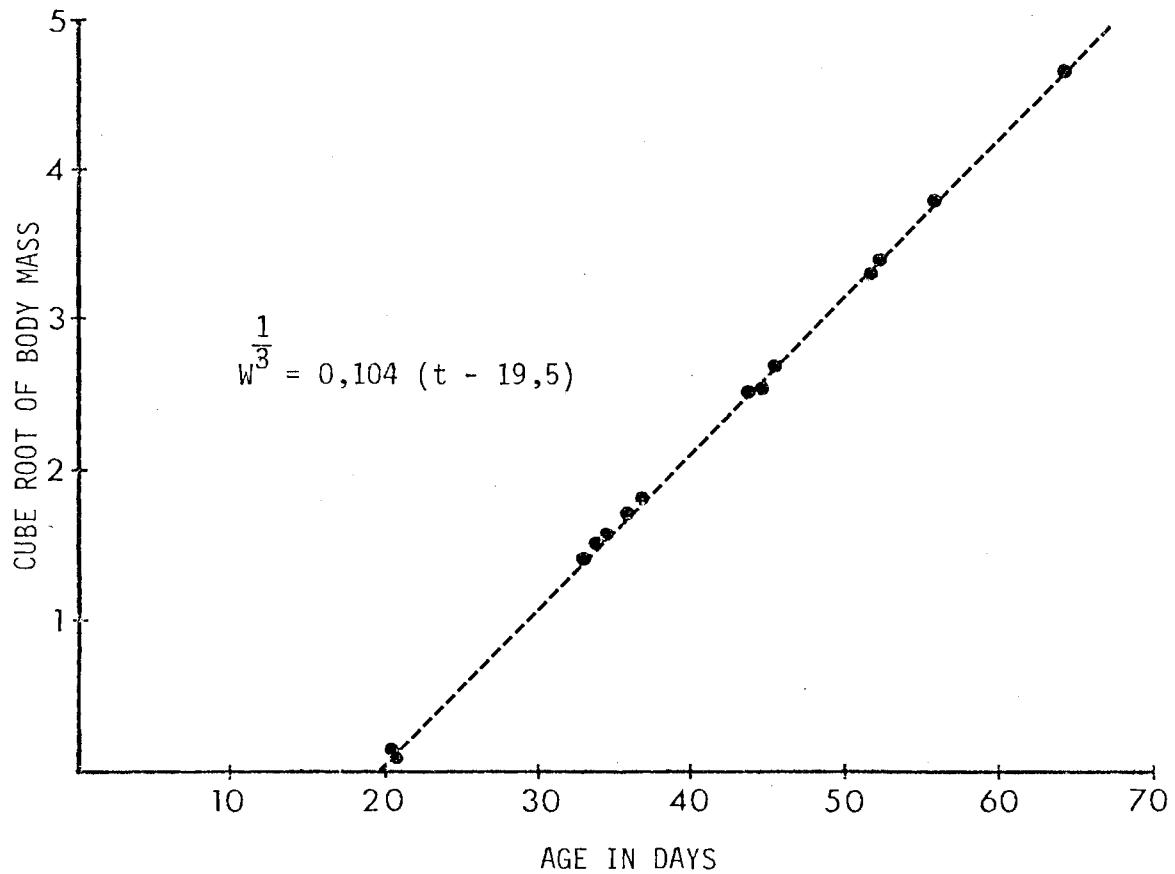


Figure 6: Cube root of mean foetus mass of each litter plotted against age.

