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Research Article

Breeding pattern of wildcat *Felis silvestris* (Schreber, 1777) studied in captivity in the iberian peninsula

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Abstract

We studied the effect of several environmental and reproductive variables on the reproductive performance of captive European wildcat (*Felis silvestris silvestris*, Schreber 1777) females in Spain. We collected reproductive data from 34 females that produced 77 litters and 295 kittens. The youngest females that gave birth were 12 months old, whereas the oldest was11+ years old. On average, females giving birth were 3.8 years old (n=62), with a mode of one+ years old. Mean litter size was 3.7 kittens±1.0 (range: one to six; n=77 litters), with three or four kittens comprising 67.5% of litters. Mean litter size declined significantly from spring to late summer. Females kept in big enclosures and during a Feline Immunodeficiency Virus (FHV-I) outbreak showed higher mean litter sizes.
Births occurred from March to August, most occurring during the spring (91% of litters; n =65). Late litters were mostly from second gestations (following the loss of the first litter of that year) and females in their first gestation. Females giving birth in March were significantly older than those giving birth later, especially from May to June-August. Experienced females gave birth in March and April.
The sex ratio was 1:1, with most of the litters containing both sexes.
Outside a disease epidemic episode, the main causes of known mortality were infanticide (54%) and diseases (44%). Kittens affected by infanticide had lower survival than those affected by FHV-I. Our results show that the wildcat has low reproductive plasticity. This may partially explain its fragmented distribution across Europe.
Although our work was in captivity, it presents new knowledge on the reproductive biology of the wildcat, which is important both for conservation of wild populations and for the management of captive ones, for example, the role of seasonality and environmental variables on litter size, or the causes of kitten mortality

Introduction

The European wildcat population has declined dramatically during the last several centuries, displaying a fragmented and discontinuous distribution in Europe (Stahl and Leger, 1992; Stahl, 1993; Nowell and Jackson, 1996). Following the atlas published in Spain (García-Perea, 2007), its distribution is fragmented and mainly overlaps the mountain systems of the Iberian peninsula, located in well preserved forest (Ruiz-Olmo et al., 1995; Aihartza et al., 1999) or Mediterranean scrubland (Lozano et al., 2003, 2013).

According to Stahl (1993) and Sunquist and Sunquist (2002), there is little information about this endangered species, including its breeding performance. For this reason, there is often a trend toward using the vast knowledge gathered from domestic cats for this species (Artois et al., 2002; also see Turner and Bateson, 2014, for a summary). The few studies on *F. silvestris* reproduction are often fragmentary, contain few data and have been carried out in several Central European countries, Scotland and Italy (Matthews, 1941; Suminski, 1962; Volf, 1968; Meyer-Holzapfer, 1968; Condé and Schauenberg, 1969, 1974; Corbett, 1979; Heptner and Naumov, 1980; Raimer adn Schneider, 1983; Kitchener, 1991; Stahl and Leger, 1992; Daniels et al., 2002; Angelici and Genovesi, 2003; Hartmann, 2005; García, 2006). They all show a seasonally polyoestrous cat, normally having a single litter in spring comprising two to five kittens. Pregnancy lasts 68 (63 to 69) days, and there is little information about the sex-ratio and other litter characteristics. None or very little of this information notes the age of the females, temporal changes in characteristics of the litters, or kitten mortality. For example, although infanticide is considered an adaptive and widespread strategy in felids, it has been studied mainly in big cats such as lion (*Panthera leo*), tiger (*Panthera tigris*) (Singh et al., 2014), leopard (*Panthera pardus*) (Balme and Hunter, 2013), puma (*Puma concolor*) and jaguar (*Panthera onca*). It has also been detected in Iberian lynx (*Lynx pardinus*) (López et al., 2010) and domestic cats (*Felis catus*) (Pontier and Natoli, 1999). However, there is very little information on infanticide in small and elusive felids like European wildcats (López et al., 2010).

Because of the difficulty of studying European wildcats in wild conditions, most of these studies were conducted with captive animals. These studies have, of course, conditions differing from those of wild animals. However, captivity offers us some other advantages and opportunities such as: controlled and standard conditions; proximity and handling of the animals (including physiological samples and veterinary care); knowledge of paternity and exact age; larger samples; and the possibility of changes in environmental conditions.

Breeding patterns are a basic tool for several management and conservation strategies. For instance, demographic models, energy and food demand assessments, and population viability analyses, can be developed only with consistent and detailed information on breeding parameters. There is no information on the European wildcat's breed-

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ing patterns in the Iberian peninsula, except for the scarce data of Ruiz-Olmo et al. (1995), which were also gathered in captivity.

The present study is the first major work published on the reproductive performance of European wildcats from the Iberian peninsula. This study was carried out in captivity and its objectives were to describe female age at breeding, seasonality of breeding, litter size, causes of kitten mortality, neonate sex-ratio, and some factors affecting these patterns. These observations yielded some new data on the effect of female age, female experience and the litter birth-month on reproductive performance and kitten mortality, which are presented here for the first time. With this new information, we contribute a more detailed picture of the breeding performance of *F. silvestris*, which can be used in conservation strategies and programmes, and in the captive management of the species.

Materials and methods

The European wildcat breeding project started in 1983 at the Vallcalent Centre (town of Lleida, Spain). The objectives of the Centre, over the study period, were:

1) At the beginning, to establish a captive stock that ensured the maximum genetic variability and make possible a recovery of the species in the wild;
2) To learn about the species' biology, behaviour, veterinary care, captive breeding and management;

A total of 295 European wildcats were managed, and 77 litters were recorded.

Facilities

The European wildcats studied in this work were held in captivity. During the study period, the facilities where we kept the animals changed from small enclosures at the beginning, to bigger and more environmentally complex facilities during the second period of the study. Each facility consists of an outside enclosure, ranging from 6.7 m^2 (during the first years, 1983–1997) to 207 m^2 (1998–2007). Females were given access to two sleeping nest boxes (0.1 m^3) per facility during the first period and six to eight boxes (0.1 m^3) per facility during the second period. Cats were fed "*ad libitum*" with mice, rats, rabbits, quails, and chickens. Veterinary care was given, including vaccinations (Fevaxyn i-CHP until 2003, and Fevaxyn Pentofel from 2004) against feline rhinotracheitis, feline calicivirus, feline panleucopaenia and feline leukaemia. Also, an anti-parasite treatment (against *Clamydia psittaci*) was applied. However, an acute episode of rhinotracheitis was detected between 2001 and 2003, which affected most of the kittens born in that period.

