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Reproductive biology of captive female Eurasian lynx, *Lynx lynx*

Abstract Studies on wild Eurasian lynx (*Lynx lynx*) have revealed variation in reproduction between areas, years and individuals. In order to explore potential causes for this variation other than food supply, we analysed data from captive lynx, which provide conditions with minimal environmental variation as all were fed ad libitum. Data from 37 individual female lynx were available from 20 zoos in Norway, Sweden, Finland, Switzerland and the Czech Republic. Data on 177 reproductive events (where a male was available to the female at mating time) are presented. Of these events, 85% resulted in litters being born. Average litter size was 1.95, with a variation from 1 to 4. The mean birth date was 26th May, and sex ratio was not significantly different from parity. The probability of reproduction was related to age, with fewer litters produced by the very young (2–3-year old), and no sign of a senescence effect. However, a clear effect of senescence on litter size was evident. The captive lynx did not have higher reproductive rates than wild lynx, indicating that either factors other than food supply are driving the variation in wild lynx reproduction, or that a factor such as stress may be causing additional variation in the captive population.

Keywords Captive lynx · Emergency life-history stage · Litter size · Reproductive pattern · Senescence · Stress responses

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Introduction

Conservation of many felid species is a challenge in the face of human population growth, increasing resource consumption and a host of other societal pressures on habitats and populations (Swanson and Brown 2004). Thus, worldwide, several species of large carnivores are on the brink of extinction (Berger 1999). Understanding the factors that most severely affect the extinction risk of populations is then crucial for maintaining biodiversity. Extinction is determined by complex interactions among variables that decrease mean population size, such as the specific growth rate, stochastic environmental fluctuations and demographic stochasticity (Sæther and Engen 2004).

In general, we expect a strong relationship between resource availability for reproducing females and their reproductive success (Stearns 1992). Thus, variation in environmental factors affecting the functional response in predators will potentially affect population growth. Such effects have been demonstrated in Canadian lynx *Lynx canadensis* (Stenseth et al. 2004) and indicated in Eurasian lynx *Lynx lynx* (Pulliainen et al. 1995). At low population densities, both long-term studies of vertebrates (e.g. Clutton-Brock 1988; Newton 1989) and recent theoretical studies (Lande et al. 2003) have shown

that both environmental variations (through spatio-temporal changes in resources) and demographic stochasticity (through a stochastic Allee effect (Engen and Sæther 2003), family effects (e.g. Gaillard et al. 1998) or cohort effects (Lindström and Kokko 2002; Gaillard et al. 2003a) may strongly influence population dynamics. In addition, such influences do not affect individuals randomly. Several studies have shown that in vertebrate populations heavy females usually are better able to cope with adverse conditions than small ones, by reproducing earlier, producing more offspring with higher reproductive value and living for longer (see examples in Clutton-Brock 1988; Newton 1989; Gaillard et al. 2000). Furthermore, age plays a determinant role in shaping variation in individual performance in vertebrates (Charlesworth 1980). Consequently, we will assess the reproductive patterns according to age after accounting for individual heterogeneity in captive lynx and compare the outcome with free-ranging lynx.

Although the Eurasian lynx numbers around 7000 individuals in Europe (von Arx et al. 2004), local population densities may be low. For example, the number of lynx in France, Germany, Switzerland and Austria totals around 300 individuals, while in Norway, where the population numbers around 300 individuals, the population is split into several smaller management units with specific management goals. Thus, the effective local population size may be low in several regions of Europe. Hence, to assure realistic management plans for lynx we need more knowledge about the variation in reproductive patterns. Here, we largely control for variation in resource abundance and other environmental factors (e.g. climatic influences) by studying reproductive output in 37 known-aged captive female lynx fed ad libitum. Ovary analyses of free-ranging lynx have shown 50% fertility in 10-month-old females and 100% fertility in 22-month-old females, but indicated that primiparous females breed later in the mating season than multiparous females (Kvam 1990). Furthermore, studies of captive felids have documented that there is a strong male-biased sex ratio in litters born to ad libitum fed animals (Tella 2001). Thus, here we will describe variation in timing of birth and birth sex ratio. Further, we will look for patterns of reproductive output in relation to age. We will contrast the data with results obtained from a large sample of free-ranging animals in Fennoscandia and Switzerland (Kvam 1990; Pulliainen et al. 1995: based on ovary analyses; Breitenmoser-Würsten et al. 2001; Andersen et al. 2003: based on counting kittens in lair, i.e. representing a minimum litter size at birth). Because of the absence of environmental constraints, we predict that captive lynx will have a lower age at maturity and higher reproductive output than wild lynx, i.e., we expect a generally higher litter size, and a high reproductive rate in all fertile ageclasses. Furthermore, we expect no age-specific variation in timing of birth, and a male-biased sex ratio. We discuss our results in the light of recent findings from studies of felids in captivity (e.g. Morato et al. 2001, 2004; Swanson and Brown 2004).

