

# Family effects on early survival and variance in long-term reproductive success of female cheetahs

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## Summary

1. While it is generally accepted that the survival of offspring within families may be correlated, the extent of correlation has been largely untested. Furthermore, the impact of such correlation on the estimated variance in females' reproductive success has rarely been quantified.
2. Here we use an exceptional data set from a long-term study of individually recognized cheetahs from the Serengeti National Park in Tanzania to formally quantify family effects in carnivores.
3. We show (i) that cubs from the same litter exhibit more similar fates than unrelated cubs when it comes to first-year survival; and (ii) that the observed variance of the long-term reproductive success of females is twice the variance expected under the assumption of complete independence of fates between cubs.
4. We suggest that family effects are likely to be widespread in vertebrates with average litter sizes  $> 1$ , and could have important consequences for population dynamics and population viability analyses.

*Key-words:* *Acinonyx jubatus*, demographic variance, population dynamics, population viability analysis, Serengeti

*Journal of Animal Ecology* (2007) **76**, 908–914  
doi: 10.1111/j.1365-2656.2007.01266.x

## Introduction

Over the past decades, the importance of individual variability in population dynamics has been recognized and well documented (Gaillard *et al.* 2000). Factors such as age (Charlesworth 1980), sex (Clutton-Brock, Guinness & Albon 1982), social status (Lott 1991), or spatial variation in habitat quality (Coulson *et al.* 1997; Pettorelli *et al.* 2003) have been shown to constrain demographic parameters, underlying the need to take into account population structure when modelling dynamics (Caswell 2001).

'Family effects' (Gaillard *et al.* 1998) has previously been used as a general term describing similarities among related individuals, leading to dependence in life-history traits among siblings (Ims 1989; Massot *et al.* 1994; Gaillard *et al.* 1998). Similarities in life histories in related individuals can be generated through various processes, including (1) maternal effects, which can occur

when an offspring's phenotype is influenced by that of its mother, independently of the direct effects of the genes that it inherits (Reinhold 2002; Wilson *et al.* 2005); and (2) litter effects, which reflect similarities of fates among siblings belonging to the same litter (Boutin, Roses & Caley 1988; Gaillard *et al.* 1998). Up to now, to our knowledge, the only polytocous mammalian species for which the existence of family effects has been formally tested and the consequences of these effects on females' long-term reproductive success has been assessed and quantified is the roe deer, *Capreolus capreolus* (Linnaeus 1758; Gaillard *et al.* 1998).

In a recent work exploring the effects of structured heterogeneity on demographic stochasticity, Fox and co-workers showed that structured heterogeneity in life-history traits such as survival decreases the effect of demographic stochasticity on population growth rate (Kendall & Fox 2002; Fox *et al.* 2006). However, population viability analyses (PVA) still rely on estimated means and variances of life-history parameters to estimate time to extinction (Lacy 1993). Family effects will increase the variation between individuals, and thus the variance associated with the average reproductive success. As a consequence, where family effects exist,

neglecting them in population viability analyses will lead to misleading results (Boyce 1992; Gaillard *et al.* 1998), such that populations that may appear viable when neglecting these effects may not be viable in reality. Carnivores are a group that may be particularly sensitive to family effects, for two key reasons. First, many of them are threatened (IUCN Red List, <http://www.iucnredlist.org>), and many remaining populations are small and fragmented. Second, the deviation between estimated demographic variability, excluding and including family effects, is expected to increase with increasing litter size, which is often large in threatened carnivores (Schaller 1972; Caro 1994; Slough & Mowat 1996; Maddock 1999).

Although family effects have not been investigated formally in carnivores, anecdotal evidence suggests that, at least, litter effects in this group are likely to exist and may be quite strong. Predation, infanticide and abandonment are generally the principal causes of cub deaths, and both these factors are likely to affect the whole litter simultaneously. All the examples of spotted hyena, *Crocuta crocuta* (Erxleben 1777) litter disappearances reported by White (2005) involved both twin cubs dying. Infanticide is likely to play an important role in lion, *Panthera leo* (Linnaeus 1758) cub mortality, which almost always results in simultaneous cub death (Schaller 1972; Packer & Pusey 1983; Funston & Hermann 2001). Smith & McDougal (1991) reported for tigers, *Panthera tigris* (Linnaeus 1758) that 'during the first year mortality was 34%, of which 73% of mortality was whole-litter loss.