Study animals

Data on breeding from a total of 45 adult animals (11 males and 34 females) were used, including a total of 18 founders (ten males and eight females) that arrived at the Vallcalent Centre from different Iberian locations: Pyrenean mountains in Lleida and Huesca provinces (Males: eight; Females: five), Cantabrian mountains in the Cantabria province (Females: one), Central System mountains in the provinces of Ávila and Madrid (Males: two; Females: two).

Births, litter size, and breeding season

Mating was detected by characteristic and insistent mewing from the males and females (animals were monitored daily to detect this behaviour). Because the cats remained undisturbed, no exact data on copulations and gestation length could be gathered. We focused our attention on births and development of litters. The exact dates of birth could be assessed by means of: (a) previous X-rays taken at about 15–30 days before the a priori estimated date of birth (38–53 days of pregnancy); (b) males that were found outside the boxes; and, (c) females that stopped eating one day before or on the day of birth (food and food remains were weighed in a daily basis). On some occasions, females that lost all the kittens of their litter at the beginning of the reproductive season would have a replacement litter at the end of the summer of the same year.

Litter size and kitten sex-ratio were recorded between three and five days after birth (paying special attention to the presence of remains of killed or dead kittens) and always while keeping the females foraging outdoors.

Age determination

For almost all of the animals born at the Vallcalent Centre, the age of the breeding was known exactly (each animal was marked by either earrings or earcuts until 1998, and thereafter by subcutaneous transponders implanted at 45–60 days after birth). For the founders, the approximate date of birth (and age) was known for animals that arrived at the centre facilities as kittens. For other adult founders, age class was determined from their teeth when they died (Condé and Schauenberg, 1978; García-Perea et al., 1996), but some ages could not be used for some analyses.

For statistical analysis we coded animals in their first year of live as 0+ (from zero to 12 months old), in their second year of live 1+ (from 12 to 24 months old), and so on.

Mortality

When possible, the cause of death was studied and established. Necropsies were carried out, and samples were collected for analysis. When it was necessary, direct immunofluorescence tests and PCR (Stiles et al., 1997; Burgesser et al., 1999) were used in order to asses which infectious agent caused death.

Reproductive experience

We assessed female reproductive experience during all the previous births of a female.

Statistics

Litter sizes were compared between enclosure size and the phase of disease outbreak by means of Mann-Whitney U tests; and between month of litter birth, age of the mother at litter birth and reproductive experience of the mother, using Kruskall-Wallis tests. To study the effect of a replacement litter on reproductive performance, we compared the mean litter size of the first litter and the second litter of the year (for females which have replacement litters), with that of females that have just one litter per year using a Kruskal-Wallis test. We examined the relationship between age of mother and month of litter birth using a Kruskall-Wallis test. We also compared the mortality curves of the three categories of litters (first litters of the year for females which later on the same year had a replacement litter; replacement litters, and just one litter per year) until 90 days old with Kaplan-Meier. European wildcat kittens are weaned at 6–7 weeks of age when they can feed on solid food. Independence and dispersal of the kittens starts at 4–5 months of age (Stahl and Leger, 1992; Nowell and Jackson, 1996). So, in captivity, we arbitrarily define 90 days old as a reasonable time frame to study the effect of mothers' performance on kitten mortality. Finally, we also compared litter sizes between one+ year old vs >two+ years old female; and between primiparous mothers experienced ones by means of Mann-Whitney U tets.

We used the Fisher test to compare the monthly distribution of litters and χ^2 test to compare the monthly distribution of kittens by enclosure size, disease and reproductive experience.

Sex ratio and the number of litters that comprised a single sex or both sexes were compared by means of χ^2 test.

We described the mortality curves of the two most important known causes of mortality (FHV-I and infanticide) during the first 90 days of life using the Kaplan Meier procedure, and compared the mortality caused by them using the Long Rank test.

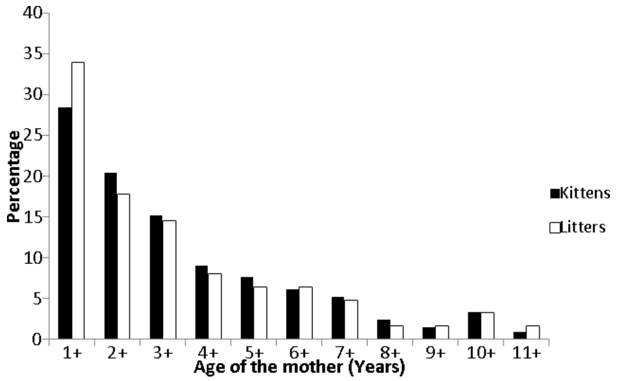

Figure 1 – Percentage of kittens or litters born from each age class of breeding wildcat females held at the Vallcalent Centre. The horizontal axis represents the age of the mother, 1+ indicating females between 12 and 24 months old, etc.

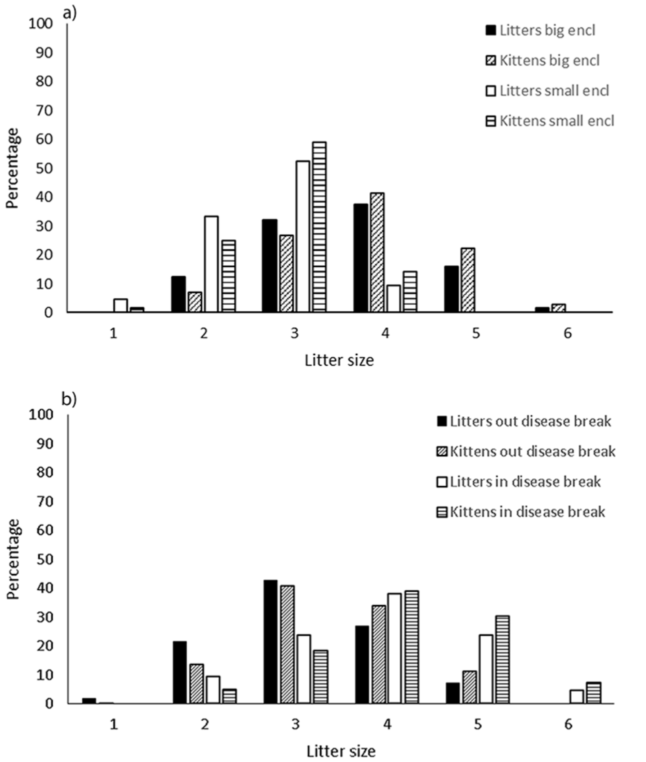

Figure 2 – Frequency distributions of kittens and litters by litter size born from captive wildcat females held at Vallcalent Centre in small vs big enclosure facilities (a) or during disease outbreak (2001-2003) vs before/after disease outbreak (b).

