One size fits all: Eurasian lynx females share a common optimal litter size

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Summary

1. Lack proposed that the average clutch size of altricial species should be determined by the average maximum number of young the parents can raise such that all females in a given population should share a common optimal clutch size. Support for this model remains equivocal and recent studies have suggested that intra-population variation in clutch size is adaptive because each female has its own optimal clutch size associated with its intrinsic ability to raise offspring.

2. Although Lack litter size and condition-dependent litter size are presented as two competing models, both are based on the concept of individual optimization. We propose a unified optimal litter size model (called 'adaptive litter size') and identify a set of conditions under which a common vs. a state-dependent optimal litter size should be observed.

3. We test whether females of Eurasian lynx (*Lynx lynx*) have a common optimal litter size, or whether they adjust their litter size according to their state. We used a detailed individual-based data set collected from contrasting populations of Eurasian lynx in Scandinavia.

4. Observed reproductive patterns in female lynx provide strong support for the existence of a common optimal litter size. Litter size did not vary according to female body mass or reproductive category, or among contrasted populations and years. A litter size of 2 was associated with a higher fitness than both smaller and larger litters, and thus corresponded to the 'adaptive litter size' for female lynx.

5. We suggest that the reproductive pattern of female lynx might correspond to a risk avoidance tactic common to all individuals, which has evolved in response to strong environmental constraints generated by a highly unpredictable food supply during lactation.

Key-words: environmental stochasticity, felids, individual optimization, Lack clutch size, life-history evolution, reproductive tactic

Introduction

Life-history theory predicts strong covariations among life-history traits (Stearns 1976, 1977). Trade-offs between current reproduction and future reproduction or survival, or between the size and number of propagules, are among the most widely studied in populations of vertebrates (Clutton-Brock 1991). These trade-offs depend on both the life history of the focal species (Hamel *et al.* 2010) and environmental conditions (Nussey *et al.* 2007).

Variability in life-history traits among individuals within a population should thus reflect the interplay between life-history strategy and current environmental conditions. On the one hand, adopting a given life-history strategy will constrain the potential for variation in most life-history traits (Stearns 1976). On the other hand, animals have to track environmental changes (Thomas 1994), leading to an increase in the variability of traits observed among individuals (Van Valen 1965).

Many studies have examined the observed variation in the number of propagules produced at each breeding attempt by individuals of iteroparous species (see e.g. Godfray, Partridge & Harvey 1991 for a review). More

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than 65 years ago, Lack (1947) proposed that clutch size in altricial birds should maximize the number of recruits and would not necessarily correspond to the maximum potential number an individual can produce. Indeed, as he formulated 1 year later when extending his model to mammals (Lack 1948:46), 'the upper limit is set by the number of young which the parents can successfully raise; that, as litter size increases, the proportionate mortality among the young increases and that eventually an optimum litter size is reached, beyond which the initial advantage of an extra youngster is more than offset by the rise in proportionate mortality'. From an extensive review of the early bird literature, Lack (1947) found support for his concept of optimal clutch size, which is currently known as the 'Lack clutch size' (Godfray, Partridge & Harvey 1991). However, experimental studies of brood enlargement have provided quantitative evidence against a 'Lack clutch size'. From a meta-analysis based on 42 studies, Van der Werf (1992) found for instance that enlarged broods produced an average of 0·55 more fledglings than nonmanipulated broods, leading them to reject the food-limitation process implicit in the 'Lack clutch size'. However, while the studies reviewed by Van der Werf (1992) included a large range of life expectancies (with adult survival probabilities in the range from 0·35 to 0·95) they were all based on short-term manipulations of brood size (from 1 to 4 years). Detailed long-term field studies involving the monitoring of known-aged individuals have become popular during the last decades (e.g. Clutton-Brock & Sheldon 2010). Among other topics, individual-based analyses of variation in clutch or litter size have benefited from the increasing availability of high-quality data at the individual level. This has allowed Lack's original model to be extended from the population level to the individual level. Indeed, following pioneering works in the mid-1970s (Smith & Fretwell 1974; Perrins & Moss 1975) and subsequent refinements developed under the optimal investment hypothesis (Morris 1985, 1987), Pettifor, Perrins & McCleery (1988) proposed the individual optimization hypothesis. According to this model, the optimal number of propagules should be state-dependent (sensu McNamara & Houston 1996) and vary in relation to individual attributes such as age, body mass or reproductive status. This individual optimization model nowadays accounts for most observed variation in the number of propagules within populations of vertebrates (Curio 1983; Murphy 2000; Risch, Michener & Dobson 2007), although other mechanisms either related to the restraint or constraint hypotheses (sensu Curio 1983) and based on adverse effects of environmental stochasticity such as bad years (Boyce & Perrins 1987), predation pressure (Skutch 1949), parasitism (Power *et al.* 1989) or uncertainty in what is the most rewarding clutch size (Mountford 1968) have all received some empirical support.

