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# Seasonality and reproduction in wild-living cats in Scotland

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The definition of the wildcat *Felis silvestris* Schreber, 1775 in Scotland is contentious, in light of long-term interbreeding with domestic cats *F. catus* Linnaeus, 1758. Two morphological groupings (Group 1 and Group 2) have previously been proposed to explain the variation found in wild-living cats in Scotland, with Group 1 cats closest to wildcats and Group 2 cats to domestic cats. Data from the reproductive tracts of 185 wild-living cat carcasses and evidence of reproductive activity in 31 live cats were analysed in order to compare reproductive activity between the morphological groups, and in relation to seasonality and existing data on wildcats and domestic cats. For males, Group 2 cats had a greater mean relative testes size than Group 1 cats. Estimated from corpora lutea, there was a suggestion that Group 1 females showed more seasonality in oestrous than Group 2 cats. In all wild-living cats, the mean litter size was 4.3 and estimated birth dates were throughout the year, but least in winter. A high number of pseudopregnancies were recorded. The results were consistent with the hypothesis that Group 2 cats are closer to domestic cats. However, the variation observed in the sample of wild-living cats reported here, suggested that reproduction was neither strictly seasonal nor outside the range observed in some feral cat populations.

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## Introduction

The definition of the wildcat *Felis silvestris* Schreber, 1775 in Scotland is contentious, in light of long-term interbreeding with domestic cats *F. catus* Linnaeus, 1758, and has been the subject of recent research (Daniels *et al.* 1998,

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2001, Beaumont *et al*. 2001, Reig *et al*. 2001). Two morphological groupings among wild-living cats were proposed by Daniels *et al*. (1998), based on a discriminant function defined by standardised intestine length and standardised bone size, and these have recently been extended to include skull morphometrics (Reig *et al*. 2001). Group 1 cats have some characteristics traditionally associated with wildcats (namely shorter intestines, longer limbs and larger skulls), while Group 2 cats are more closely associated with domestic cats (having larger intestines, shorter limbs and smaller skulls) (Daniels *et al*. 1998, Reig *et al*. 2001).

While these groupings are neither considered definitive nor exclusive by the authors, they are intended to provide a means of investigating the hypothesis that a group of cats with a higher proportion of 'original' wildcat genes can be defined in the face of long-term interbreeding. The collection of carcasses (Daniels *et al*. 1998) and data on live captures (Daniels 1997, Daniels *et al*. 2001) therefore provided an opportunity to investigate potential differences between Group 1 and Group 2 cats with respect to reproductive activity.

To date, few data are available on reproduction in wildcats. Most field guides consider wildcats to be seasonal breeders with one litter per year (Easterbee 1991, Macdonald and Barrett 1993). Mathews (1941) found no indication for seasonality in male wildcat sexual activity and there was evidence of two oestruses (in spring and summer) and occasionally a third (in late autumn) in females. On a larger sample size, Condé and Schauenberg (1969a, b) concluded that any later births were attributed to failed or lost litters earlier in the year.

Male domestic cats maintained indoors do not exhibit seasonality in sperm production (Goodrowe *et al*. 1989), but do exhibit a photoperiodic effect on testes weight (Kirkpatrick 1985) as do some feral cat populations (van Aarde 1978). Other feral populations appear to have no seasonal variation in testes mass, but do show differences in other reproductive parameters (Jones and Coman 1982).

Under natural climatic conditions, female domestic cats are seasonally polyoestrous with peaks in sexual activity in the northern hemisphere in spring, summer, and autumn (Goodrowe *et al*. 1989, Nelis 1995, Johnston *et al*. 1996). For free-ranging females, periods of anoestrus are dependent on photoperiod, geographical location and also genetic effects – for example, long-haired breeds have longer anoestrous periods (Goodrowe *et al*. 1989). Feral cat births occur in most months but peak in spring and summer (Kerguelen Island – Derenne 1976, Pascal 1980; Marion Island – van Aarde 1978; SE Australia – Jones and Coman 1982; USA – Warner 1985, Jöchle and Jöchle 1993).