Cheetah, *Acinonyx jubatus* (Schreber 1775) in the Serengeti represent an ideal opportunity to test formally for the presence of family effects in carnivores, as the population has now been monitored for over 30 years (Caro 1994). Moreover, the species is one of the rarest large African carnivores, due to a combination of anthropogenic factors acting on unusual ecological constraints. Low interspecific competitive abilities (Durant 1998) and high predation from other large carnivores (Laurenson 1994) ensure that cheetah remain at much lower population densities than those of coexisting large predators, with the exception of wild dogs, *Lycyaon pictus* (Temminck 1820; Creel & Creel 1998). On the other hand, human population and expansion are increasing in most countries where cheetah occur (Gros 1998; Gros & Rejmanek 1999; Gros 2002), leading to increases in both the fragmentation of cheetah populations and human–carnivore conflict outside protected areas (Treves & Karanth 2003). A thorough understanding of factors affecting long-term viability of this species therefore has potentially important consequences for the management and conservation of cheetahs.

In large mammals, survival during the juvenile stage is lower and more variable than during adulthood, enhancing its role in population dynamics (Gaillard *et al.* 2000). Cheetah show particularly high levels of juvenile mortality, with only 5% of cubs born reaching independence (Laurenson 1994). The possible existence of maternal effects has been suggested previously, as there

is evidence that some mothers perform much better than others (Kelly 2001). There is, moreover, some evidence to suggest that there should be strong litter effects in cheetahs. Laurenson (1994) observed high levels of mortality in cubs while confined to a den in their first 2 months, the majority of which were through whole litter loss. However, there is no quantitative information about the linkages of the fates of siblings once they have left the den and become mobile, when litter effects should be less marked. Here we address two key questions: (1) Do mother and litter identities influence first-year survival in cheetahs? (2) If family effects exist in cheetah, what are their consequences for the long-term reproductive success of female cheetah? As predicted by Crow & Morton (1955) and previously reported for roe deer (Gaillard *et al.* 1998), family effects should increase the variance in the number of surviving offspring per female and therefore the variance in long-term reproductive success.

## Materials and methods

### STUDY SITE AND DATA

Cheetah of the south-eastern plains of the Serengeti National Park, Tanzania, have been studied continuously since 1969 (Caro 1994). Approximately 2800 lions, up to 1000 leopards, *Panthera pardus* (Linnaeus 1758), 8700 spotted hyenas and 210 cheetahs live within the ecosystem (Caro 1994), but these numbers fluctuate from year to year (Sinclair & Arcese 1995). Within the study area (2200 km<sup>2</sup>), considerable fluctuations occur in local prey and predator abundance due to seasonal migrations of prey (Durant *et al.* 1988). These migrations follow the rainfall, which falls mainly between November and May, the wet-season months. Female cheetah follow the migration of their main prey, Thomson's gazelle (*Gazella thomsonii* Blainville 1816; Schaller 1972), which means they have annual home ranges averaging 833 km<sup>2</sup> (Caro 1994).

Cheetahs in the study area are located by eye by scanning through binoculars from high vantage points. Once located, they are approached slowly in a zig-zag fashion to avoid scaring them, and are identified individually according to unique spot patterns on their pelage (Caro & Durant 1991); at the same time details are noted about their location, reproductive status and the presence of dependent cubs (Durant, Kelly & Caro 2004). In this manner, the history of individual cheetah is tracked through their lifetimes. The population in the study area has fluctuated between 50 and 80 adult cheetah since 1982, after which point the study area was clearly defined and individual cheetah within it were identified and monitored in a continuous and systematic manner.