Both Lack clutch (resp. litter) size and the state-dependent clutch (resp. litter) size models are based on the concept of individual optimization. Therefore, instead of interpreting these models as being mutually exclusive, we propose a general framework involving a unified model of optimal litter size. We present this model as involving two contrasted modes of optimization represented by Lack clutch (resp. litter) size (Fig. 1a) predicting a common optimal number of propagules shared by all females in a given population and the fully state-dependent model ('state-dependent optimal litter size', Fig. 1b) predicting that each female has its own optimal number of propagules at each reproductive event, respectively. To identify which mode of optimization is observed in a given population, we identify three criteria. First, if there is a common optimal litter size shared by all females in the population, no relationship between individual state and litter size is expected (Fig. 1aI). On the other hand, if each female has its own state-dependent optimal litter size, a positive relationship between individual state and litter size is expected, as good condition values will increase the optimal litter size (Fig. 1bI). Individual state might vary between individuals, due to differences in size, condition, age, social status, reproductive category and due to variation in environmental conditions. Second, if there is a 'common optimal litter size' (i.e. a common optimal litter size shared by all females in the population), the modal average of the litter size distribution should be the optimal litter size, such that most females in the population will produce the optimal litter size (Fig. 1aII). On the other hand, if each female has its own state-dependent optimal litter size, litter size distribution should match the distribution of the key state variable in the population. Thus, the distribution of litter sizes should be uni-modal only when the key state variable is uni-modal (Fig. 1bII). Third, if there is a common optimal litter size shared by all females in the population, fitness should peak at this 'adaptive litter size' that also corresponds to the most commonly observed litter size (Fig. 1aIII). On the other hand, if each female has its own state-dependent optimal litter size, fitness should increase monotonically with increasing litter size (Fig. 1bIII).

We take advantage of a long-term study of radiocollared Eurasian lynx (*Lynx lynx*) females conducted in contrasting populations across Scandinavia, to test whether a common optimal litter size exists, or whether each individual has its own state-dependent optimal litter size.

Material and methods

STUDY AREAS

Study areas included two sites in Sweden (Bergslagen and Sarek) and two sites in Norway (Hedmark and Akershus). The study areas have been described in more details elsewhere (Andrén *et al.* 2006; Nilsen *et al.* 2012), so we will only present a brief description here.

The northernmost study area is partly located within the Sarek National Park (67°00′ N, 17°40′ E) and consists of a mixture of
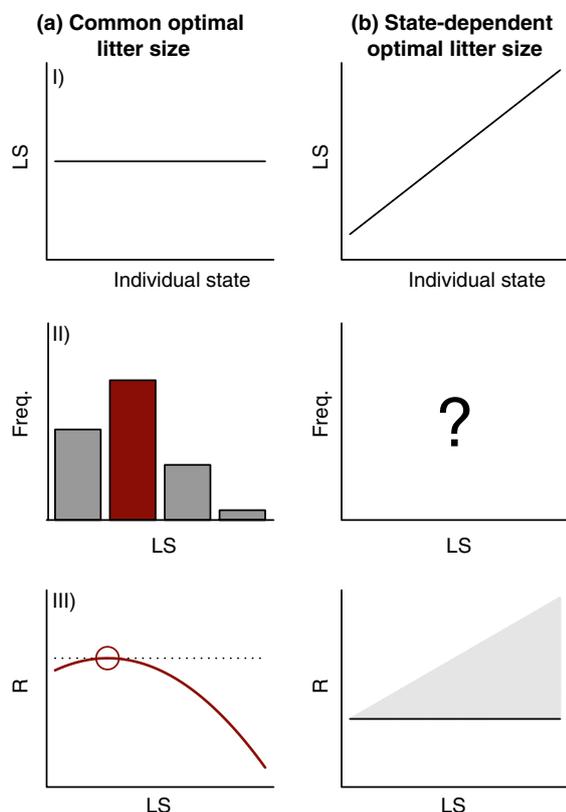
Fig. 1. A schematic representation of the criteria used to distinguish between two modes of optimization of litter size: 'common optimal litter size model' (left panel) and 'state-dependent optimal litter size model' (right panel). I) If there is a common optimal litter size (aI), no relationship between individual state and litter size is expected, whereas a positive relationship is expected under the state-dependent optimal litter size model (bI). II) If there is a common optimal litter size litter size distribution should be uni-modal and the modal average of the distribution should correspond to the optimal litter size (aII), whereas under the state-dependent optimal litter size model, the litter size distribution should match the distribution of the key state variable (bII). III) If there is a common optimal litter size fitness should peak at the common optimal litter size that also corresponds to the most commonly observed litter size (aIII). In contrast, fitness should increase monotonically with litter size under the state-dependent optimal litter size model (bIII).