Female domestic cats are generally considered induced reflex ovulators, requiring successful mating stimuli for the release of eggs. Therefore, the presence of corpora lutea (CL) in the ovaries is an indicator of mating (Goodrowe *et al*. 1989, Nelis 1995). However, female domestic cats can also undergo spontaneous ovulation resulting in pseudopregnancy (Johnston *et al*. 1996). In pseudopregnancies, or in failed pregnancies, CL continue their progesterone-secreting activity for 10–15 days before declining, in comparison to the 25–30 days if implantation is successful

(Tsutsui and Stabenfeldt 1993). Therefore CL are an indicator of the timing of reproductive activity but not necessarily an accurate indication of litter size – since not every ovulated egg is likely to be successfully fertilized or implanted after fertilization and also CL of previous pregnancies can persist for some time in the ovary (Matthews 1941).

Below we report on an investigation into reproduction in wild-living cats in Scotland based on an examination of the reproductive tracts of carcasses and evidence of reproductive activity in live captures. Reproduction is then discussed in relation to the proposed morphological groups, potential seasonality and in comparison with published data on wildcats and domestic cats.

## Material and methods

Reproductive tracts from 185 cats (103 males and 82 females) were obtained from 148 carcasses collected as described in Daniels *et al.* (1998) and a further 37 carcasses collected from throughout Scotland between April 1994 and April 1996. Cats of known domestic origin (ie with cat food in their stomachs or pet collars) were excluded from analysis but all other cats were considered. Captured males (13) from Daniels *et al.* (2001) were examined to determine whether testes were descended or not. Females (18 captures plus 17 recaptures) were examined for signs of pregnancy or lactation with respect to date.

Cats were classified according to sex, age, month and season of capture (see Daniels 1997), with age classed on the basis of body weight (Jones and Coman 1982) as: females: < 1.6 kg = 'juvenile', 1.6–2.5 kg = 'subadult', > 2.5 kg = 'adult', males: < 2.2 kg = 'juvenile', 2.2–3.5 kg = 'subadult', > 3.5 kg = 'adult'.

However, this classification was mediated by the use of tooth eruption, canine laminations and epiphysial closure of all limb bones. For example, if a cat was classed as juvenile on the basis of its weight but was found to have complete adult teeth and epiphysial closure, it was reclassed as an adult. For a subsample of carcasses (for which relevant intestine and limb bone data were available), cats were classed as one of two morphological groups following the discriminant function of Daniels *et al.* (1998) – where Group 1 cats are characterised by short intestine length and long limb bones (humerus, ulna, radius, femur and tibia) and Group 2 by long intestine length and short limb bones.

To determine estimated age (and hence birth date) for non-adult live captures (once all adult teeth are present it is not possible to accurately determine age), cats were examined orally for the presence of milk teeth, erupting adult teeth or adult teeth. The age (in months) for juvenile and subadult cats was then estimated from published age ranges associated with the eruption and replacement of milk with adult teeth (Silver 1969, Condé and Schauenberg 1978, Corbett 1979). Two further estimates were obtained from two graphs plotting age in months against: (a) body weight and (b) head and body measurements, by Stahl and Leger (1992: 19–22). A final estimated age was then obtained from the mean of these three methods.

Cat carcasses were frozen as soon as possible after collection, although unavoidably the time between cat death and freezing was variable (often up to several days or even weeks). On thawing, for collection of data on morphology, diet and parasites, the reproductive tracts of males and females were removed, re-frozen and stored prior to analysis. On dissection, pregnancy in females was recorded along with the number and size of their foetuses to enable estimation of birth dates.