### Litter survival data

Cubs generally become observable around emergence, when they leave the lair, at  $\approx 8$  weeks of age: more than

72% of litters have been reported previously to die in the lair, before they emerge (Laurenson 1994). With the exception of the 3 years of Laurenson's in-depth study, we generally do not have information on litter size at birth. Cubs become independent on average at 18 months (range 12–22 months; Durant *et al.* 2004). To maximize the number of litters in the analysis, we considered cubs that were first seen up to 92 days (3 months). The mean first date of observation of these litters was  $73.33 \pm 14.94$  days ( $n = 212$  cubs). Survival was assessed until 1 year of age, as independence does not occur before this age and survival from 1 year old to independence is relatively high (Laurenson 1994). Because cheetah are located by sight, intervals between sightings are unpredictable (Durant *et al.* 2004). We therefore neglected litters from the analysis if the mother was not resighted within 10 months of the first sighting. This reduces the probability that cubs are deemed not to have survived up to 1 year of age, when in fact they may have survived but are simply not seen. A total of 212 emerged cubs from 73 litters and 55 females fitted these requirements. All cubs were born between 1981 and 2003, and 128 of them (60%) survived to 1 year old.

#### *Reproductive success data*

According to Crow & Morton's (1955) model, family effects are expected to increase the variance in the number of survivors per female and therefore the variance in female reproductive success (Gaillard *et al.* 1998). Ultimately, they thus affect the variance associated with the annual reproductive output of females in population viability analyses. Cub production and female longevity are expected to account for a large amount of variance in females' reproductive success. We examined a female's ability to raise cubs while controlling for the impact of longevity, by excluding females from our analysis for which we did not have continuous data over a consistent number of years (we used 5 years) from the age of first reproduction. Considering continuous data also allowed us to control for the possible number of reproductive events (as all females considered were monitored continuously for the same number of years). Under these constraints, we obtained suitable data from 38 females. These females were observed between 1970 and 2001, and reared a total of 137 cubs. The females produced an average of  $3.60 \pm 2.48$  cubs over 5 years (ranging from 0 to 11). We neglected adopted cubs from all analyses.

#### STATISTICAL ANALYSIS

##### *Modelling cub survival*

The relationship between cub survival and litter size, age when the cubs were first seen, and female age class (distinguishing between young females and females >3 years old; Durant *et al.* 2004) was assessed using general linear mixed models, with a binomial error structure (lmer procedure in R, [www.r-project.org](http://www.r-project.org)). We

compared models, considering (a) the mother's identity as a random effect; (b) litter as a random effect nested within mother; and (c) no random effect. Model selection was performed using Akaike's information criterion (AIC; Burnham & Anderson 1998). Annual rainfall, the number of female cheetahs, and lion density in the study area were previously found to influence annual reproductive success (Durant *et al.* 2004), and were accounted for in this analysis. Because of the sample size, cheetah and lion density classes (0: below the average density over the study period, 1: above) were considered for this analysis.

##### *Variance in female reproductive success*

We obtained the frequency distribution of females according to their first 5 years' reproductive success and calculated the mean and variance of observed reproductive success. We then estimated the frequency distribution of females according to their reproductive success expected under a null hypothesis of no family effects (see Appendix S1 in Supplementary material).

In contrast to roe deer, cheetah do not reproduce seasonally and can breed all year long. The average litter size at birth for a female cheetah is 3.5, with more than 70% of the litters having a size of 3 or 4 (Caro 1994). Gestation period varies between 90 and 95 days, and a subsequent litter can be produced within months if cubs die at an early age (Caro 1994). If cubs survive, they are not independent until 18 months of age, on average (Caro 1994), but this can vary from 12 to 22 months (Durant *et al.* 2004), and a new litter is generally produced around that time. Early litter losses are rarely detected. Therefore it is impossible to obtain data on the exact number of cubs born per female per year (or over 5 years).

We know that those 38 females produced 137 cubs that reached 1 year old. The question is to estimate how many cubs were born over 5 years to those 38 females. To answer this question, we considered various scenarios. Assuming a litter size of 3.5 and that all litters are successful (low-mortality scenario), with a 12-month minimum time to independence and a 3-month gestation, we would get an average of 14 cubs per female over 5 years. But a female could produce many more cubs if all the litters produced did not survive. Laurenson (1994) estimated cub survival to be around 5%. To match this estimate (high-mortality scenario), we need a total of 68 cubs that were on average born over 5 years for each female ( $137 / (68 \times 38) = 5\%$ ). We thus used a range of possible numbers of cubs to be born over 5 years, from 12 to 68 cubs per female. The real number of cubs produced by the 38 females is expected to fall within this range.