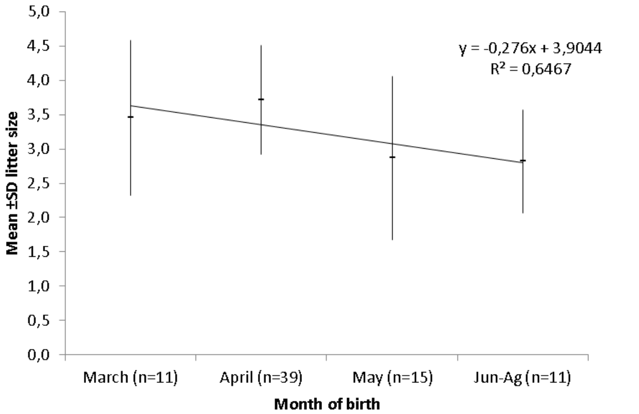

Figure 3 – Mean litter size of captive wildcats from Vallcalent according to the month of birth of the kittens. n indicates the number of litters in each month, considering just the litters with precisely known birth month and number of kittens born.

Results

Age of breeding

The youngest mating female was ten months old, and the youngest female that gave birth was 12.3 months old. Fig. 1 shows the age of breeding females for all birth events. One+ year old females accounted for 32.8% of the litters gathered. On average, females giving births were 3.8 ± 2.7 (mean±SD) years old (n=62), with a mode of one year old. The oldest breeding female was 11+ years old when she gave birth.

Litter size at birth

Statistical differences were found in litter size before and after change in enclosure size (Mann-Whitney U test=271.5; $p<0.0001$); with bigger litter sizes in big enclosures (n=56; 3.6 ± 1.0) than in small enclosures (n=21; 2.7 ± 0.7), and also during and outside the disease outbreak (Mann-Whitney U test=355; p=0.005), with smaller litter size outside the disease outbreak (n=56; 3.2 ± 0.9) than during it (n=21; 3.9±1.0). Litter size ranged from two to six, with four kittens being the most frequent size in big enclosures and during the disease outbreak, while it ranged from one to four in small enclosures, and one to five outside the disease outbreak, with three kittens being the most frequent litter size in both cases (Fig. 2). Overall three and four kittens accounted for 67.5% of litters and 69.1% of kittens respectively (n=77 and n=259).

We found statistical differences in mean litter size according to month of birth (Kruskall-Wallis test, df=3, p=0.003); litters were bigger in April with 3.7 ± 1.2 kittens (n=39 litters and 145 kittens) and declined through to late summer, when mean litter size was 2.8 ± 0.8 kittens (June to August n=11 litters and 31 kittens) (Fig. 3).

We did not find statistical evidence of the effect of age (Kruskall-Wallis test=10.3, df=6, p=0.113) or the reproductive experience of the mother (Kruskall-Wallis test=9.7, df=6, p=0.137) on mean litter size. However, we found statistical differences between females one+ year vs all others females grouped (Mann-Witney U test=243; n=62; p=0.003) and between inexperienced primiparous females vs experienced ones (Mann Witney U Test=483.00, p=0.007). Females one+ years old had a mean of 2.9 ± 0.9 kittens/litter (n=21), while all older females had a mean of 3.7 ± 1.0 kittens/litter (n=41). With respect to the effect of experience, primiparous females had a mean of 3.0 ± 1.0 kittens/litter (n=34), while experienced ones had 3.7 ± 1.0 kittens/litter (n=43) (Fig. 4). Overall, the mean litter size was 3.4 ± 1.0 kittens per litter (n=77).

Seasonality

No differences were found when comparing the monthly distribution of litters before and after the change in enclosure size (n=76 litters, Pearson χ^2=6.689, p=0.075), and during and before/after the disease outbreak (n=76 litters, Fisher test=3.068, p=0.382). However, we found differences in the monthly distribution of kittens born before and after the change in enclosure size (n=271, Pearson χ^2=15.150; df=3; p=0.002) and during and before/after the disease outbreak (n=274, Pearson χ^2=13.650; df=3; p=0.003). In big enclosures there were more kittens born in April and fewer in March than in small enclosures. With respect to disease, there were more kittens in April during the disease outbreak, and fewer in March and from June to July than before/after the disease outbreak.

Considering all the data, a seasonal pattern was found for births, which occurred only from March to August (Fig. 5). Most births occurred from March to May (85.5% of litters, n=65; 88.0% of kittens, n=241), especially in April (51.3% of litters and 55.5% of kittens). However, the remaining 11 litters were born in the summer. Three of these were from second gestations of females who had lost all the kittens of their first litters, and five were primiparous females.