In order to compensate for the potential effects of long-term freezing on the mass of gonadal tissues, testes, ovaries and uteri were fixed in 10% formalin for one week. Formalin was replaced after 24 hours to avoid possible reversible reactions with formaldehyde (Bancroft and Stevens 1996) and then left for a further 6 days prior to weighing. Fixed testis mass (TM) excluding the epididymides, was measured for one testis. Relative testes size (RTS – see Kenagy and Trombulak 1986), the percentage of testes mass in relation to body mass, was calculated as: (TM × 2 / body mass) × 100. Testis volume

(TV), the volume of one testis, was estimated as an eliptical sphere V = $\pi$ (L × A × B) / 6 (after Diem 1962), where L, A and B are the length and perpendicular diameters respectively. A transverse slice of tissue (4–5 mm) was removed slightly inferior to the widest point of one testis for histometric studies.

Both male and female gonads underwent standard tissue processing and embedding procedures using a Histokinette type E7326 tissue processor (Columbia Industrial Developments, Ltd), following Bancroft and Stevens (1996). Slides were stained using haematoxylin and eosin, mounted and examined under a light microscope. For males, the epididymides and seminiferous tubules of sectioned testes were examined for the presence or absence of spermatozoa. For females, sectioned ovaries were examined for the presence or absence of CL. The largest cross sectional areas ($\pi r^2$) of all CL (where present) were measured using an eyepiece graticule. The size of the CL and the cytological condition of the luteal cells enabled an estimation of its approximate age (Mathews 1941).

The time of year was expressed either in 'standard weeks' (ie 7-day intervals numbered sequentially from January 1st) or by seasons (spring: March–May, summer: June–August, autumn: September–November, and winter: December–February – as defined in Daniels 1997) to overcome two limitations of the data. Firstly, small sample sizes, and secondly to allow for errors in estimation of oestrus dates and birth dates. This was particularly relevant for CL which remain active for 35–44 days and may persist in lactating cats for 63 days *post partum* (see Goodrowe *et al.* 1989).

## Results

### Males

For cats trapped alive, nine classified as adult had scrotal testes but neither one subadult nor three juveniles did. For carcasses, 74% were classed as adults, 18% subadults and 8% juveniles (Table 1). No cats classified as juvenile had sperm present in their testes, whereas 33% of all cats classified as subadults and 86% of adults did. These differences were highly significant (Fisher's exact test: $p < 0.001$). Differences between adults and subadults were also highly significant for TV ($t$-test: $t = 4.9$, $n = 87$, $p < 0.01$), TM ($t = 5.6$, $n = 78$, $p < 0.01$) and RTS ($t = 2.6$, $n = 78$, $p < 0.01$; Table 1). Therefore in the following analyses, for comparison of Group and seasonal data, only data from adult carcasses were used.

Group 1 adult males had relatively smaller testes (RTS) than Group 2 adult males ($t = -2.7$, $n = 38$, $p < 0.01$). However, there were no significant differences between Groups for any other characteristics: the numbers of cats with and without sperm in their testes (Fisher's exact test: $n = 6$, $p = 0.99$); TV ($t = -1.3$, $n = 45$, $p = 0.22$) or TM ($t = -1.2$, $n = 44$, $p = 0.13$), Table 1. Since there was also no difference between the Groups for the numbers of samples collected in different seasons (Fisher's exact test: $n = 72$, $p = 0.61$, all adult male cats, ie Groups 1 and 2) were considered together for comparing seasonal differences.

Sperm was found in cats' testes all year and there was no difference in the frequencies of cats with or without sperm in their testes between seasons (Chi-square test: $\chi^2 = 4.7$, $n = 72$, $p > 0.05$). There was also no difference across seasons in body mass (ANOVA: $F = 4.7$, $n = 68$, $p = 0.98$) or TM (Kruskal-Wallis test: $H = 0.327$, $n = 64$, $p = 0.95$). However, there were significant differences in median TVs between seasons, with the highest in spring and the lowest in autumn ($H = 13$, $n = 71$, $p < 0.01$) but this was not related to Group. There was also a

Table 1. Reproductive characteristics for wild-living cats based on different age classes and (for adults only) different morphological groups. TV – testis volume, TM – testis mass, RTS – relative testes size, CL – corpora lutea.