Materials and methods

Reproductive data were collected from 37 female lynx for which a total of 177 reproductive events were recorded (i.e. access to adult males was provided during the mating season) between 1968 and 2002. Three females were born to wild lynx and brought to the zoos as kittens, and the other 34 females were all born in captivity. The females were raised in 20 different zoos from Norway (4), Sweden (10), Finland (4), Switzerland (1) and the Czech Republic (1). Data regarding the age of the female, date of birth, litter size and sex ratio were collated from questionnaires sent to all zoos and from the Eurasian Lynx Studbook (The Eurasian Lynx Studbook 1944–1997). All lynx were given food ad libitum. As a result, these captive females had particularly high body weights, averaging 23.0 ± 2.2 kg (mean $\pm$ SD) (4) compared to 16.6 ± 1.0 kg (58) for adult wild lynx (Andersen et al. 2003). The mating season for lynx is mid February to early April, and kittens are normally born in May and June after a gestation length of around 70 days (Tumanov 2000). Lynx that conceive at the age of approximately 22 months are referred to as 2-year olds.

Data analysis

We analysed two components of reproductive output separately. That is, we analysed variation in reproductive rates as the proportion of females reproducing (given access to an adult male during the rut). We then analysed litter size as the average number of kittens produced per reproductive event, including only reproducing females (see Hewison and Gaillard 2001 for a similar approach on roe deer). We looked for age-related patterns of variation in these two reproductive parameters. In particular, we expected (1) a lower reproductive output in young and prime-aged females due to the positive effects of reproductive experience, and (2) a lower reproductive output in old ages due to negative effects of senescence. Because our data included repeated measures of reproductive events for a given female (average = 4.78), we needed to account for pseudoreplication problems (*sensu* Hurlbert 1984). To analyse age variation in reproductive rates, we included mother identity as a random factor in a mixed model procedure. For binomially distributed dependent variables such as sex ratio and proportion of reproductive females, we fitted a Generalised Linear Mixed Model. For litter size that was approximately normally distributed, we fitted a Linear Mixed Model. In both types of analyses, we assessed the effects of age by including age either as a continuous linear independent variable, continuous quadratic independent variable or a fixed factor with different numbers of classes. According to Burnham and Anderson's (1998) recommendations, we selected the best model to describe the data on the basis of Akaike

Information Criterion (AIC) values (i.e., the model with the lowest AIC value corresponded to the best compromise between accuracy and precision and was retained). The significance of effects of size was tested by using Wald tests. All the analyses were performed using the R software (R Development Core Team 2004).

Results

Timing of birth and sex ratio in captive lynx kittens

A total of 292 lynx kittens were born in 150 litters. Exact time of birth was known for 169 young (excluding 1 birth on 2 September). Mean birth date was 25 May, and 50% of the births were between 19 and 31 May. Males were born on average 3 days later than females (27 and 24 May, respectively, $Z = 1.53$, $p = 0.13$).

Sex ratio was known for 102 complete litters, producing 186 kittens with a global sex ratio of 0.495 not significantly different from parity. Although females tended to produce more male kittens when aging (slope of 0.0748), this difference was not significant ($p = 0.147$). A quadratic model suggested that offspring sex ratio first increases with age and then decreases at old ages but not significantly (age: $p = 0.234$, age^2: $p = 0.392$). Likewise, there was a slight tendency for large litter size to be female-biased (slope of -0.114, $p = 0.547$). The best model was a constant sex ratio (AIC = 791.72 vs. 794.10 for the second best model including the effect of litter size).