Some females lost all the kittens in their first litter during a reproductive season. In some of these cases, they had a replacement litter later in the same year (late summer, July or August). We did not find statistical differences between mean litter size of females who lost all the kittens in their first litter of the year, their replacement litters (second litter in the same year) and the litters of females which had

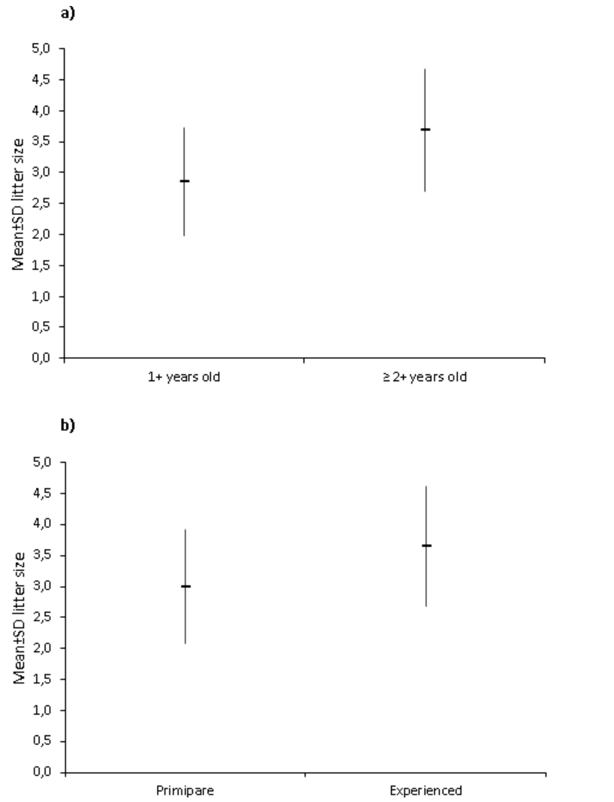

Figure 4 – Mean litter size of captive wildcats according to the age (a) or reproductive experience (b) of the mother. Data were grouped as females reproducing while they are between 1 and 2 years old (1+) vs females older than 2 years (a), and primiparous females vs experienced females in their second or later reproductive event (b).

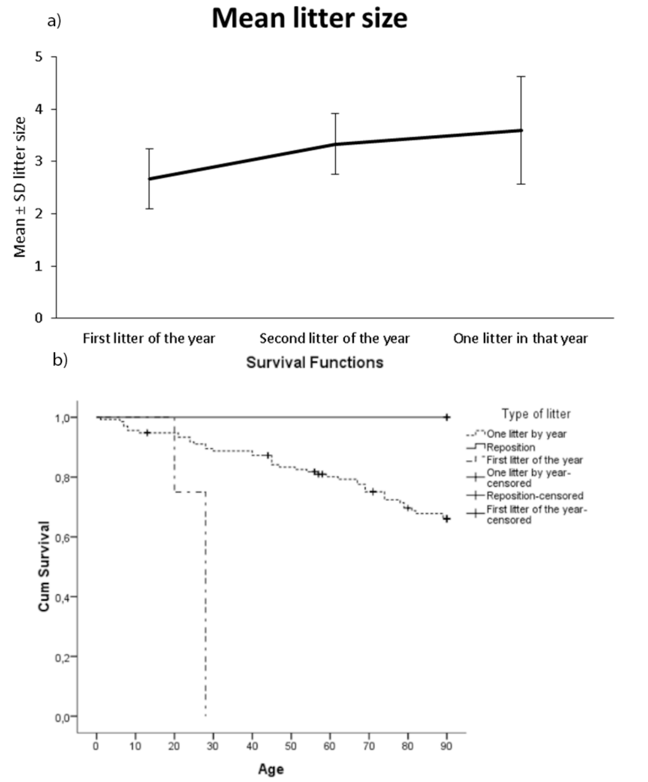

Figure 6 – (a) Mean litter size for first litter of the year (for females which lost all their kittens in that litter, and gave birth to a replacement litter in the same year), second litters (replacement litters, usually in late summer, from those females which lost all the kittens in their first litter of the year) and females that had just one litter in that year. (b) Cumulative survival curve until 90 days of living kittens born from different types of litter.

just one litter per year, (n=77, Kruskal-Wallis=1.793, df=2, p=0.458), although the results suggest that replacement litters had higher mean litter size (3.3 ± 0.8 kittens/litter, n=3) than the same females had in the first (lost) litters of the year (2.7 ± 0.8 kittens/litter, n=3), and similar to litters from females with just one litter per year (3.6 ± 1.0 kittens/litter, n=71) (Fig. 6 a). We found statistical differences (Log Rank test=49.715, df=2, p=0.000) in the survival time of kittens for each type of litter, with kittens from the first litter of the year having the lowest survival time (Mean Survival time±SE=26.0 ± 1.3, n=8), followed by the kittens from females with just one litter per year (Mean Survival time±SE=76.1 ± 2.2, n=135), while none of the kittens born in replacement litters died before 90 days old (Fig. 6 b).

Considering all the litters with precisely known birth dates and mother age, we found statistical differences between the ages of mothers giving birth in different months (n=62, Kruskal-Wallis=12.969, df=3, p=0.005). On average, the oldest females gave birth in March (n=9, 6.6 ± 3.0 years old), and the youngest gave birth in May, (n=11, 2.0 ± 1.2 years old), while those giving birth in other months were intermediate in age (Fig. 7).

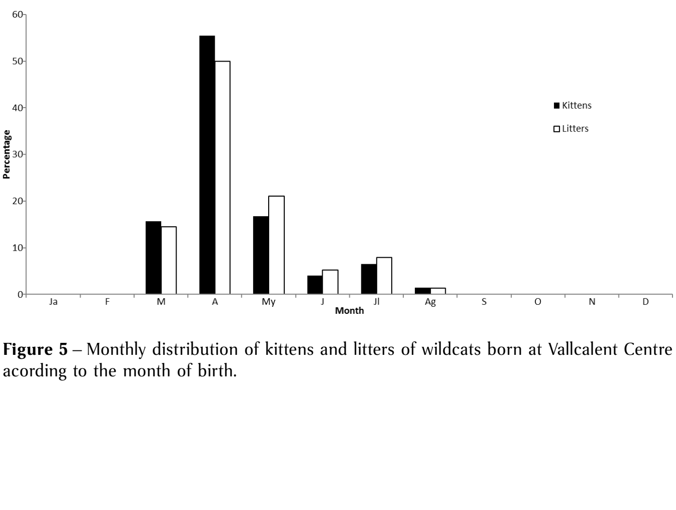

Figure 5 – Monthly distribution of kittens and litters of wildcats born at Vallcalent Centre acording to the month of birth.

Regarding the litters of known birth date and the number of reproductive events for each mother, we found a significant relationship between the number of reproductive events and the month in which they gave birth (n=76 litters, Fisher test=25.9, p=0.021). Females with greater previous experience were more likely to give birth in March and especially in April. Until their fourth reproductive event, some females gave birth in May, June and July, but after that all subsequent births took place in March or April (Fig. 8).