We used this range of values to calculate the variance of reproductive success among females that should be expected when family effects do not occur. To do so, we determined the probability for a female to raise 0, 1, 2, ... 12, ... up to 68 cubs during the 5-year period, given

**Table 1.** Model selection for cub survival

Model	AIC
No random effect	230.25
Mother identity as a random effect	231.87
Litter as a random effect nested within mother	225.35

In all models, fixed effects include litter size, mother's age class, adult cheetah female density (density class), and age when cubs were first seen.

AIC, Akaike's information criterion.

**Table 2.** Cub survival as a function of female cheetah density, mother age class, age when cubs were first seen and litter size

Parameter	Estimate	SE	Z	P
Intercept	-1.19	1.65	-0.72	0.47
Female cheetah density	-1.05	0.54	-1.94	0.05
Litter size	-0.44	0.25	-1.79	0.07
Age when cubs first seen	0.04	0.02	2.17	0.03
Mother age class	0.79	0.55	1.44	0.15

the mean cub survival observed (Appendix S1). By multiplying these probabilities by the total number of females sampled, we obtained the frequency distribution of females according to reproductive success expected when survival chances of cubs are independent across females and across years (no family effects). We used an *F*-test (Lewontin 1966) to compare this variance with the observed variance in reproductive success.

## Results

Litter identity strongly affected cub survival between 3 months and 1 year ( $7.50 \pm 2.74$ ,  $F = 2.74$ ,  $P < 0.001$ ; Table 1). Cub fates within a litter were thus strongly dependent. Mother identity, however, did not significantly affect the model ( $0.006 \pm 0.07$ ,  $F = 0.07$ ,  $P = 1$ ).

The age at which the cubs were first seen (between birth and 3 months old) and female cheetah density significantly affected cub survival (Table 2). Cub survival to a year increased with increasing cub age when first seen, and decreased with cheetah density. Litter size tended ( $P = 0.07$ ; Table 2) to affect cub survival, with larger litters having lower chance of surviving to a year. Mother's age class marginally affected cub survival in

this data set, with younger females performing less well than older ones (<3 years old). Lion density and rainfall effects were not significant.

Over 5 consecutive years, the reproductive success of females varied from 0 to 11 cubs surviving to 12 months. The maximum number of years a female successfully reproduced was in 3 out of the 5 years, and this was achieved by four females, while three never reproduced successfully. There was a highly significant difference between the expected distribution of reproductive success among females assuming independence between siblings and the observed distribution of reproductive success (all  $\chi^2 > 48.40$  for  $df = 1$ ; Table 3; Fig. 1). The main differences occurred at the extreme values of reproductive success: too many females were very unsuccessful (14 females raised fewer than three cubs in 5 years) and too many females were very successful (two females raised more than eight cubs). This led to a significant increase in the variance of 5-year reproductive success among females (Table 3). The observed variance in female reproductive success was, on average, twice the variance expected under the assumption that fates of siblings were independent between years. This variance forms one of the components of demographic variability in the population, hence our results suggest that this component is much higher than predicted under the assumption of independence.

## Discussion

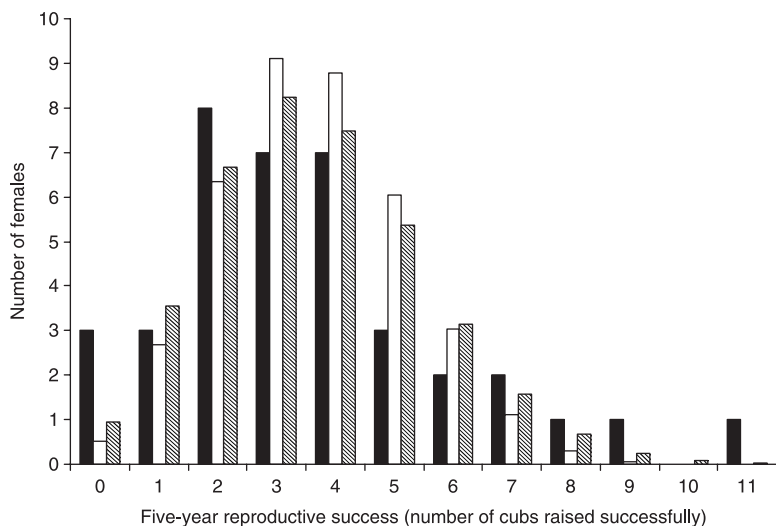
This study allows us to answer our two original questions: (1) litter effects on cub survival are strong in this species, even after emergence; (2) as predicted by Crow & Morton (1955), the variance of the long-term reproductive success of cheetah females is therefore much higher than expected under the assumption of complete independence of fates between cubs within a litter. Results previously obtained on a European, non-predated, herbivore species are thus confirmed on this African, predated, carnivore species. However, we report a two-fold increase in the variance of reproductive success among females, while a threefold increase was reported for roe deer in Trois Fontaines (Gaillard *et al.* 1998).