| Reproductive characteristics | Adults | Subadults | Juveniles | Adults only | |
|---|---|---|---|---|---|
| | | | | Group 1 | Group 2 |
| | | Males | | | |
| Frequency (%): sperm present | 64 | 6 | 0 | 20 | 17 |
| sperm absent | 10 | 12 | 8 | 4 | 2 |
| Mean TV ($mm^3$) | 885 | 371 | 96 | 816 | 950 |
| SE | 46 | 71 | 12 | 67 | 85 |
| $n$ | 71 | 16 | 8 | 26 | 19 |
| Mean TM (g) | 0.69 | 0.31 | 0.08 | 0.65 | 0.76 |
| SE | 0.03 | 0.05 | 0.01 | 0.05 | 0.05 |
| $n$ | 64 | 14 | 7 | 27 | 17 |
| Mean RTS (%) | 0.03 | 0.02 | 0.01 | 0.03 | 0.04 |
| SE | 0.001 | 0.002 | 0.00001 | 0.002 | 0.002 |
| $n$ | 64 | 14 | 7 | 21 | 17 |
| | | Females | | | |
| CL present | 13 | 0 | 0 | 6 | 4 |
| CL absent | 29 | 9 | 4 | 9 | 9 |

positive correlation between TV and standard weeks (starting at week 20) for cats with sperm present in their testis ($r_S = 0.67$, $n = 21$, $p < 0.01$; Fig. 1).

There were no significant correlations between standard weeks (starting at week 20) and TM or RTS either for cats with sperm present or absent in their testis (all $p > 0.05$). All cats with TVs greater than 800 $mm^3$ had sperm present in their testis as did those with TMs greater than 0.6 g. No cats weighing less than 2.5 kg or with RTS less than 0.02% had sperm present in their testis (Fig. 2).

**Females**

For carcasses, 77% were classed as adults, 16% as subadults and 7% as juveniles (Table 1). No females classed as subadults or juveniles had evidence of CL present but 31% of adults did (Table 1). Although these differences were not significant (Fisher's exact test: $n = 42$, $p = 0.1$), subadults and juveniles were excluded from the following analyses, to compare differences between Groups and seasons.

There was no significant difference between Group 1 or Group 2 females in the proportion of animals with CL present (Fisher's exact test: $n = 15$, $p = 0.49$), but the sample size was too small to account for seasonal and group differences together (Table 2). Thirty one percent of cats had CL present but the majority of these appeared to be pseudopregnancies (ie unfertilised); two of them had two

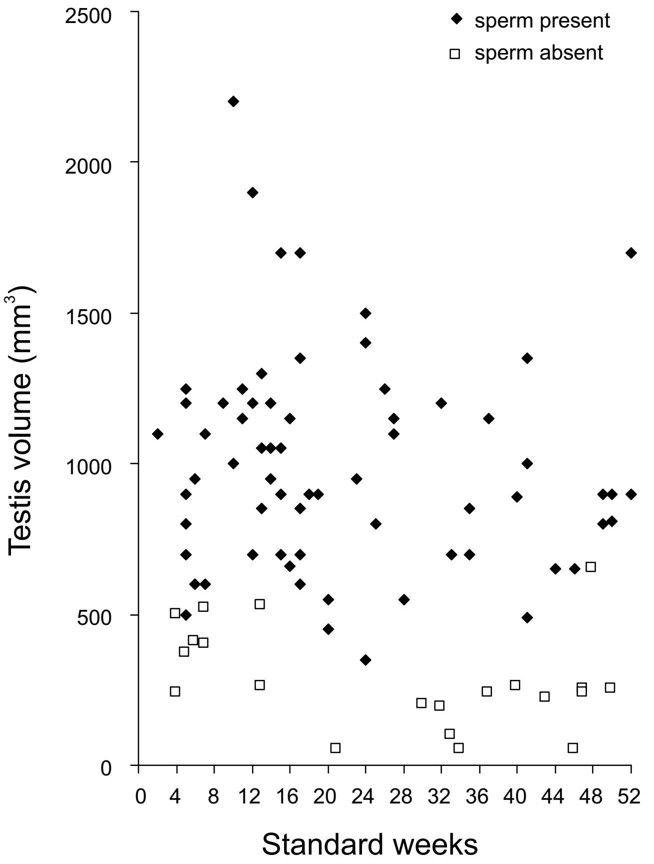


Fig. 1. The relationship between time of year and testis volume for wild-living cats with both sperm present in their testis and those with sperm absent.