coniferous forests, mountain birch *Betula* sp. forest and alpine tundra in mountainous terrain. The central area is situated in the county of Hedmark in south-eastern Norway (61°15′ N, 11°30′ E). The topography of the area consists of several parallel river valleys running from north to south, and about 72% of the area consists of coniferous forest. The Akershus study area (59°45′ N, 11°15′ E) is situated around the Norwegian capital, Oslo, and is similar to the Hedmark area although the proportion of farmland and human density is much higher and the topography is less hilly. The Bergslagen study area is located around Grimsö wildlife research station (59°30′ N, 15°30′ E) in south-central Sweden. The area is dominated by coniferous forest, and the proportion of agricultural land is higher in the southern parts (about 20%) and decreases towards the northern parts (<1% of the area). Roe deer (*Capreolus capreolus*) are the main prey in the Hedmark, Akershus and Bergslagen study areas, while semidomestic rein-

deer (*Rangifer tarandus*) are the main prey in the Sarek area where roe deer are absent (Odden, Linnell & Andersen 2006; Mattisson *et al*. 2011; Nilsen *et al*. 2012).

FIELD PROCEDURES

Field data were collected from 143 reproductive events by 56 individual female lynx monitored in the four contrasting areas described above. At the time we performed the analysis, the different studies had lasted for 7–13 years. Female lynx were equipped with either VHF or GPS collars following standard handling protocols approved by the Swedish Animal Ethics Committee and the Norwegian Experimental Animal Ethics Committee. Details on lynx capture can be found elsewhere (Arnemo *et al*. 1999, 2006; Andrén *et al*. 2002). At capture, females were weighed and aged (two age-classes: yearling and older). The exact age was known for 30 females that were either captured as kittens or yearlings or recovered after death and aged using tooth sectioning (Kvam 1984) and then retrospectively classified. For the analysis, female lynx were classified into three reproductive categories: primiparous females at 2 years of age (including only known-aged females), primiparous females at 3 years of age (including only known-aged females with known reproductive history) and multiparous females (including all females that had reproduced before the focal reproductive attempt irrespective of their first age of reproduction). Although senescence in litter size has been reported for captive lynx (Henriksen *et al*. 2005), it only occurs from 12 years of age so that only 1 of 143 reproductive events was possibly influenced by senescence in our study.

In May and June, the reproductive status of all female lynx was examined by more frequent localizations of radiomarked females, and by counting the kittens in the natal lair if movement data indicated that she had given birth (Schmidt 1998). Potentially reproductive females were localized as often as possible (most often several times each week, but much more frequently following the introduction of GPS collars) during the birth period in May and early June. Because females adopt a central place foraging behaviour centred on a natal lair for the first 6–8 weeks of the kittens lives, it was almost impossible to have failed to detect a reproductive event where kittens survived the perinatal period. At each reproductive event, we recorded the number of offspring (litter size) in the natal den. For a more detailed description of field procedures, we refer to Andrén *et al*. (2006).

Regular visual observation of lynx is almost impossible, thus we were not able to monitor kitten survival through the snow-free season, although the status of the radiocollared females could be assessed. With some exceptions, kittens were not radiomarked but marked with ear-tags in early years and pit-tags in later years. Thus, after snowfall, we used observations of snow tracks from radiocollared female lynx to assess the number of kittens that had survived. The number of recruits was then defined as the number of offspring with the mother at the onset of winter (between November and January), as the hunting season starts for lynx in February in both countries, this means that female or kitten mortality due to hunting was not a possible cause of variability in recruitment as we have defined it. Unfortunately, it was not often possible to determine the individual identity of those kittens that survived and those that died. Lynx tend not to disperse before February to April (Samelius *et al*. 2012), so there is little chance that dispersal would be misinterpreted as mortality.

