POPULATION ECOLOGY - ORIGINAL PAPER

The cost of maturing early in a solitary carnivore

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Abstract Central to the theory of life history evolution is the existence of trade-offs between different traits, such as the trade-off between early maturity and an extended period of body growth. Based on analysis of the reproductive tracts of harvested Eurasian lynx (*Lynx lynx*) females in Norway, we find that females that mature early are generally heavier than those that postpone maturation. A higher proportion of 1.5-year-old females showed signs of ovulation in areas with high prey density, where they were also heavier. Further, we show that female Eurasian lynx that mature early have the same number of placental scars (an index of breeding investment and litter size) as older females, suggesting that they have a relatively high investment in their first litter. This induces a cost in terms of body weight development, as those females that had matured at the age of 1.5 years were substantially lighter by the age of 2.5 years than those that postponed breeding. This effect tended to be more pronounced in areas with low prey density. We discuss to what extent this might affect their future fitness prospects, and suggest that such costs of maturing early in terms of body weight development might be high in terrestrial large carnivores due to a prolonged period of postnatal care.

Keywords Cost of reproduction · Life history ·
Litter size · *Lynx lynx*

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Introduction

A central tenet in life history theory is that there is a trade-off between early maturation and continued body growth (Stearns 1992). Age at first reproduction can greatly affect individual fitness and population dynamics (Cole 1954; Stearns 1992; but see also Oli and Dobson 2003). While early breeding could increase the number of lifetime breeding attempts (Lambin and Yoccoz 2001), it might come at the cost of decreased survival (Descamps et al. 2006), and/or body growth (Green and Rothstein 1991). The concept of a trade-off between life history traits rests on the assumption that energy is allocated to different fitness traits (Williams 1966), and a negative relationship between competing traits at the population level then rests on the assumption that energy acquisition and use is constant among individuals. As this is rarely the case, individual heterogeneity might override the costs of reproduction resulting in co-variation between fitness components (see, e.g., Weladji et al. 2008). Thus, comparing body development and future fitness prospects of early and late breeders might not reveal costs of reproduction if only high quality individuals mature at an early age (Langvatn et al. 2004). Further, these costs might be manifested only under certain unfavorable conditions (Tavecchia et al. 2005). Detecting costs of early maturation at the population level despite individual heterogeneity should thus provide strong evidence of a trade-off.

Among large mammals, the cost of reproduction has been most frequently studied in large herbivores (e.g., Tavecchia et al. 2005), and relatively little is known about such relationships in carnivores. This asymmetry in our understanding of the demographics of predators and prey is just one factor hindering our ability to predict how predator–prey dynamics will operate. Large mammalian

carnivore females have to provide food for their young for an extended period after weaning, and their hunting success might be hampered by having to train the offspring to hunt (Caro 1987) or by spatial constraints when the offspring are in the den (Laurenson 1995), potentially causing costs of early maturation (e.g., Pettorelli and Durant 2007). We used data from harvested Eurasian lynx (*Lynx lynx*) to study costs of early maturation in terms of body growth. In Eurasian lynx, females are able to give birth at the age of 2 years, but there is considerable variation in the proportion that do so (see, e.g., Henriksen et al. 2005 for examples from wild and captive lynx). Lynx are solitary like most other felid species (Breitenmoser-Würsten et al. 2007), but females provide maternal care for their offspring until broods break up in early to mid-winter after a period of investment lasting for around 12 months: 2 months pre-natal and 10 months post-natal (Schmidt 1998; Zimmermann et al. 2005). During this period, females accompanied by offspring have high energetic needs resulting in high kill rates (Nilsen et al. 2009), putting heavy pressure on the hunting skills of lynx females. In other words, a lynx giving birth at 2 years of age will face energetic demands for an entire year which could otherwise have been invested in growth. Therefore, it could be expected that lynx face a potential cost of early maturation. Based on earlier findings in mammals as well as the relatively long period of parental care in lynx, we expect that: (1) early maturing females are heavier as 1.5 years old than late maturing females; and if individual heterogeneity (e.g., in hunting skills) overrides potential costs of early maturation, then (2a) we expect that this difference in body condition is also evident at the onset of the next breeding season, and if, on the contrary, early maturation is traded-off against sustained body growth, then (2b) we expect late maturing females to be heavier at the onset of the next breeding season.