Sex-ratio

From kittens of known sex, 110 neonates were males and 102 females, which was not statistically different from a sex ratio of 1:1 (χ^2=0.302; df=1; p=0.583).

Litters comprising kittens of both sexes were more frequent than expected (χ^2=5.918; df=1; p=0.015), representing 65.6% of litters of

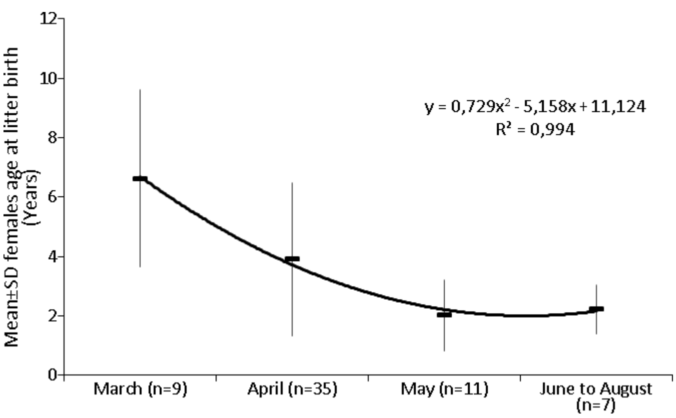

Figure 7 – Mean age of wildcat females according to birth month for those litters with precisely known date of birth. n indicates the number of litters in each month considering just those with precisely known age of the mother and the birth date of the kittens.

Table 1 – Causes of kitten mortality for captive European wildcats in Vallcalent Centre.

	All kittens		Excluded FIV-I outbreak[1]	
Cause of kitten death	**n**	**%**	**n**	**%**
Infanticide	28	23.93	21	35.59
Accident	1	0.85	1	1.69
Feline Herpes virus (FHV-I)	61	52.14	14	23.73
Panleucopedia	1	0.85	1	1.69
Ascitis	1	0.85	0	0
Anal prolapse	1	0.85	1	1.69
Diaphragmatic hernia	1	0.85	1	1.69
Starvation	1	0.85	0	0
Unknown	22	18.8	20	33.9
Total	**117**	**100**	**59**	**100**

[1] Excluding all the kitten death during the 2001-2003 rhinotracheitis epidemic episode (FHV-I)

known sex (n=61), compared with 34.4% of single-sex litters (14.8% of litters were only males and 19.7% were only females).

Factors affecting kitten mortality

Considering all dead kittens, the main cause of kitten mortality was diseases (55.6%, Tab. 1), practically all of them infectious. Considering only the cases in which mortality causes were established, 68.4% of kitten deaths were due to diseases. However, FHV-I alone was responsible for most of these deaths, affecting 61 cats (12 adults, 35 kittens and 14 of unknown age at death), especially during the FHV-I epidemic episode of 2001-2003.

Excluding this episode and considering only those kittens with a known cause of death (n=39), infanticide accounted for 53.9% cases, and diseases caused an additional 43.6% of deaths.

Among diseases, we must pay special attention to rhinotracheitis caused by Feline Herpes Virus (FHV-I). This disease was responsible for the deaths of 10.8% of the kittens born from 1983–2000 at the Vallcalent facilities (n=93), 47.1% born in 2001 (n=17), 46.2% in 2002 (n=26) and 62.8% in 2003 (n=43), and just 3.9% from 2004 to 2007 (n=102). This acute episode coincided with the change to the new and bigger facilities. Some isolated cases during the second week of age (a single litter) led us to consider a foetal infection as the infection vector.

Survival time of kittens affected by infanticide (Mean Survival time $\pm$SE=27.1$\pm$4.6 days, n=23) was significantly lower (Log Rank test=35.02, df=1, p=0.000) than those affected by FHV-I (Mean Survival time $\pm$SE=70.7$\pm$3.7, n=47). Half of the kittens affected by infanticide died at 28.0$\pm$1.5 days of life, while half of those affected by FHV-I died at 81.0$\pm$6.3 days of life (Fig. 9).

Infanticide was recorded for 12 of 34 monitored breeding females, affecting 19.5% of the monitored litters (n=77). However, a single female caused three, and another female caused two of the 15 recorded cases of infanticide. In five of these cases, all kittens in the litter (n=16) died from infanticide. We found statistical differences (Mann-Whitney U-test=216; n1=48: n2=14; p=0.043) between the mean ages of females who lost some kittens from infanticide (n=14, 3.0$\pm$3.0 years old, ranging from one to ten years old), compared with those females who did not lose any kittens from infanticide (n=48, 4.0$\pm$2.6 years old, range from one to 11 years old).

Discussion

Basic breeding patterns

The general breeding parameters of captive European wildcats in Spain were within the normal range reported for the species (Matthews, 1941; Volf, 1968; Meyer-Holzapfer, 1968; Condé and Schauenberg, 1969, 1974; Corbett, 1979; Raimer adn Schneider, 1983; Eisenberg, 1986; Stahl and Leger, 1992; Angelici and Genovesi, 2003; Hartmann, 2005; García, 2006): a seasonally polyoestrous species; giving birth mostly in spring; and more often a litter size of three to four kittens. European wildcat females were able to breed from their first year of life (Hartmann, 2005), until a maximum of 11 years old. We had ten females that gave birth at 12 month old, so they must have been sexually mature at ten months old, in agreement with other authors, who determined that sexual maturity for both sexes was attained at ten months old (Meyer-Holzapfer, 1968; Volf, 1968; Condé and Schauenberg, 1969; Schauenberg, 1980). Females of one+ year old accounted for 32.8% of the litters and 27.4% of the kittens recorded, contrary to the pattern described by Condé and Schauenberg (1969), who found that older females accounted for most of the litters. Our results can probably be explained because our captive management, for example, by keeping young females together with males. In our study, no effect on litter size due to female age was observed. The sample for females older than six years old was too small, preventing the possibility of studying the effect of senility on litter size. Very little is known about the energetic requirements of European wildcats. However in domestic cats, the mean maintenance energy requirements are about 50 to 60 kcal/kg of body weight (Bermingham et al., 2010), but for a female with more than two kittens, the energy requirements increase, during the lactation, 2 to 2.5 times the maintenance energy requirements (National Research Council, 2006). On the other hand, Kienzle (2006) and Bermingham et al. (2010) show that females of domestic cats younger than two years old, have higher maintenance energetic requirements than older females. Then, in situations when the food resources are a limiting factor, younger females will have less available resources to allocate to breed than older females. Nevertheless, in captivity, with individuals fed ad libitum, young females can also satisfy their maintenance and breeding energetic requirements.