We first analysed variation in litter size according to individual attributes of mothers using loglinear mixed models with Poisson-distributed errors. We included log-transformed female body mass (including only females with weight measurements obtained in the focal year) and reproductive category as fixed factors, and study area year (nested in study area), and female identity as random factors. To assess differences in fitness generated by observed variation in litter size and reproductive categories, we fitted generalized linear mixed models. We considered three different metrics for assessing fitness: the reproductive success defined as the probability to successfully raise at least one offspring (analysed using a binomial error term and a logit link function), the number of recruits (analysed using a Poisson error term and a log link function) and the geometric mean of the number of recruits (calculated from the raw data for a given litter size in a given reproductive category) to account for the influence of variance in the number of recruits on fitness in stochastic environments (Boyce 1977), as increased variance generally leads to decreased fitness (Tuljapurkar 1989).

We modelled litter size as a covariate (with linear and quadratic constraints to assess the robustness of the linearity assumption) and reproductive category as a fixed factor variable, and also looked for possible interactive effects between those female attributes. We included random effects of study site, year (nested within study area) and female identity. To assess the magnitude of variation in recruitment associated with different litter sizes, we calculated the coefficient of variation. All analyses were run using R version 2.12.1 (R Development Core Team 2010). We used functions from the lme4 package (Bates, Maechler & Dai 2008) to perform these analyses. We used Akaike's Information

Criterion (AIC) as a criterion for model selection (Burnham & Anderson 2002).

Results

LITTER SIZE VARIATION

Litter sizes of female lynx varied from 1 to 4. The most frequently observed litter size was 2 in all populations but one (Akershus, with the lowest sample size, Fig. 2). After accounting for the effects of study area, year and female identity (entered as random effects), the model without any fixed effects received the largest statistical support (higher AIC weight, Table 1). Thus, lynx litter size did not vary according to female attributes (Fig. 1d). Litter size did not increase with body mass (slope of -0.46, SE $= 0.47$, $P = 0.33$). Likewise, litter size was not smaller for first-time breeders than for multiparous females ($P = 0.31$). When using the entire data set ($N = 143$ when also considering litter size of females in years where body mass data were missing), estimated litter sizes were 2.42, 2.22 and 2.11 for primiparous at 2 years of age, primiparous at 3 years of age and multiparous females, respectively. Litter size did not vary markedly among years (from 1.91 in 2002 to 2.54 in 2005, for years with $n > 5$) or among study areas (from 2.05 in Akershus and Østerdalen to 2.35 in Grimsö). Lastly, the repeatability (*sensu* Hayen, Dennis & Finch 2007) of litter size was low (0.085) because both the within-individual and the among-individual variation in litter size was low. Overall,
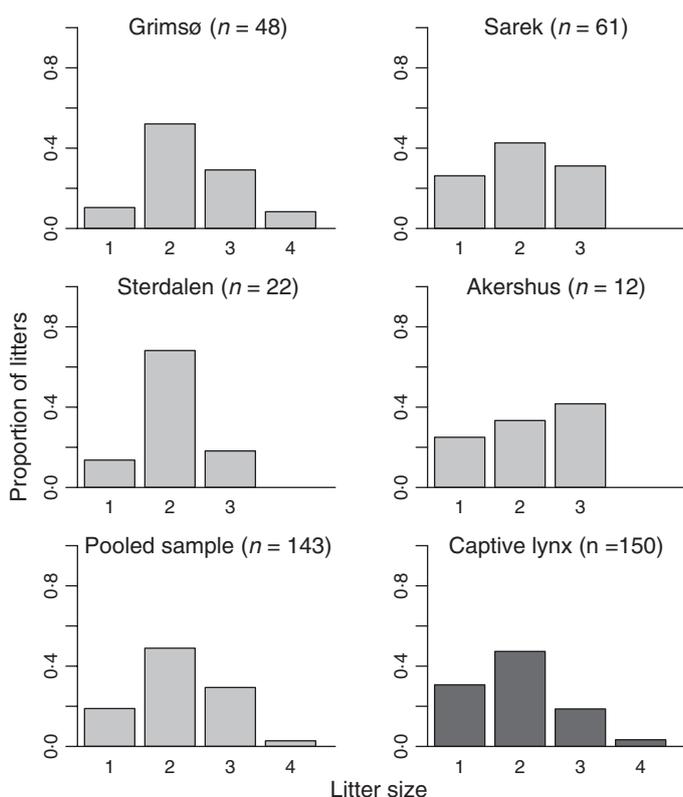

Fig. 2. Frequency distributions of lynx litter sizes in four Scandinavian populations, and their pooled distribution, as well as in captive populations in Europe. Note that the sample size is very low in Akershus ($n = 12$) where the pattern deviates from the other populations. Data from captive lynx were taken from Henriksen *et al.* (2005).