Materials and methods

Data collection

To investigate if early maturation had an effect on body mass development in Eurasian lynx, we focused on the relationship between body weight and reproductive status. More precisely, we used the occurrence of luteal bodies as an index of maturity, and placental scars as an index of previous years' breeding effort. Our analyses are based on data from Eurasian lynx harvested in Norway from 1993 to 2009, of which successful analysis of reproductive tracts were available for 70 females 1.5 years old, 54 females 2.5 years old, and 152 females >2.5 years old. Information about body weight, sex, age (determined by incremental lines in the tooth cementum; see Kvam 1984) and breeding

status (see below) were obtained from autopsy. The lynx were harvested in the period January–March, with 70% harvested in February. We initially assessed any difference in weight related to the time of harvest; however, neither for the 1.5-year-old animals ($R^2 < 0.001$, $p = 0.965$) nor for those of 2.5 years old ($R^2 = 0.023$, $p = 0.263$) could we find any clear relationship between weight and month of harvest. Also, there was no general increase or decrease in the proportion of the 1.5-year-old females that had signs of ovulation in relation to month of harvest ($p = 0.483$). Thus, we did not control for time of harvest in further analyses.

To assess breeding status, we sampled the reproductive tracts with ovaries from harvested females. All ovaries and uterine tracts were from frozen or newly harvested lynx, so no further processing was conducted prior to sectioning. Both ovaries were sectioned to search for Graafian follicles or ruptured follicles. Positive identification of such bodies on either of the ovaries were interpreted as sign of ovulation and thus sexual maturity. Uterine tracts were searched for presence of placental scars (Kvam 1991), and we did not aim to distinguish the age of the scars. As lynx are generally not giving birth before the age of 2 years (Henriksen et al. 2005), and only about 10% of 1.5-year-old females in our sample showed signs of placental scars, we assumed that all scars from females aged 2.5 years were from the same reproductive event. Visible placental scars were interpreted as signs of previous pregnancy and the likely birth of kittens. As some of the ovulating females might not become pregnant, and some of the pregnant females might have lost their kittens at an early stage, our test is conservative.

Geographical regions based on prey density and distribution

We used data sampled across all of Norway where prey densities and distributions vary greatly; we thus controlled for sampling location in the analysis. In general, roe deer (*Capreolus capreolus*) is the preferred prey of Eurasian lynx when available (Odden et al. 2006), whereas semi-domestic reindeer (*Rangifer tarandus*) often form the main prey at higher latitudes (Sunde et al. 2000a). We used roe deer hunting statistics from the municipality level averaged over 1997–1999 to make a coarse division between areas with high (HR) and low (LR) roe deer densities (see also Nilsen et al. 2009 for the use of hunting statistics for this purpose). Maps of reindeer areas were obtained from the Norwegian Reindeer Management Authority. Based on the municipality where the lynx was harvested, it was placed in HR (>0.75 roe deer harvested 10 km^2 forested area), LR (<0.75 roe deer harvested 10 km^2 forested area), or SM (semi-domestic reindeer). Some municipalities contained

both reindeer and high densities of roe deer, and in these cases the lynx was classified as HR. This is because the lynx prefer areas with roe deer habitat rather than those containing reindeer (Sunde et al. 2000b), and there is a likely bias in the harvest towards lynx in lowlands where lynx prey on roe deer (Sunde et al. 1998). Lynx use very large territories (600–1,500 km^2 for males and 300–800 km^2 for females; Linnell et al. 2001) that can typically span several municipalities (Herfindal et al. 2005). However, although some lynx will have access to prey outside the municipality where it is shot, we believe our classification is functional for a study area as large as Norway.

Although lynx densities varied across regions and years (Linnell et al. 2010), we did not further control for potential density-dependent effects in the analysis, as we did not have adequate population level data available for this purpose. More importantly, quota harvest keeps the lynx population in Norway well below the level where any density-dependent effects are likely to occur (Linnell et al. 2010). We are thus confident that prey density is a more important factor in explaining inter-individual and regional differences in food availability.

Statistical analysis

To test the hypothesis outlined in the "Introduction", we used a combination of generalized linear models (GLM), and generalized mixed effects models (GLMM). In general, we used GLMs to test and conduct model selection, and GLMMs with a binomial error term implemented in the procedure *glmer* (with add-on library "lme4") in software R 2.8.1 (R Development Core Team 2008) to estimate population-level parameters. In the mixed effects models, body weight was fitted as an independent fixed effect, with year and prey region fitted as random intercept terms. The maximum likelihood was obtained by using the Laplace-approximation, as there is no general analytical solution to the likelihood maximization in models with a mixing of binomial (fixed error terms) and Gaussian (random effects) distributions (Skrondal and Rabe-Hesketh 2004).