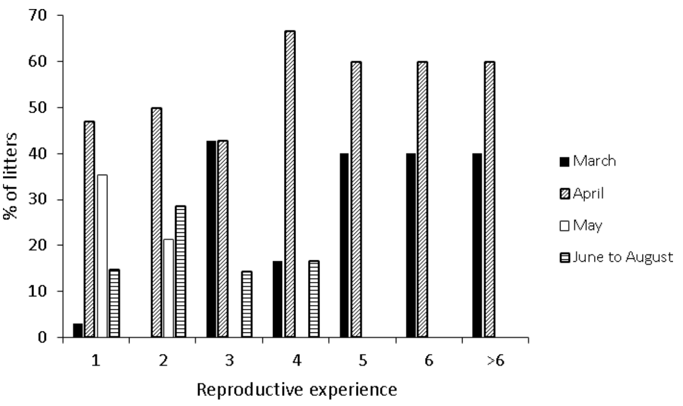

Figure 8 – Monthly distribution of litters according to the females' reproductive experience (number of previous litters per female).

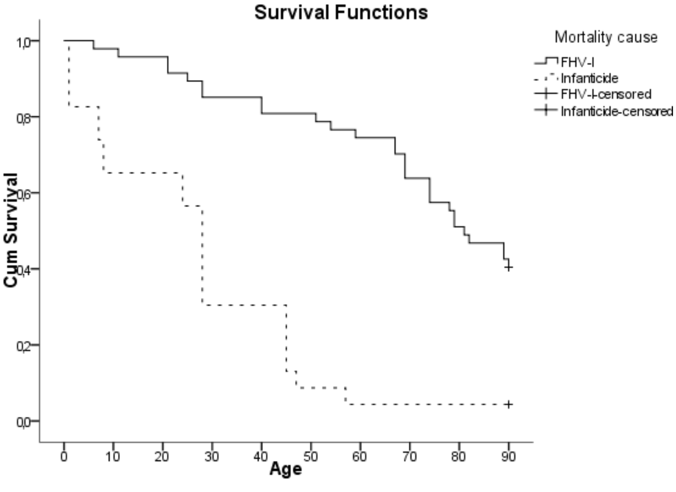

Figure 9 – Cumulative survival curve until 90 days of living kittens affected by the two most common causes of mortality, infanticide and FHV-I.

Among felid species, a standard fecund female seems to produce on average about two to four litters during its life, mainly due to the short mean life expectancy (Caro, 1994; Kruuk, 1995; Sunquist and Sunquist, 2002). This also seems to be the case for feral and European wildcats from Scotland (Balharry and Daniels, 1998). Based on the mean number of kittens per litter, this represents six to 16 kittens. Although we observed females with as many as nine litters during their lives, this occurred because in captivity European wildcats tend to live longer than in the wild and also captive management promotes reproduction, which consequently increases chances to reproduce.

Our work gives some new findings. On one hand, litter size was significantly correlated with birth month, since litters born in April produced one more kitten per litter than those born later (June-August), with the litters of March and May being intermediate in size.

On the other hand, our results show that one-year-old females and primiparous females have smaller litters than older or experienced females. Many females breeding in March and April were mainly middle-aged females (four to eight years old), while those breeding in May to August were more often younger (one to three years old). As said before, younger females have to allocate more resources to maintenance requirements than mature females, and then have fewer resources available to reproduce. So if younger females gave birth during late spring and summer, these litters from females with higher maintenance requirements will tends to be smaller.

European wildcat females may rarely have two litters in a single year. Indeed, Sunquist and Sunquist (2002) considered that two or three successful litters in a year seem unlikely, except in times of peak food resources, i.e. high rodent populations. In contrast, domestic cat females often breed twice a year, and almost ten per cent can breed three times annually (Liberg, 1983; Artois et al., 2002; Nutter et al., 2004). However, as Condé and Schauenberg (1974) and Volf (1968) reported, some females presented a second oestrus and a second litter in late summer or early autumn after losing their first litter. Sunquist and Sunquist (2002) added the possibility of new breeding females failing to conceive during the previous oestrous cycles also could have a litter in late summer or early autumn. In line with this, our study never found a female with two successful litters in a year, despite "*ad libitum*" food, which was, therefore, not a limiting factor, and the 11 late litters observed in this study correspond to females losing their first litter, females in their first gestation (after failing to conceive during the first oestrus) or breeding females of one year old. Our results suggest that females that lost all the kittens in their first litter of the year, subsequently have a larger litter, and their kittens have a higher survival probability in that second (replacement) litter, which are comparable to those of females that have just one litter per year, although these results should be considered with caution because of the small number of replacement litters.

In our work, the sex ratio was 1:1, with most litters containing both sexes, in agreement with that stated by other authors for European wildcats (Tryjanowski et al., 2002), for domestic cat (Liberg, 1980) and for other medium-big felid species (Macdonald et al., 2010) and small monogamous felids (Faust and Thompson, 2000). Condé and Schauenberg (1974) found that the sex ratio in the wild was biased towards males, but in the captive population it was balanced, as in our case.