Table 1. Models used to evaluate the effects of female body mass (log-transformed) and reproductive category on litter size at birth (using a Poisson error structure and a log link) in Eurasian lynx in Scandinavia studied at four study sites. All models are fitted using the g*lmer*-function in the add-on library lme4 in the R software, with log likelihood maximized by Laplace approximation, and year (nested in study site), study site and individual fitted as random intercept terms

Model	AIC	ΔAIC	w_i
Intercept only	**16·0**	**0·0**	**0·449**
BM	17·0	1·0	0·272
RC	17·7	1·7	0·192
BM + RC	19·6	3·6	0·074
BM + RC + BM:RS	23·0	5·0	0·014

BM = female body mass, RC = reproductive category (primiparous 2 years old, primiparous 3 years old, and multiparous). Model selection was based on Akaike's Information Criterion (AIC; Burnham & Anderson 2002), with Akaike's weights calculated as described in Burnham & Anderson (2002). The selected model occurs in boldface. Sample size was 40.

the average litter size was 2·16 [95% confidence intervals (1·93; 2·42)]. The variation in litter size in relation to female mass, female parity, year and site was low although most of these factors were highly variable. Female mass averaged 15·9 kg and varied from 9·0 to 21·4 (with a coefficient of variation of 19·2%). Likewise, a large amount of variation in environmental conditions occurred among sites (with latitude ranging from 59°N to 67°N and the density of the main ungulate prey going from 0·3 to >5 per km^2, Nilsen *et al.* 2012). Lastly, our sample included both primiparous and multiparous females, which usually display marked differences in reproductive effort in vertebrates (with a lower effort in primiparous females, Curio 1983; Linden & Möller 1989). Such low variability in litter size across contrasting situations combined with low consistency of litter size within female reproductive trajectories supports the common optimal litter size mode of optimization.

FITNESS CONSEQUENCES OF PRODUCING DIFFERENT LITTER SIZES

When considering reproductive success, only two models received substantial statistical support (AIC weights higher than 0·02, Table 2a). These models included quadratic effects of litters size and differences among reproductive categories, and only differed by including or not interactive effects between litter size and reproductive categories. As the statistical support (as measured by the AIC weights) for the model including the interaction was about three times higher compared with the model without the interaction, we finally retained the model including the interaction between litter size and reproductive categories (Table 2a and Fig. 3a). From this selected model, the predicted reproductive success of primiparous female lynx at age 2 increased from a litter size of 1 to a peak at a litter size of about 2, and then decreased for lar-

Table 2. Models used to evaluate the effects of litter size at birth on reproductive success (binomial error structure and logit link) in Eurasian lynx in Scandinavia studied at four study sites. All models are fitted using the g*lmer*-function in the add-on library lme4 in the R software, with log likelihood maximized by Laplace approximation, and year (nested in study site), study site and individual fitted as random intercept terms

Model	AIC	ΔAIC	w_i
(a)			
Intercept only	201·9	13·5	0·001
LS	203·9	15·5	<0·001
RC	197·9	9·5	0·006
LS + RC	199·9	11·5	0·002
LS + RC + LS:RC	196·8	8·4	0·011
LS + LS^2 + RC	190·8	2·4	0·219
LS + LS^2 + RC + LS:RC	**188·4**	**0·0**	**0·727**
LS + LS^2	194·6	6·2	0·033
(b)			
Intercept only	161·5	13·5	0·001
LS	155·9	7·9	0·014
RC	153·5	5·5	0·048
LS + RC	**148·0**	**0·0**	**0·744**
LS + RC + LS:RC	150·7	2·7	0·193

LS = litter size at birth, RC = reproductive category (primiparous 2 years old, primiparous 3 years old, and multiparous). Model selection was based on Akaike's Information Criterion (AIC; Burnham & Anderson 2002), with Akaike's weights calculated as described in Burnham & Anderson (2002). The selected model occurs in boldface. (a) Model selection performed on the entire data set (with a sample size of 143), (b) Model selection performed on the data set restricted to litter size of 2 and larger to avoid the quadratic effect of litter size (with a sample size of 116).

ger litters (slope of the linear term on a logit scale: 4·48, SE = 1·73, slope of the quadratic term on a logit scale: −1·03, SE = 0·34, Table 2a, Fig. 3a). Similar patterns of variation occurred for multiparous females, the only difference being a higher intercept and a steeper slope of the linear term (Fig. 3a). For primiparous females at 3 years of age, too few data (only 1, 5 and 3 females for litter size of 1, 2 and 3, respectively) prevented us from obtaining robust estimates.