generations of CL present. There were significant differences in the proportions of cats with CL present per season ($n = 14$, $p < 0.05$) with the lowest numbers in winter (Table 2). There were no significant differences in the proportions of pseudopregnancies across seasons ($n = 7$, $p = 1.0$), but there were differences across seasons in the occurrence of CL in carcasses: 43% occurred in spring, 29% in summer, 21% in autumn, and only 7% in winter. When CL and the size of foetuses were used to estimate the time of oestrus, oestruses were found in all seasons. Five of 6 females of Group 1 had CL present in summer and autumn whereas CL-bearing Group 2 cats were found in all seasons except autumn. This may suggest a greater seasonality in Group 1 cats or may simply be an artifact of the small sample size.

The mean litter size of wild-living cats (ie Group 1 and Group 2 cats) based on nine litters was 4.3 (range = 3–6). From forward estimates based on foetus size of

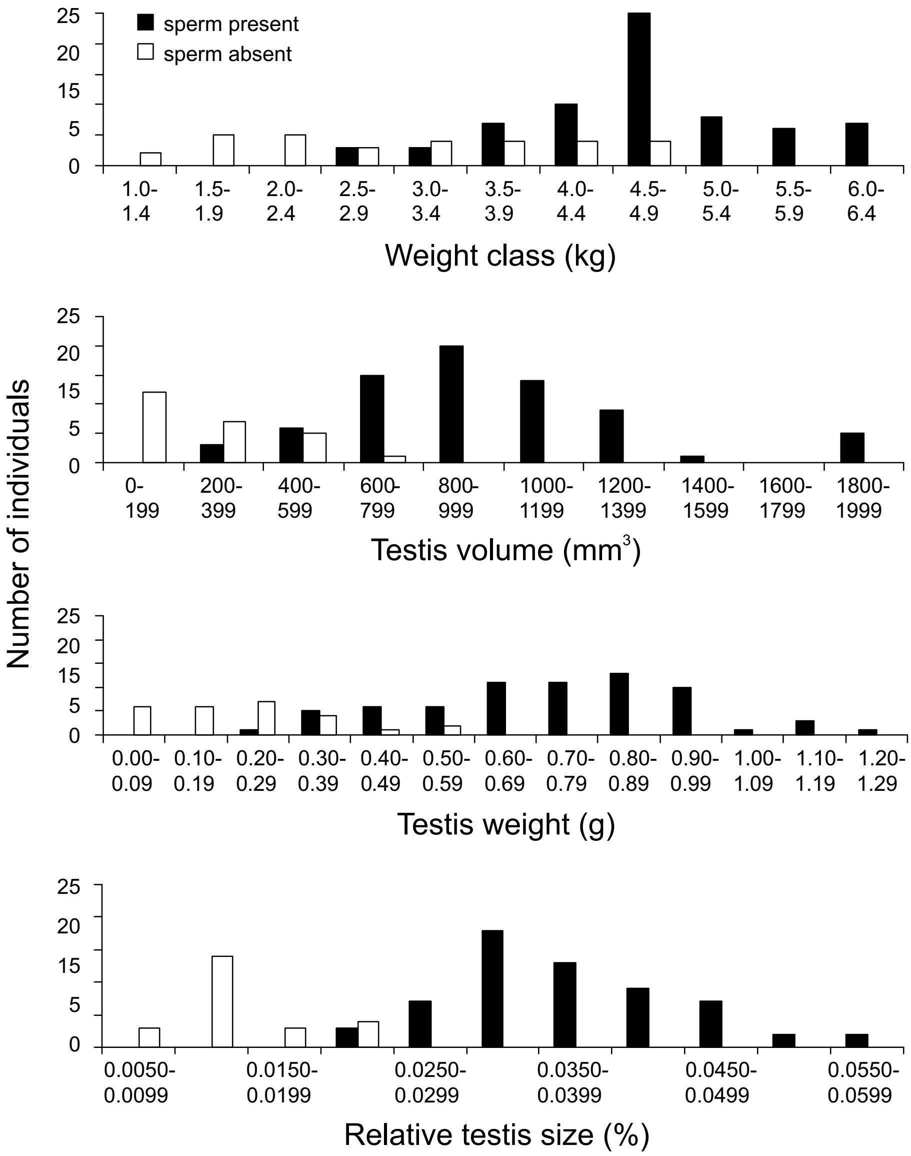


Fig. 2. Frequency of wild-living male cats with sperm present in their testis and sperm absent by body weight, testis volume, testis mass and relative testis size.