Kitten mortality

There is very little information on European wildcat kitten mortality, especially during the first few weeks of life. In our study, 45% of the kittens died before 90 days old. High mortality rates of kittens in domestic cats have been detected in some studies. For example Nutter et al. (2004) reports that 48% kittens die or disappear before 100 days, although she reported a case where 90% of kittens died before they were six month old. In our case, under normal conditions (outside disease outbreak) and among the confirmed cases of mortality, infanticide was the main cause of death. Infanticide is widespread amongst felids (Schaller, 1967, 1972; Hornocker, 1970; Packer, 1984; Quinn et al., 1987; Emmons, 1988; Kitchener, 1991) and is often caused by non-parental males (Lukas and Huchard, 2014), although it can be perpetrated by both sexes (Palombit, 2015). However, there is very little information on infanticide in small cats such as *F. silvestris* and practically none about maternal infanticide. In our work at Vallcalent Center, all the infanticide events were perpetrated by females, since males were kept away from females and their kittens once they gave birth. Whatever the adaptive value (if any) of maternal infanticide, it is a very extreme strategy used seldom in the wild (von Schmalz-Peixoto, 2003). Two possible explanations have been proposed for maternal infanticide: it could be a social pathology triggered by conditions of captivity (Hrdy, 1979); or it could be a tool for maternal manipulation of the offspring (for example manipulating the sex ratio by killing or neglecting the kittens of the most costly sex Hrdy, 1979; Eshel and Sansone, 1994). von Schmalz-Peixoto (2003) found that amongst predators which feed on large prey, females perform infanticide without cannibalism, which suggests that for these species, kittens are too small to be consumed outside of starvation times. The European wildcat feeds mainly on rabbits or rodents (Malo et al., 2004). In the case of *Felis silvestris*, von Schmalz-Peixoto (2003) reported active female infanticide in 67% of the 29 litters produced by 7 dams studied in captivity, all of them with cannibalism, showing that maternal infanticide and cannibalism may occur in this species in captivity. This agrees with her prediction that kittens should be consumed, as they are of similar size to the natural prey of European wildcats. In our case, most of the females which committed infanticide also ate their kittens, although the dams were fed "*ad libitum*". This together with the fact that few females (12 of 34) were involved in infanticide, and only two of them were responsible for one third of all cases (5 cases and 13 kittens) suggests that it is caused by individual aberrant behaviours that could appear in some circumstances (Hrdy, 1979), perhaps due to captivity, stress, or early management and could explain most of these cases.

The second most important cause of death under normal conditions was infectious disease and related complications. In many cases a single kitten per litter was affected, revealing that these were occasional cases. *F. silvestris*, like most felids, is susceptible to some viruses such as feline leukaemia FeLV, feline respiratory disease ("cat flu"), including rhinotracheitis virus FHV-I and a calicivirus FCV, feline immunodeficiency virus (FIV), feline parvovirus (FPV), also known as feline panleucopaenia, feline coronavirus FcoV, and rabies (Ashton and Jones, 1980; Boid et al., 1991; Kitchener, 1991; McOrist et al., 1991; Artois and Remond, 1994; Nowell and Jackson, 1996; Daniels et al., 1999; Leutenegger et al., 1999; Fromont et al., 2000; Ostrowski et al., 2003; Munson et al., 2010). Some of theses infectious diseases are present in wild populations of the European wildcat in Spain, and are considered as a risk factor in their conservation (López-Martin et al., 2007). Most of these diseases were absent from the Vallcalent's facilities, especially the new enclosures. However, we had a severe infection caused by rhinotracheitis virus, FHV-I, which affected, and normally killed, most of the kittens born between 2001 and 2003. The origin of this disease was unknown, spreading within the adults which presented some symptoms (but did not kill them), but affecting severely their kittens. This episode is related to changes at the facilities which could have stressed the animals; and which may contributed to the spread of the disease, as has been documented by Munson et al. (2010). The successful treatment of this outbreak allowed us to reduce its impact in subsequent years.

Although the most common cause of mortality was FHV-I, kittens affected by infanticide died earlier and had lower probability of survival than those affected by FHV-I. This was because infanticide generally occurs during the first few days of life of the kittens (Pontier and Natoli, 1999; von Schmalz-Peixoto, 2003), while FHV-I, as with many other infectious diseases in cats, is not necessarily lethal (Lozano and Malo, 2012). The infected individuals spread the disease, and finally, some of them recovered from the disease and showed a good physical condition, while others died.

Reproductive patterns of a low reproductive plasticity species: ecological and conservation implications

Reproductive plasticity has been defined as the ability of an animal to modulate its reproductive functions in response to environmental changes (Jeong and Paik, 2017). It has been observed in a variety of animals, but in some cases, the environmental cues, and the mechanisms through which these cues affect reproductive biology are poorly understood (Sowa et al., 2015).

The European wildcat has a wide distribution area (especially longitudinally), and occurs in a wide range of environmental conditions. Photoperiod varies less geographically than other environmental factors like temperature, rain, prey density or prey type, etc. Despite these wide range of environmental conditions, the general picture of the reproductive pattern is almost the same throughout its distribution area: a seasonally polyoestrous species; giving birth mostly in spring; and more often a litter size of three to four kittens.

Recent studies show that photoperiod is crucial for seasonal reproduction (Rani and Kumar, 2014; Weems et al., 2015), and that the signalling pathway downstream of light detection and signalling is fully conserved between mammals and birds ((Nishiwaki-Ohkawa and Yoshimura, 2016)). The fact that mammals and birds share the same route illustrates the importance of the photoperiod in vertebrates. Brown (2010) found that seasonality of reproduction is highly sensitive to the photoperiod for some felids (Pallas' cat, *Octolobus manul*), while others (ocelot (*Leopardus pardalis*), tigrina (*Leopardus tigrinus*), margay (*Leopardus wiedii*), lion (*Panthera leo*), leopard (*Panthera pardus*), fishing cat (*Prionailurus viverrinus*)) are not influenced at all by the photoperiod. On the other hand, domestic cats in tropical latitudes, (as other tropical felids) are not seasonal breeders, while domestic cats living in northern latitudes are seasonal breeders (Hurni, 1981; Sunquist and Sunquist, 2002). Long daylight periods following periods of shorter daylight induce oestrus in domestic cats (Hurni, 1981). Although the photoperiod varies from North (North of Scotland) to South (South of Spain) of the European wildcat's distribution, the first sudden change from short daylight to long daylight occurs from mid January to mid February (2 hours more of light in North Scotland and 1 hour in South Spain, respectively). Assuming that at that time females are in oestrus, and considering a gestation length of 63-69 days, most births will occur in April. Is worth noting that Daniels et al. (2002) found that wild-living cat females (including wildcats, domestic cats and their hybrids) gave birth throughout the year, but less in winter, and that cats more related to wildcats were more seasonal than those closer to domestic cats. However, in Scotland long-term hybridisation with domestic cats explains this weaker seasonality, since domestic cats can reproduce all year round (Nutter et al., 2004). There are other European carnivorans that also have litters all year round, e.g. common genet (*Genetta genetta*) (Camps et al., 2017).