As the quadratic model retained from previous analyses could arise mainly as a consequence of a lower reproductive success of females producing singletons, we replicated the analysis after discarding litter size of 1 from the data set. The best model included additive effects of litter size and reproductive category (highest AIC weight, Table 2b). From this model, reproductive success markedly decreased with increasing litter size (slope on a logit scale of −1·06, SE = 0·39). Multiparous females did slightly better than 2-year-old primiparous females and clearly better than 3-year-old primiparous females although the low sample size for this group requires cautious interpretation. All these results clearly support the mode of optimization involving a common optimal litter size (Fig. 1aI).

We found very similar patterns when using the number of recruits (Table 3a, Fig. 3b). Only the models including additive or interactive effects of litter size (quadratic
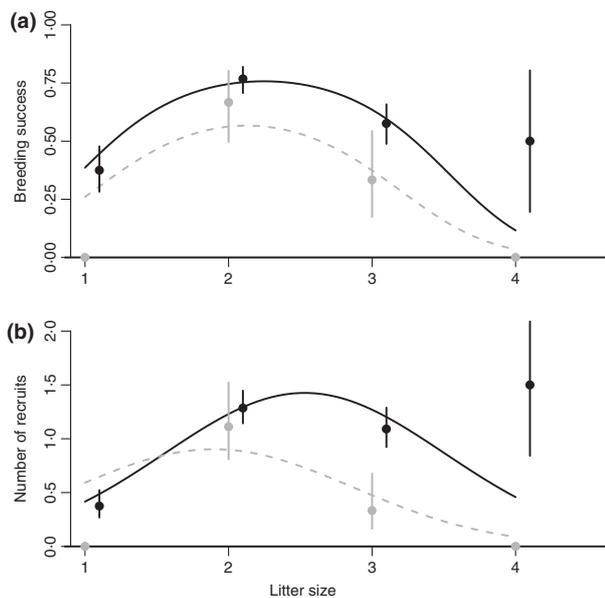
Fig. 3. Relationship between litter size and (a) reproductive success (i.e. probability of producing at least 1 recruit) and (b) number of recruits for lynx females in different reproductive categories. Smooth curves correspond to the prediction from the selected model (see Table 2a and 3a). In the panel, only the curves for 2-year-old primiparous (grey) and multiparous (black) individuals are shown, as the sample size was limited for 3-year-old primiparous. The observed data for 2-year-old primiparous (grey filled circles) and for multiparous (black filled circles) are shown as unconditional means with SE. Note that the sample size for litter sizes of 4 was very limited (only 2 observations in each of the depicted reproductive stages).

Table 3. Models used to evaluate the effects of litter size at birth on the number of recruits (Poisson error structure and log link) in Eurasian lynx in Scandinavia studied at four study sites. All models are fitted using the *glmer*-function in the add-on library lme4 in the R software, with log likelihood maximized by Laplace approximation, and year (nested in study site), study site and individual fitted as random intercept terms

Model	AIC	ΔAIC	w_i
(a)			
Intercept only	173·3	18·2	<0·001
LS	172·9	17·8	<0·001
RC	167·5	12·4	0·001
LS + RC	166·5	11·4	0·002
LS + RC + LS:RC	163·9	8·8	0·009
LS + LS^2 + RC	157·3	2·2	0·245
LS + LS^2 + RC + LS:RC	**155·1**	**0·0**	**0·735**
LS + LS^2	164·5	9·4	0·007
(b)			
Intercept only	140·5	11·7	0·001
LS	140·4	11·6	0·001
RC	**129·8**	**1·0**	**0·273**
LS + RC	129·8	1·0	0·273
LS + RC + LS:RC	128·8	0·0	0·451

LS = litter size at birth, RC = reproductive category (primiparous 2 years old, primiparous 3 years old, and multiparous). Model selection was based on Akaike's Information Criterion (AIC; Burnham & Anderson 2002), with Akaike's weights calculated as described in Burnham & Anderson (2002). The selected model occurs in boldface. (a) Model selection performed on the entire data set (with a sample size of 143), (b) Model selection performed on the data set restricted to litter size of 2 and larger to avoid the quadratic effect of litter size (with a sample size of 116).

effects) and reproductive status had non-negligible statistical support, and the model including the interaction received about three times as much support as the model without interaction (Table 1b). Predicted number of recruits produced by primiparous females at 2 years of age increased from a litter size of 1 to a litter size of about 2, and then decreased for larger litters (slope of the linear term on a log scale: 1·99, SE = 0·94, slope of the quadratic term on a log scale: −0·53, SE = 0·18, Table 3a, Fig. 3b). For multiparous females, the predicted recruitment was higher than for primiparous females (Fig. 3b). For primiparous females at 3 years of age, too few data were available.