pregnant females ($n = 10$) and back estimates based on live captures of juvenile or subadult cats ($n = 16$), births occurred throughout the year although the number of lactating females ($n = 6$) peaked in summer (Fig. 3).

Table 2. Seasonal characteristics of corpora lutea (CL) in wild-living adult female cats (Group 1 and 2 pooled).

| Females | Spring | Summer | Autumn | Winter |
|---|---|---|---|---|
| with CL | 6 | 4 | 3 | 1 |
| without CL | 8 | 1 | 5 | 16 |
| pseudopregnant | 3 | 2 | 1 | 1 |

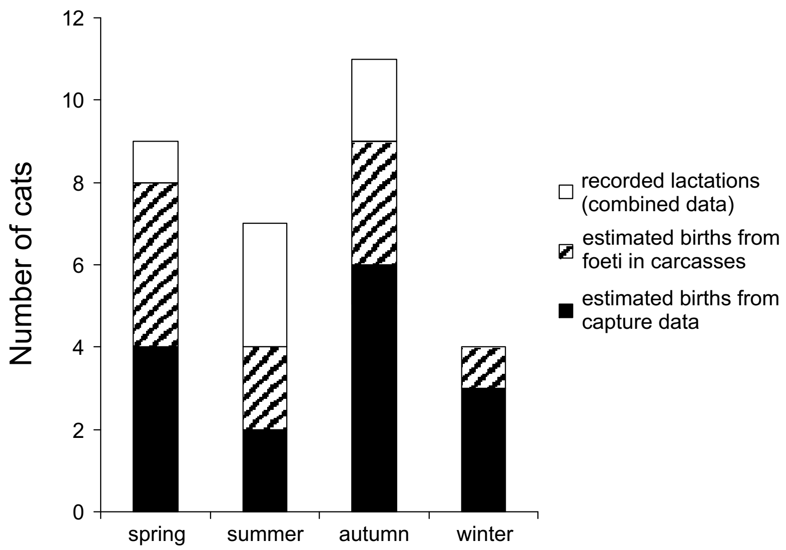


Fig. 3. Seasons of estimated births and recorded lactations in female wild-living cats.

## Discussion

### Morphological groupings and the definition of a wildcat

The classification of cats into adults, subadults and juveniles based on weight (Jones and Coman 1982) proved useful as long as tempered with other criteria. A larger number of adult males had sperm present in their testes and had larger testes volumes, testes mass and relative testes size than subadults, while corpora lutea were only found in females defined as adults.