Results

In total, 60% of the 1.5-year-old females showed signs of ovulation (42 vs 28), whereas 63% of those 2.5 years old had one or more placental scars (34 vs 20). In general, lynx females showing signs of ovulation at 1.5 years old were heavier than those that were not sexually mature ($\beta = 0.522$, 0.201 SE; Table 1; Fig. 1a: GLMM). This pattern was similar in all regions ($p = 0.608$ for the interaction between prey region and body mass on ovulation rates; GLM with binomial error term), but with some indications

Table 1 Statistics from generalized linear mixed effects models fitted to estimate the population level difference in body weight and ovulation rates (indexed by Luteal bodies) among Eurasian lynx (*Lynx lynx*) females 1.5 years of age, and the presence of placental scars (indicating breeding last season) among lynx females 2.5 years old

	AIC	ΔAIC	w_i
Luteal bodies			
Φ_1	84.9	–	0.998
Φ_2	96.9	12.0	0.002
Placental scars			
Φ_1	65.6	–	0.896
Φ_2	69.9	4.3	0.104

All models were fitted as generalized mixed effects models, with year and region fitted as random intercept terms. Akaike information criterion (AIC) is reported together with the difference in AIC (ΔAIC) and Akaike's weight (w_i). In both cases (luteal bodies and placental scars), we compared two models; Φ_1 including the effect of body weight, and Φ_2 with no covariables
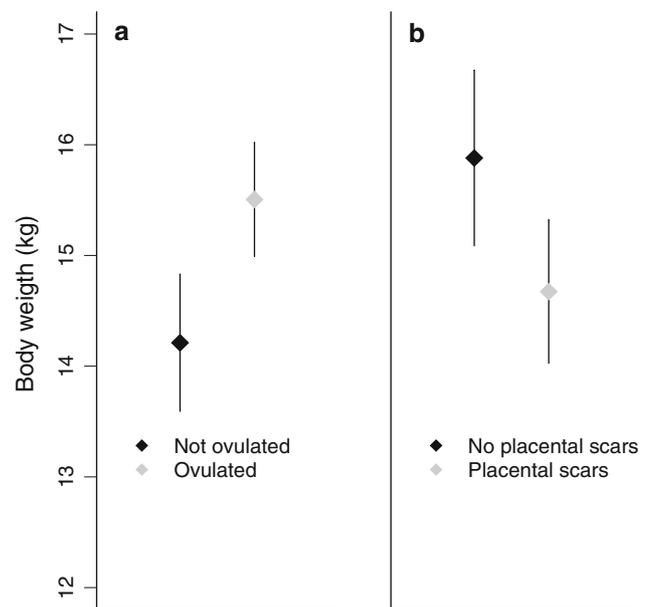

Fig. 1 Breeding status of the female lynxes in the current study in relation to body mass. **a** Signs of ovulation in 1.5-year-old female lynxes, **b** the presence of placental scars in 2.5-year-old female lynxes

that the ovulation rates differed between prey regions ($p = 0.061$; GLM with binomial error term) when controlling for the effect of body mass. Removing body mass from the model further indicated that the proportion that showed signs of ovulation differed between regions ($p = 0.013$; GLM with binomial error term), being somewhat higher in HR areas [0.83 (95% CL: 0.63−0.94)] than in LR [0.44 (0.24−0.67)] and SM areas [0.52 (0.33−0.70)]. There was, however, a tendency for a difference in body mass at 1.5 years of age between regions ($p = 0.085$; linear model), with heavier individuals in HR (15.62 kg, 0.39 SE) and

lighter in LR (14.73 kg, 0.40 SE) and SM (14.48 kg, 0.35 SE), suggesting that both terms should not enter the model simultaneously. Fitted alone, a model with body mass only (AIC = 83.16) had more support than a model with regions only (AIC = 84.91) as indicated by the lower AIC value (note that ΔAIC < 2, so both models should be considered; Burnham and Anderson 2002).

Among females 2.5 years old, those that had placental scars were significantly lighter than those that did not have scars ($\beta = -0.462$, 0.238 SE); Table 1; Fig. 1b). There was some indication, although not statistically significant, that this pattern varied among regions ($p = 0.078$; GLM with binomial error term), being most pronounced in SM-areas ($\beta = -1.684$, 0.823 SE) and weaker in HR ($\beta = -0.285$, 0.334 SE) and LR areas ($\beta = -0.111$, 0.290 SE).

Comparing the number of placental scars among females 2.5 years of age with those of older females (including only females with ≥ 1 scar), we found no difference (2.5 years vs older; $p = 0.370$; Poisson regression). Also, the number of placental scars did not differ among prey regions ($p = 0.840$; Poisson regression), and there was no indication of different relationship between age and placental scars in the different prey regions ($p = 0.895$ for the test for an interaction between age and region; Poisson regression).