After discarding litter sizes of 1 from the data set, three models received substantial statistical support. The best of these models included interactive effects between litter size and reproductive category (Table 3b). From this model, the number of recruits produced by primiparous females at 2 years of age tended to decrease with increasing litter size (slope on a log scale of −1·37, SE = 0·72), whereas the number of recruits produced by multiparous females was rather constant across litter size (with an increase in slope relative to primiparous females of 1·27, SE = 0·74 leading to an estimated slope of −0·10). However, based on the parsimony principle, we retained the simplest model that only included the effect of reproductive category

(Table 3b). The number of recruits tended to decrease with increasing litter size, especially for primiparous females. Although not statistically significant, these results support the mode of optimization involving a common optimal litter size (Fig. 1aIII) rather than the mode of optimization involving a state-dependent optimal litter size because under this latter model, the number of recruits should have increased with increasing litter size (Fig. 1bIII).

In both primiparous and multiparous females, the variability in the number of recruits from litter sizes of 3 was higher compared with litter sizes of 2 (Table 4). When accounting for the expected negative effect of variation in the number of recruits on fitness, the geometric mean of the number of recruits was consistently highest for females producing litters of 2, indicating that the modal average of the distribution of litter size corresponded to the litter size with the highest fitness (Fig. 1aIII and Fig. 2). These results perfectly match the expectation from the mode of optimization involving a common 'adaptive litter size'.

Discussion

We found that twinning is the most commonly observed litter size and consistently corresponds to the common

Table 4. Observed fitness (measured either as the arithmetic mean or as the geometric mean of the number of recruits) associated with different litter sizes and different reproductive categories in Eurasian lynx in Scandinavia studied at four study sites

LS	RC	N	Arithmetic mean	CV	Geometric mean
1	P2	2	0·00	0	0·00
1	M	24	0·38	132	0·30
2	P2	9	**1·11**	84	**0·90**
2	M	55	1·27	68	**1·09**
3	P2	6	0·33	154	0·26
3	M	24	1·09	101	0·81
4	P2	2	0·00	0	0·00
4	M	2	**1·5**	141	1·00

LS = litter size at birth, RC = reproductive category (P2; primiparous 2 years old, M = multiparous), N = sample size, CV = coefficient of variation (in percentage). Data on primiparous 3 years old females are not reported due to low sample size. The highest arithmetic and geometric mean fitness for both P2 and M females are in bold.

optimal litter size for Eurasian lynx. The litter size we observed (2·16) is remarkably similar to previous studies of both wild (2·0 based on 26 litters in Switzerland, Breitenmoser-Würsten *et al.* 2007) and captive (1·95 based on 150 litters, Henriksen *et al.* 2005) Eurasian lynx, indicating that 2 likely corresponds to a common optimal litter size across a wide range of ecological conditions. Litter size was independent of female mass and reproductive category, two maternal attributes commonly reported to influence reproductive effort in vertebrates (Clutton-Brock 1991). Moreover, litter size did not vary markedly among years and sites, and most females produced litter sizes of 2 in most years, leading to a very low repeatability in litter size (i.e. due to a low degree of both between- and within-individual variation in litter size). Our results also provide clear evidence that this most commonly observed litter size of 2 resulted in higher fitness, partly because increased variation in recruitment leads to reduce fitness as the decrease in the mean number of recruits with increasing litter size was not strong for multiparous females. The fitness benefit of producing a litter size of 2 was mainly shaped by the selective pressure against variation in fitness components, which generally leads to a decrease in the average individual fitness (Bulmer 1985). However, for a given litter size, we found clear evidence of individual heterogeneity in recruitment among females of different reproductive categories. In general, multiparous females recruited more than primiparous ones, especially when producing large litters. Such difference might be due to increased experience (e.g. Weladji *et al.* (2006) on reindeer, Broussard, Dobson & Murie (2008) on Columbian ground squirrels *Spermophilus columbianus*) or better skills at providing food (e.g. Rutz, Whittingham & Newton (2006) on goshawks *Accipenter gentilis*). After the fixed effects of litter size and reproductive category were taken into account, the number of recruits did not vary

among years or study sites despite marked environmental differences between study sites, regarding latitude (from 59°N in Grimsö to 67°N in Sarek), prey type (reindeer in Sarek vs. roe deer elsewhere) and prey density (from 0·3 km^{-2} in Hedmark to >5 km^{-2} in Akershus, Nilsen *et al.* 2012, 2009a).