There was some evidence of differences between the two pre-defined morphological groups: relative testes size was larger in Group 2 males, and there was a suggestion that Group 2 females showed less seasonality in oestrous. These differences are consistent with the suggestion that Group 2 cats are closer to domestic cats (Daniels *et al.* 1998, Reig *et al.* 2001). Woodall *et al.* (1993) showed that domestic dogs *Canis familiaris* had significantly larger epididymal weights and sperm numbers (but not testes mass), than sympatric dingoes *Canis familiaris dingo* in Australia. Testes are also relatively larger in species that adopt a promiscuous or polygynous mating system (Kenagy and Trombulak 1986). Under certain circumstances feral domestic cats are intensely promiscuous (Natoli and De Vito 1991). Furthermore, Price (1984) claims that, in general, domestic animals demonstrate increased fertility with respect to their wild counterparts. However, no other reproductive characteristics suggested increased fertility in Group 2 cats.

**Seasonality in reproduction**

The only previous reproductive data on wildcats from Scotland was based on a very small sample with no cats collected in the summer (Mathews 1941). Mathews (1941) found, for a sample of six adult wildcats, sperm in the testes for all months in which they were collected: February, March, April and December (corresponding to spring and winter as defined here). Corbett (1979) reported three adult males with sperm present in January, March and April (winter and spring) but also four in non-reproductive condition in January, October and December (autumn and winter). Meyer-Holzapfel (1968) in Switzerland and Volf (1968) in the Czech Republic both record 'exceptional cases' of captive wildcats producing litters in August (summer), while Condé and Schauenberg (1969a) claimed the breeding season for captive wildcats in France was from December to June (winter, spring and summer).

Unlike the pattern described for male domestic cats maintained indoors and for some feral cats (van Aarde 1978, Kirkpatrick 1985, Goodrowe *et al*. 1989), the adult wild-living cats described here did not exhibit seasonality in testes characteristics (apart from TV which may have been influenced by five large values – Fig. 1). These results are very similar to those reported by Jones and Coman (1982) for another population of feral cats, for which there was no seasonal variation in cats with sperm present in their testes nor in TM, but for which there were monthly differences in epididymis weight, which coincided with peak female conception rates.

For females, although few data were available, estimated oestruses occurred in all seasons (for Group 2 cats) but with a suggestion of a peak in summer and a trough in winter (for Group 1 cats) although the sample size was very small. A surprisingly high proportion of CL present appeared to be the result of unfertilised pseudopregnancies. There are four possible explanations for this. Firstly, that the CL were the result of spontaneous ovulations, an occasional occurrence in domestic cats (Johnston *et al.* 1996), although there are no data for wild-living cats. Secondly, that pregnancies were aborted, although there was no evidence that these cats had been pregnant (ie they did not have enlarged uteri). Thirdly, pseudopregnancy could be expected to increase in times of nutritional stress (ie food shortage), as described for other wild mammals (for example harp seals *Phoca* *groenlandica* – Renouf *et al*. 1994). Finally, pseudopregnancy could be the result of sterile matings by infertile males or (late) castrated domestic cats.

The mean litter size presented here (4.3), albeit from a small sample size, is similar to that cited for wildcats (4, 3 and 5.5 in captivity – Meyer-Holzapfel 1968, Volf 1968, Condé and Schauenberg 1969a, respectively; and in the wild: 4 and 3.7 – Kolb 1977 and Macdonald and Barrett 1993) but also for feral cats (3, 4.6, 2, and 4.4 – Derenne 1976, van Aarde 1978, Corbett 1979, Jones and Coman 1982) and domestic cats (4–4.5 – Tsutsui and Stabenfeldt 1993). There was also evidence that the cats described here had litters in all seasons but with the lowest numbers in winter (Fig. 3).

In conclusion, there was tentative evidence of some reproductive differences between Group 1 and Group 2 cats, consistent with the hypothesis that Group 2 cats are closer to domestic cats. There was limited evidence of seasonality in reproduction among female Group 1 cats but overall reproduction was not strictly seasonal. Furthermore, the variation observed in the sample of wild-living cats in Scotland reported here, also fell within the range of reproductive seasonality described for feral cats. Part of the variation recorded in reproductive characteristics may be due to the introgression of domestic cat genes into the wild population.

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