Age-related reproductive output

In 150 litters, we observed 46 litters with only one kitten, whereas we observed 71 litters with twins, 28 with triplets and 5 litters with four kittens. Comparing the mean litter size and distribution of litters with data collected from 124 litters from wild lynx (Andersen et al. 2003), we found no significant difference in the mean litter size (Wilcoxon rank test $Z = 1.49$, $p = 0.14$) or the distribution of litter sizes ($k_s = 0.50$, $p = 0.77$, Kolmogorov goodness-of-fit test), although wild lynx had slightly larger litters [2.07 ± 0.73 (mean $\pm$ SD, Table 1)] than captive lynx (1.95 ± 0.79).

Litters were produced in 150 of 177 reproductive attempts (85%); however, the reproductive rate (proportion of females reproducing) varied between the age groups. In fact, only two of three 2-year-old and three of four 3-year-old females produced litters. Although the best model was a constant proportion of reproductive females at all ages (AIC = 904.492), the two age class model-opposing young (2 to 3-year old) to older females indicated a much lower output for young females (0.745 vs. 0.904). Hence, from 4-year old onwards the reproductive rate was high, with no sign of a senescence effect (all females older than 9 years of age were breeders).

The best model to describe age-related variation in litter size was a two-class model (AIC = 349.572 vs. 353.675 for the constant model), with young and prime-age females (2 to 11-year old) producing 0.78 (SE = 0.29) more offspring per litter size than old females ($p = 0.008$). Hence, a clear effect of senescence on litter size was evident. In particular, differences between young and prime-age females (0.16, SE = 0.12) were not significant ($p = 0.203$). Excluding the female giving birth for the first time when 7 years old, the mean age of first reproduction was 2.4 ± 0.68 years (mean $\pm$ SD).

Discussion

Contrary to our expectation, captive female lynx did not give birth to larger litters than wild lynx. Although captive lynx were much larger, they tended to produce smaller litter sizes than wild lynx. Likewise, captive lynx did not have an earlier age at maturity. Therefore, the reproductive output of captive lynx was at best similar to, but not higher than, reproductive output of wild lynx. However, once we accounted for individual heterogeneity, the age-related variation in reproductive output fitted our expectation. Thus, we found a clear senescence in litter size causing reproductive output to fall among old (12-year old or more) females. Likewise, 2– to 3-year-old females showed a similar reproductive rate to wild lynx of the same age.

Timing of birth, sex ratio and age at maturity

In a sample of 23 known birth dates for wild lynx (Andersen et al. unpublished), the mean birth date was

Table 1 Reproductive parameters in captive (this study) and wild lynx in Scandinavia and Switzerland

Mean litter size in reproducing lynx (number of litters)	Mean litter size of 2-year olds (including non-reproduction)	Mean litter size of >2-year olds (including non-reproduction)	Proportion of 2-year olds breeding (range)	Proportion of all females breeding (range)	References
1.95 ± 0.79 (150)	1.27 ± 1.08	1.70 ± 0.99	67%	85%	This study
2.07 ± 0.73 (124)	1.35 ± 0.51	1.70 ± 0.15	50% (25–80)	73% (65–82)	Andersen et al. (2003)[a]
2.10 ± 0.87 (22)		1.71 ± 1.10		87%	Breitenmoser-Würsten et al. (2001)

[a] Represents mean values from four different wild populations (columns 2 and 3; mean $\pm$ SE)

Table 2 Model selection procedure for the analysis of the effects of age on reproductive output (*A* proportion of females breeding and *B* litter size) of captive lynx in Europe

Model	AIC
A	
No age effect	**904.492**
Linear effects of age	933.562
Quadratic effects of age	931.700
Two age classes (2–3 vs. older)	939.738
Two age classes (2–11 vs. older)	1053.480
Three age classes (2–3, 4–11 and older)	1086.635
B	
No age effect	353.675
Linear effects of age	361.285
Quadratic effects of age	366.565
Two age classes (2–3 vs. older)	357.570
Two age classes (2–11 vs. older)	**349.570**
Three age classes (2–3, 4–11 and older)	353.063