The low variability in litter size that we found in Eurasian lynx seems to be rare for polytocous mammals for which clear relationships between female body mass and litter size are generally reported (Rieger 1996; Hewison & Gaillard 2001; Servanty *et al.* 2009). The restraint (involving a prudent (sensu Drent & Daan 1980) tactic leading individuals to allocate less to reproduction than would be possible so as to avoid any fitness costs) and constraint (involving a limitation of the reproductive allocation generated by poor individual condition or harsh environments) hypotheses have most often been supported, especially in long-lived species (Linden & Möller 1989). Alternatively, a constraint could prevent the mode of optimization involving state-dependent optimal litter size in species producing small average litter sizes. As a given individual can only produce integer number of offspring, any increase in offspring number will represent a higher relative increase in species producing twins like lynx (i.e. a 50% increase when going from 2 to 3) than in species producing say 10 offspring (i.e. a 10% increase when going from 10 to 11). Such a constraint might prevent female lynx from adjusting their litter size to their current maternal condition and is consistent with current support for the mode of optimization involving a state-dependent optimal litter size that has been documented in several species with large litters (e.g. great tits Pettifor, Perrins & McCleery 1988; Richardson's ground squirrels Risch, Michener & Dobson 2007).

In female lynx, constraints generated either by poor individual condition, bad years or less productive environments do not appear to affect litter size. It rather seems that all female lynx are limited in their ability to wean more than 2 offspring. This limitation occurs despite the low energy female lynx allocate during gestation relative to some similar-sized mammals facing with similar environmental conditions. Thus, a 20 kg female lynx produce two kittens of about 350 g at birth (J.D.C. Linnell, J. Odden & H. Andrén, unpublished data), whereas a 20 kg female of the main lynx prey, roe deer, produces 2 fawns of about 1·4 kg at birth (Andersen *et al.* 2000), leading to a fourfold difference of reproductive allocation at birth for a given size. Such a low reproductive effort, whatever its cause, should allow lynx females to adjust, at low cost, their litter size to the environmental conditions prevailing at conception. Adjustment in litter size has been previously reported in other large mammals giving birth to small newborns. For instance, in wild boar females with relative offspring sizes at birth similar to lynx (i.e. a typical 60 kg sow produce piglets of about 800 g at birth in the forest of Arc-en-Barrois, France, E. Baubet, pers. comm.), litter size is highly variable (Servanty *et al.* 2009)

and tracks temporal variation in food supply (Bieber & Ruf 2005). The existence of a common 'adaptive litter size' among female lynx despite a broad range of individual and environmental conditions raises the question of the limited, but still occurring, variation in lynx litter size: if producing twins consistently is optimal, why do all female lynx not produce twins at each reproductive attempt? One possible explanation might be that the unpredictable risk of abortion or stillbirths might lead females to have more than 2 ovulations, as reported in female pronghorn (*Antilocapra americana*) that ovulate between 3 and 9 eggs at each oestrus to consistently produce twins (Byers 1997).

Producing twins appears to be the common optimal litter size that allows female lynx to maximize recruitment under most conditions. Lynx are income breeders that cannot rely on stored body reserves (Jönsson 1997) and only depend on resource availability to meet the increased energetic demands of late gestation-early lactation which mammals have to face (Clutton-Brock, Albon & Guinness 1989). Moreover, both the annual abundance and distribution of ungulate prey (Mattisson *et al.* 2011) and hunting success (Nilsen *et al.* 2009b) are potentially highly unpredictable, and the proportion of breeding females varied among study areas (Nilsen *et al.* 2012). This unpredictability is enhanced in systems where kleptoparasitism occurs (Krofel, Kos & Jerina 2012) and may be enhanced by the fact that lactating lynx become central place foragers and must use reduced hunting ranges during the first 6–8 weeks postpartum (Schmidt 1998). This can lead to a great deal of variation in both kill interval and kill utilization, which can lead to fluctuations in energy availability being an intrinsic property of lynx lactational ecology. As lynx kittens are altricial and cannot starve for long-time periods, a lynx female has to dampen the stochasticity of food supply. Lynx females are thus likely bet-hedgers (sensu Slatkin 1974) that should minimize the probability of offspring starvation generated by unpredictable food supply. Such a life-history tactic involving the risk avoidance component of bet-hedging (Philippi & Seger 1989) might be widespread in income breeders producing small average litter size and facing day-to-day unpredictability in food availability during the critical period of rearing offspring. This will require further investigation and we suggest that large mammalian carnivores might be ideal candidates for study.

Acknowledgements

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