On the other hand, the mean litter size of the European wildcat shows little variability throughout the whole distribution range of the species (means of 3-4 kittens/litter), which contrasts with the flexibility of other felid species, like Canadian lynx (*Lynx canadensis*) and bobcat (*Lynx rufus*), which adapt their litter sizes and rates of pregnancy to the cycles of their main prey *Lepus americanus* (Rolley, 1985; Tumlison, 1987; Lovallo et al., 1993; Sunquist and Sunquist, 2002; O'Donghue et al., 2010), or other species of medium-sized European carnivorans like red foxes (*Vulpes vulpes*), which predict vole (*Microtus arvalis*) availability at the birth date, and adjust their litter sizes to the abundance of the voles (Lindström, 1988) or change their productivity according to a decline in seabird availability (Zabel and Taggart, 1989); the Eurasian otter's (*Lutra lutra*) reproductive parameters vary with available environmental resources (Ruiz-Olmo et al., 2002; Ruiz-Olmo and Jiménez, 2009; Ruiz-Olmo et al., 2011). This shows that for these species, the effort allocated to reproduction is timed and adjusted to maximise reproductive output to the food energy available.

In the domestic cat, it is estimated that the maximum milk yield is attained during the third or fourth week of lactation (National Research Council, 2006). So if the European wildcat has to adjust its reproduction to satisfy its maximum nutrient requirements, births should occur three or four weeks before the highest food availability. This period will depend on the main prey species. The European wildcat is considered a facultative specialist, which changes from rabbits to rodents as main prey, depending on variation in their local abundance and availability (Malo et al., 2004). The African wildcat, *F. lybica*, a related species, is also considered as a facultative specialist, which changes from murids to other preys depending in their abundance and availability (Herbst and Mills, 2010). In Spain, rabbit abundance is higher in June than in October (Barrio et al., 2010). In Scotland, where European wildcats prey mainly on rabbits, the abundance of young rabbits was higher in summer, and the abundance of rabbits with myxomatosis (these two categories of rabbits were supposed to be more vulnerable to capture) was higher in autumn (Corbett, 1979). In Ports de Tortosa i Beseit, where *Apodemus sylvaticus* represents 3/4 of the prey of the European wildcat (Such-Sanz et al., 2007), availability of rodents is highest in spring (Such-Sanz et al., 2003), while in Piñeiro and Barja (2011), the abundance of *Apodemus sp.* (also the main prey) was highest in summer, although it was consumed more in autumn, when its vulnerability to capture was highest.

Because there are few variations in seasonality of births and litter size of the European wildcat despite its wide distribution area, and its varying trophic ecology, we argue that it displays low reproductive flexibility. However, within this stable reproductive framework, the European wildcat can make minor adjustments, like replacement litters, or variations in litter size in agreement with intrinsic (age of female) or extrinsic (disease outbreaks, enclosure size) factors. In addition, in our case, these minor variations occurred in captivity with unlimited food, which would normally influence reproductive output.

According to the data above, it seems than there are two main factors that affect the main parameters (seasonality and litter size) of reproduction in carnivorans: seasonal changes in food availability or risk of capture, and photoperiod. In the case of the European wildcat, the mechanisms underlying the translation of environmental cues to reproductive strategies are not well understood. We suggest that photoperiod plays a more important role in determining the seasonality of reproduction in the European wildcat. However, we think that more research is needed to elucidate the role of photoperiod and food resources, and their interactions and impacts on seasonality and litter size in the European wildcat. Low reproduction flexibility is important because births should be timed such that most energy expenditure coincides with most food availability in the environment (Hauer et al., 2002; Sunquist and Sunquist, 2002), but a lower plasticity is disadvantageous by making it more difficult to adapt to different prey abundance patterns geographically and temporally (Heggberget, 1993; Kruuk, 1995; Ruiz-Olmo et al., 2002; Ruiz-Olmo and Jiménez, 2009; Ruiz-Olmo et al., 2011).

In felids there is a high energy cost during pregnancy and lactation which limits felid litter size (Deag et al., 2000; National Research Council, 2006). Large litters compromises female hunting success during its pregnancy, need much more milk, have a lower individual birth weight, grow more slowly, and are weaned earlier (Loveridge, 1986; Deag et al., 1987, 2000; Oftendal, 1989; Kitchener, 1991). Litter size is often small (two to four young), except in the case of the "domestic cat lineage", including jungle cat (*Felis chaus*), sand cat (*Felis margarita*), and European and African wildcats, where following Sunquist and Sunquist (2002), litters are somewhat larger and reach means of three to five young. Thus, the litter size of *F. silvestris* is intermediate compared with that of other felid species. European wildcat females, on average, can contribute to a population through giving birth to a low number of kittens during their lives (estimated between 6 and 16). As kitten (young) and subadults have high mortality rates (Kitchener, 1991; Caro, 1994; Sunquist and Sunquist, 2002), the mean female contribution in terms of cats reaching the adult age class is very low. Thus, the European wildcat is a sensitive species to changes in the environment or persecution that affect breeding or mortality. Hauer et al. (2002) found that otters (*Lutra lutra*) also have a low reproductive rate and lifetime reproductive success, as a long-term survival strategy. This also seems to be the case for the European wildcat, as it is a typical K-selected species when considering its small litter size and the low number of litters per female (Macdonald, 1985). However, this strategy is even more disadvantageous for European wildcats, owing to their relatively quickly development, shorter dependence on their mother (Kitchener, 1991; Sunquist and Sunquist, 2002) and low reproductive plasticity. Therefore, the European wildcat breeding strategy reacts to changes in environment slower than other felid species, including feral and domestic cats. This may partially affect its ability to recover after a population decline. The European wildcat is one of the medium-sized European carnivorans with the slowest recovery since the reduction of its population and distribution after World War II. As a consequence, the species still displays a fragmented and discontinuous distribution across Europe (Stahl and Leger, 1992; Stahl, 1993; Yamaguchi et al., 2015).

These findings should be considered when planning conservation efforts.

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