Discussion

In support of our first expectation, females maturing at 1.5 years old were heavier than those that postponed breeding. However, comparing the age class 1 year later, there appeared to be clear costs of breeding early in terms of body weight development. Our results thus indicate that Eurasian lynx females that mature early are generally of high phenotypic quality (as indexed by body weight), and that there are considerable costs in term of body weight development associated with their life history strategy. Such a cost, although central to life history theory, has to our knowledge not been demonstrated before for a large terrestrial mammalian carnivore.

In our analysis, we found some indication that the proportion of females 1.5 years of age that showed sign of ovulation differed between regions, being higher in areas with a higher and more predictable prey density. As the relationships between body mass and ovulation rates were similar across regions and there were differences in body mass among 1.5-year-old females between regions, we speculate that these regional differences in ovulation rates are caused by different growth patterns. Similar regional differences in lynx body size has been reported for lynx in Sweden with larger individuals in areas with high prey density (Yom-Tov et al. 2010), and negative correlations between population density and body size has been reported in Canadian lynx

(*Lynx canadensis*) (Yom-Tov et al. 2007). It is well known from studies of, e.g, large ungulates that age of maturity is often strongly dependent on environmental conditions through its effects on body mass (Gaillard et al. 1992, 2003). Previous studies based on counts of kittens at the natal den have indicated lower reproductive output for lynx in northern compared to southern Scandinavia (Andrèn et al. 2002), and our results might suggest that this is at least partly caused by different maturation rates between areas due to differences in body mass development. Our study was carried out with lynx density well below the level where density-dependent effects are likely to occur (Linnell et al. 2010), and we do not know how density-dependent effects would have affected the patterns reported here.

It has frequently been reported for mammals that the heaviest individuals survive better and produce more offspring than lighter ones (Gaillard et al. 2000; Stearns 1992). To which extent the cost reported here in terms of body mass development manifests itself through future fitness in Eurasian lynx (potential fecundity costs; sensu Bell 1980) is currently unknown. Our data on shot lynx, and the fact that we cannot specify the timing of reproductive events more accurately, makes such analysis impossible with the material at hand. If delaying maturity leads to further growth and larger body mass is correlated with increased fecundity, then delayed maturity leads to higher fertility in the first breeding attempt (Stearns 1992). However, in our analysis, there was no general difference in the number of placental scars among age classes (see also Henriksen et al. 2005), indicating a relatively high investment in their first breeding attempt of female lynx that mature early. Similar patterns are found from observations at the den of radio-collared lynx in Norway (Linnell et al., unpublished data). This contrasts with the expectations from the "differential effort hypothesis" (Forslund and Part 1995) which predicts that prime aged females should have a higher effort in each reproductive event; a patterns reported from a wide range of taxonomic groups (Stearns 1992). Potential effects of reduced body mass development among early breeders on future fitness prospects in lynx await further examination.

In Eurasian lynx where females have to provide food for their young for almost 1 year (Schmidt 1998; Zimmermann et al. 2005), one might also expect considerable parental effort after weaning. Lack of foraging skills among young females might have a strong limiting effect on first time breeding (Rutz et al. 2006), forcing some to postpone the first breeding (Stearns 1992) and others to pay a high cost when maturing early. While lynx females with kittens have much higher food provisioning rates than solitary individuals (Nilsen et al. 2009), it is unknown if young mothers are able to meet these requirements. Reduced body development of early breeders might suggest that they are not. Our analysis

also indicated that the cost of breeding at 1.5 years old was higher in SM areas, suggesting that the cost in terms of early maturation might be context-dependent, and that it manifest itself stronger under harsh conditions (Tavecchia et al. 2005). Reindeer areas are characterized by extreme fluctuations in prey density. In some seasons when reindeer are present, there is a high abundance of relatively easily killed prey (Pedersen et al. 1999). However, reindeer are herded between distinct seasonal home ranges and lynx do not follow these movements (Danell et al. 2006). In seasons when reindeer are absent, lynx are forced to hunt much smaller prey such as lagomorphs and tetraonids, which are much harder to kill (Odden et al., unpublished data) and represent much smaller meals. It is exactly under such conditions that we expect that experience is likely to be most important and where costs of reproduction are likely to be highest. The costs of reproduction in large terrestrial mammalian carnivores deserve more attention, due to potentially high costs related to their prolonged period of food provisioning to dependent young, and the impact that such demographic mechanisms have on our ability to model large carnivore viability and better understand the interactions between predators and prey.

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