As described above, we already knew from the work of Laurenson (1994) that sibling fates were likely to be highly correlated in the lair. But until now, no informa-

**Table 3.** Chi-square, first year survival (from birth to a year), theoretical and observed variances in number of cubs produced per female over 5 years for each possible average number of cubs produced per female over 5 years

No. cubs	$\chi^2$	Survival	Theoretical variance	Observed variance	<i>F</i>	<i>P</i>
12	1772.27	0.30	2.59	6.14	2.37	0.005
16	301.93	0.22	2.87	6.14	2.14	0.01
20	157.26	0.18	3.03	6.14	2.02	0.02
32	77.25	0.11	3.28	6.14	1.87	0.03
48	56.81	0.07	3.41	6.14	1.80	0.04
68	48.40	0.05	3.49	6.14	1.76	0.04

Significance of difference between theoretical and observed variances tested for each possible number of cubs.



**Fig. 1.** Observed (solid bars) number of females producing 0, 1, ... , 11 cubs over 5 consecutive years ( $N = 38$  females). Expected number of females producing 0, 1, ... 11 cubs over 5 years: open bars (for an average number of 12 cubs produced per female over 5 years); dashed bars (for an average number of 68 cubs produced per female over 5 years).

tion was available on how the fates of siblings were (or were not) correlated after emergence. This study demonstrates that, even after emergence, the survival of siblings is correlated. Lions and, to a lesser extent, hyenas are the main predators of cheetah cubs, and explain most of the mortality observed in cheetah cubs during their first year (Laurenson 1994). Are our results regarding independence of fates among siblings affected by the fact that we consider survival from emergence to a year and not from birth to a year? Presumably yes: large carnivore predation and abandonment were two major causes of cub death before emergence (Laurenson 1994), and those two factors are likely to affect the whole litter simultaneously: in 26 out of the 36 litters monitored by Laurenson (1994), all cubs indeed died before emergence. But do all the cubs from the remaining litters survive? Only two litters of the 36 exhibited partial mortality, meaning that eight litters remained complete after 8 weeks. This indicates that the strength of family effects in cheetah is likely to be substantially higher than that estimated here.

Maternal and litter effects can both generate family effects in cub survival. If some mothers are better at raising cubs than others, two cubs from the same mother will have a higher chance of survival (or death) than unrelated cubs (maternal effect). If some litters are of better quality than others, two cubs from the same litter will have a higher chance of survival (or death) than unrelated cubs (litter effect). Of course, these two effects can also interact, as good mothers might raise the whole litter, while bad ones might lose the whole litter. Here we have shown that litter identity plays a role in determining cubs' fates, but mother identity did not significantly affect cub survival. This result suggests that litter effects are probably more important than maternal effects; however, in our data set few females had more than one reproductive event ( $73/55 = 1.33$  litter per female,

nine females out of 55 produced two or more litters). This reduces the power of our test, and makes it difficult to draw firm conclusions on the relative importance of both effects in shaping cub survival.

Cheetah density had a negative effect on cub survival, confirming previous results on recruitment (Durant *et al.* 2004). Mother age class affected cub survival only marginally, probably because we only considered a reduced data set. However, as demonstrated previously (Kelly *et al.* 1998; Durant *et al.* 2004), young females tended to perform less well than older females. Litter size tended to affect survival, with larger litters surviving less well than smaller ones. Previous results on other species report contrasting results – no relationship between survival and litter size: Boutin *et al.* (1988) on wild muskrats, *Ondatra zibethicus* (Linnaeus 1766), Nur (1984) in blue tits, *Cyanistes caeruleus* (Linnaeus 1758); a negative relationship: Klomp (1970) in birds; a positive relationship: Hogstedt (1980) in birds. In cheetahs, litter size might be correlated with detectability by predators such as lions and hyenas. Further research is needed to determine the possible causes of such observed relationships.