The selected model (i.e., the model with the lowest AIC value) is indicated in *bold*

27 May, i.e. 2 days later than in captive lynx in this study. Synchronisation of births in captive lynx (50% of the births within a 13-day period) was slightly less than in wild lynx (50% of births in an 8-day period between 26 May and 2 June). Sex-ratio theory predicts that in species with large variance in male reproductive success, females in better condition may maximise their fitness by producing more male offspring (Trivers and Willard 1973). Tella (2001) suggested that provision of supplementary food could lead to the male-biased offspring sex ratios seen in many zoos. The overall 1:1 sex ratio found in this study is in line with other lynx studies both from captive (47.6% males, Kaczensky 1991) and wild populations (48.7% males, Breitenmoser-Würsten et al. 2001).

Several studies report that the age at maturity for female lynx is 2 years, both for captive (Lindemann 1955; Stehlik 2000) and wild lynx (Kvam 1991), although both Pushmann (1983) and Kaczensky (1991) confirm the ovary analyses by Kvam (1991), reporting the production of kittens by two 1-year-old females. None of the 11 zoos included in our study reported reproducing females at the age of 1 year.

Reproductive output

Estimating fecundity in a large sample of wild Norwegian lynx based on ovulation rates and known prenatal mortality, Kvam (1991) found the mean litter size to be 2.828. In a sub-sample of eight lynx with embryos (varying in size from 0.4 to 356 g), the mean litter size was 2.5 ± 0.53 (mean $\pm$ SD) (Kvam 1991). In Finland, Pulliainen et al. (1995) found a mean litter size of 2.33 ± 0.73 after counting placental scars in 82 adult females. Both these figures are higher than those found in other wild populations in Scandinavia (2.07 ± 0.73, Table 1) and Switzerland (2.10 ± 0.87, Table 1). In another study of captive lynx, Kaczensky (1991) found 142

litters (14 included in our study) to vary between 1.7 and 2.8 in 11 zoos, with a mean of 2.1 ± 0.10 (SE), which is close to the figures reported in this study (1.95 ± 0.79), indicating that litter size in captive lynx is certainly not higher (and may be lower) than in wild lynx.

In our data set, a clear senescence effect regarding litter size was apparent in the age group of 12–15 years. Although Kvam (1991) could not find any evidence for a decrease in fecundity with age in a large sample from shot animals in Norway, one obvious reason for that is related to the fact that only 13 of the 899 shot lynx (1.4%) were older than 10 years. This implies that in managed wild populations lynx seldom reach the stage of senescence, while in captivity female lynx could be older than 20 years (Stehlik 2000; Kazcensky 1991). Alternatively, the lack of occurrence of reproductive senescence in previous studies of lynx could also be accounted for by the lack of control of inter-individual heterogeneity in such studies. As commonly reported in other vertebrates, the average quality of an individual increases with age as a result of non-random mortality, potentially masking any decrease in performance with increasing age in transversal studies (see Vaupel and Yashin 1985; Gaillard et al. 2003 for further details).

More surprising is the demonstration of the same reproductive rates in captive and wild lynx (Table 1). Despite the fact that ovary analysis of a large sample of wild lynx clearly shows that all female lynx are fertile in their second spring (Kvam 1991), a significant proportion of females in this age group do not produce young. Indeed, this lower reproductive rate was also evident for 3-year-old females in our data set, indicating that prime-age reproductive output is not achieved until 4 years of age. In fact, only two of three 2-year-old and three of four 3-year-old females produced litters. Age-specific body weight development in lynx is not published. However, the fact that body weight in three 21- to 22-month-old wild females averaged 16.2 ± 1.5 kg (mean $\pm$ SD, unpublished data) whereas average body weight in old females (> 2 years) varied between 15.7 and 18.0 kg in four different Scandinavian populations (Andersen et al. 2003) clearly indicates that body weight per se could not be the factor explaining low reproductive rates in 3-year-old females.