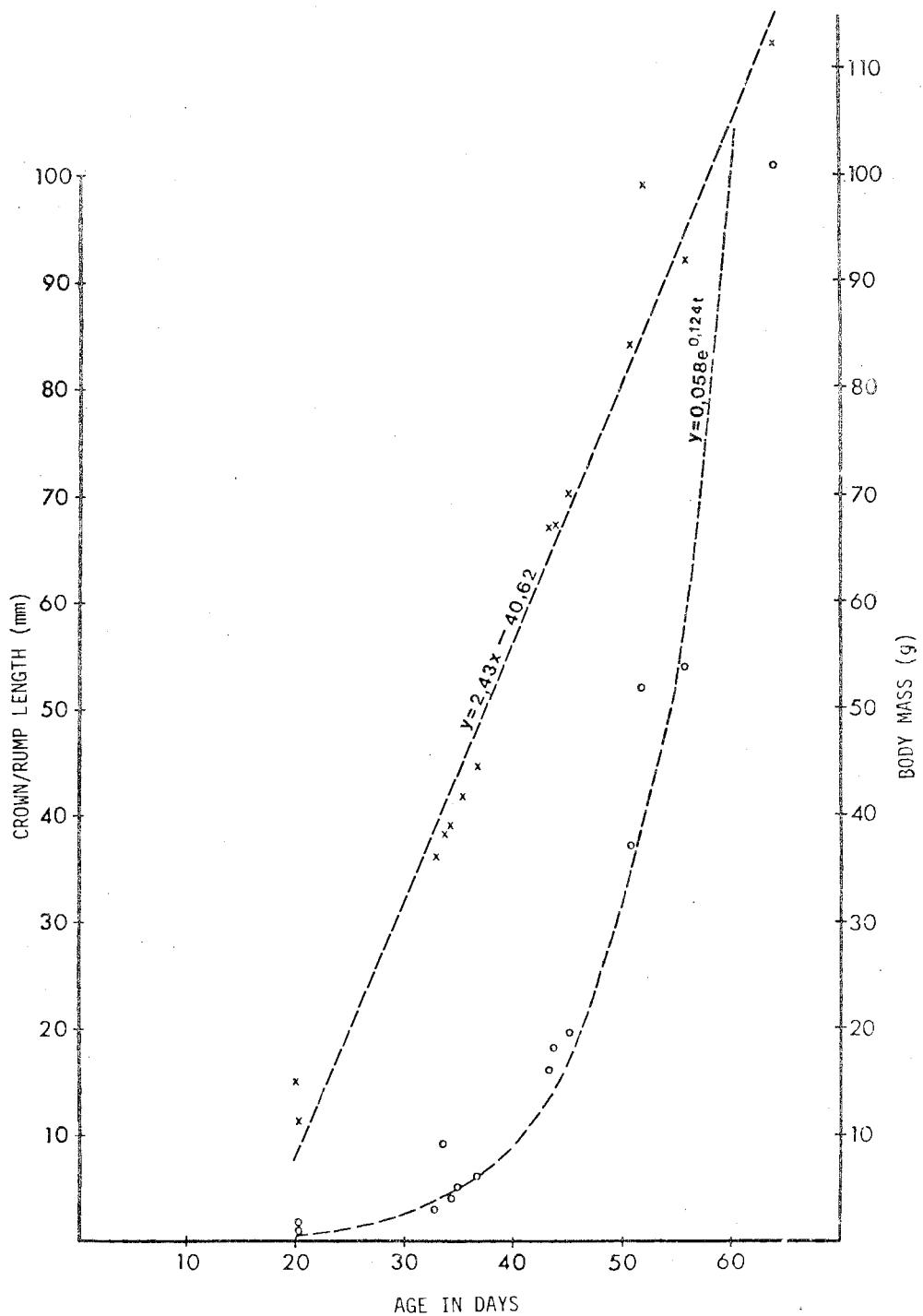


Figure 7: Mean foetus mass (o) and crown/rump length (x) for 14 litters collected on Marion Island

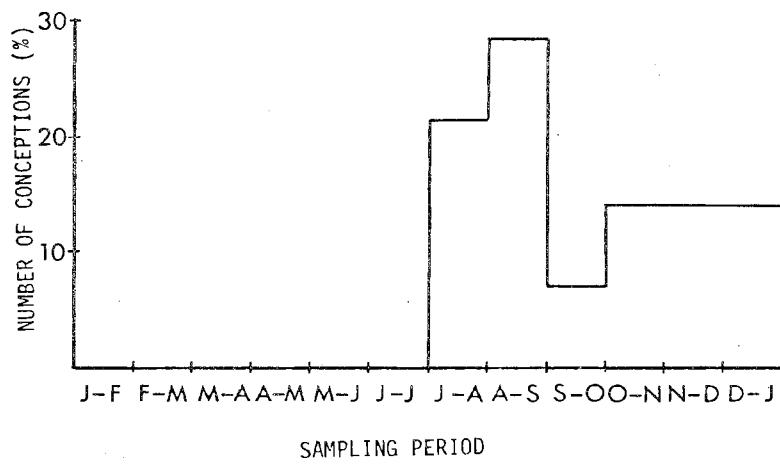


Figure 8: Number (percentage) of births during each sampling period
from January 1975 to January 1976

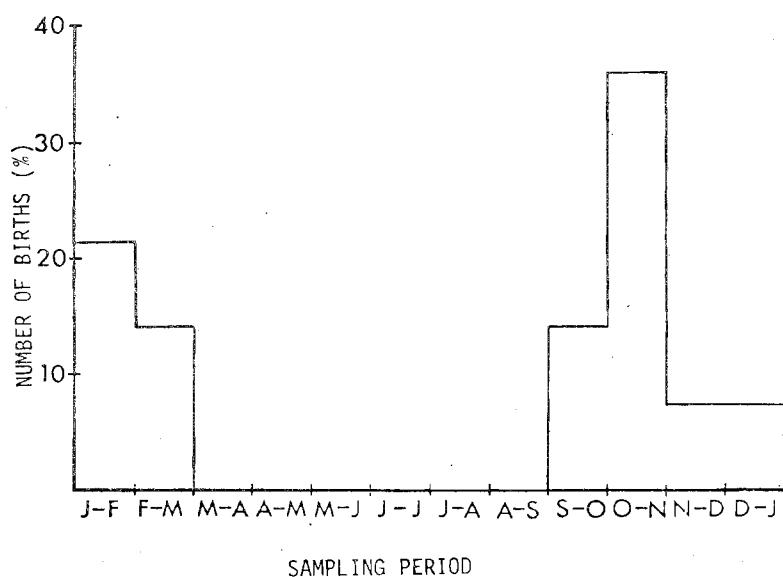


Figure 9: Number (percentage) of births during each sampling period
from January 1975 to January 1976.