Under captive conditions, there are at least three factors that can explain the relatively high number of non-reproducers in our sample. As seen in captive cheetah (Marker-Kraus and Grisham 1993), females do not display overt oestrous behaviour, and some cases of such random periods of anoestrous behaviour may be due to cage-mate suppression (Brown et al. 1996), i.e. dominant con-specifics could suppress the oestrous activity of subordinates. Second, reproductive studies of captive lynx clearly show that optical, acoustical, olfactory and tactile signals are necessary for reproductive synchronisation of partners (Stehlik 2000). It is not unlikely that the youngest age groups, lacking mating experience, have a lower reproductive rate than older animals. Third, some cases of failed reproductive

attempts could be due to low-quality sperm from males. Some species with low genetic variability have a high incidence of teratospermia, and a high number of sperm with acrosomal defects (e.g. cheetah *Acinonyx jubatus*: Wildt et al. 1992; lions *Panthera leo*: Wildt et al. 1987; pumas *Felis concolor*: Roelke et al. 1993). A comprehensive study from Latin America (Swanson et al. 2003), describing reproductive status in 185 males (>95% wild-born) from eight different felid species, showed that more than 80% of the males had never reproduced in captivity, more than 50% had low sperm counts and in four of the species more than 50% of the males had morphologically abnormal spermatozoa. Other studies of felid males in captivity showed that males housed alone or paired had improved reproductive traits compared to males held in group exhibits, possibly reflecting varying stress levels under different social conditions (Swanson and Brown 2004; Morato et al. 2001). No information on male lynx with which to test this hypothesis was available for the present study.

We hypothesise that these factors may be expressed as a stress response. It has been demonstrated that some vertebrates may enter an "emergency life-history stage" (*sensu* Wingfield et al. 1998), characterised by reduced aggressive and reproductive behaviour, after being exposed to various sorts of stress. The emergency life-history stage can be sustained for a short period without lasting effects, as in the case of abandoning a reproductive attempt (Ricklefs and Wikelski 2002), or for longer periods resulting in reduced growth, loss of body condition and impaired reproduction (Buchanan 2000). It has been found that chronic or acute stress can negatively affect reproductive function (see Liptrap 1993 for a review). In domestic cats and three non-domestic felids, Carlstead et al. (1992, 1993) found significant changes in baseline urinary corticosteroids after exposing the animals to novel or stressful environments. That is, the reproductive pattern observed in captive lynx may reflect individual variation (both in males and females) in tolerance of stress related to being kept in captivity. Such increase in individual heterogeneity would lead to an increased demographic stochasticity in captive populations.

Much of the variation in life histories reflects phenotypic responses of individuals to environmental stresses and perceived risks (Ricklefs and Wikelski 2002). Because stress responses affect the balance between survival and reproductive success, animals should favour those aspects of their life histories that contribute most to fitness. As lynx are relatively long-lived (up to 22 years in captivity, Stehlik 2000), and reported to reproduce until they are 15 years old (this study, Stehlik 2000), females should favour their own survival at the expense of current reproduction. Although few data exist to test this idea, several studies of birds (e.g. Ghalambor and Martin 2001) and mammals (Gaillard and Yoccoz 2003) have demonstrated stress responses in a manner consistent with predictions of such a hypothesis. Following the same line of argument, old lynx reaching the end of their reproductive phase may have higher tolerance for stress, and take more risks, thus investing more in offspring than in their own survival (terminal investment concept, e. g., Clutton-Brock 1984).

If the high proportion of failed reproductive attempts in the youngest age groups is a stress response in line with the emergency life-history stage concept, this may have some relevance for lynx-management practice in Norway, and other areas where the lynx-hunting season overlaps with the mating season for lynx. Although Kaczensky (1991) has confirmed two cases of repeated rutting, indicating a poly-oestrous breeding tactic, both these cases occurred after the loss of kittens in May. Consequently, if human disturbance during the mating season causes a stress response in some individuals, most likely in young unexperienced animals, this can subsequently affect individual reproductive rate. Furthermore, in wild managed populations of lynx the age distribution seems to be heavily biased towards the youngest age groups; in fact, 73% of the shot animals in Norway in 1960–1990 (Kvam 1990) were less than 4 years old, i.e. they have not reached their prime reproductive age. Hence, the population growth rate in wild lynx populations may be lower than previously predicted (Kvam 1990).

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