The likely proximate cause for family effects and similarities among litter mates is thus linked to the mother's attributes, with more mothers than expected performing really well, and more than expected performing extremely badly (Kelly 2001). This is illustrated by a higher than expected variance in long-term reproductive success of females. For example, while one female reared nine cubs in two breeding events, three were unable to rear a single cub in 5 years. High variance in female reproductive success has been suggested in other carnivores: in lions, Schaller (1972) reported that 18 females (all monitored from June 1966 to September 1969) raised about 23% of the expected number of young to be raised, and added that 'only one female approached her potential'. Smith & McDougal (1991) reported that in tigers, 22 breeding females monitored over 15 years produced from 0 to 12 dispersal-aged offspring, with a mean and variance in lifetime reproduction of 4.54 and 11.48. However, it is difficult to judge from these studies whether the reported variance in female reproductive success is higher or lower than what should be expected, as none of these studies tried to quantify whether the number of 'good' and/or 'bad' females observed was significantly different from what would be expected under the assumption of independence between cub fates. Moreover, they did not control for the effect of longevity on the variability in reproductive success.

In order to test whether the number of cubs produced differed from those expected, we needed correctly to estimate the average number of cubs produced by a female over 5 years. However, as we have outlined, this is not an easy task. To account for this, we considered a range of possibilities. In all cases, the distribution of the number of females according to the reproductive success over 5 years was significantly different from that expected under the assumption of complete

independence of fates for cubs within a litter. It is, however, interesting to note that an average number of more than 60 cubs born per female over 5 years was necessary to approach the estimate of survival from birth to 14 months of 5% found by Laurenson (1994). If this survival was the same throughout our study, this would indicate that, on average, cheetah females produce three litters a year in order to produce the number of surviving cubs observed in our population, highlighting a high reproductive potential for this species.

Population viability analysis makes use of stochastic demographic models to predict extinction risk. All else being equal, higher variance in a demographic rate will lead to a greater extinction risk (Boyce 1992). Here we have demonstrated that family effects result in a variance in female reproductive success or recruitment nearly twice that under the assumption of complete independence of fates between litter mates. In addition, as we have already noted, this estimate is likely to be an underestimate of the true impact of litter effects, as it neglects the extreme dependence of fates observed in litters still in their den. Estimates of the variability in demographic parameters is a fundamental component of PVA analysis; however, these analyses usually assume that the fates of individuals are independent. Our results show that if this is the case, and family effects are neglected, demographic variability will be substantially lower than in reality. This will result in an underestimation of extinction rate. In the case of highly threatened carnivores such as cheetah, this can have serious consequences on recommendations for conservation and management.

### Acknowledgements

We gratefully acknowledge TANAPA, TAWIRI and the Tanzania Commission for Science and Technology for providing permission to conduct the long-term study in the Serengeti. We would also like to thank all the following who have contributed to the field work of the Serengeti Cheetah Project, G. & L. Frame 1974–77; T. Caro 1980–90; A. Collins 1984; C. FitzGibbon 1985–87; S. Cleaveland 1990; L. Gilby 1992; L. Turnbull 1993; I. Graham 1994; J. Milner 1995; J. Wisbey 1996; G. & I. Sayers 1997; T. Maddox; J. Shemkunde 1999–2002; S. Bashir; A. Hilborn 2004-present. Marcella Kelly identified all of the cheetahs between 1980 and 1990. We are grateful to the many organizations who have funded the project, principally The Howard G. Buffett Foundation, Wildlife Conservation Society, Frankfurt Zoological Society (FZS), National Geographic Society, Leverhulme Trust, Royal Society UK, Times Christmas Appeal 1998, Messerli Foundation and People's Trust for Endangered Species. Numerous people and organizations in Tanzania and Kenya have provided much needed logistical support, including B. Allen, O. Newman, A. Barrett, J. Driessen, J. Jackson, A. Geertsema, P. and L. White and the staff and management of Nduvu Safari Lodge, the late H. van Lawick and his team, fellow scientists at SWRC, G. and M. Russell and M.

Borner and the staff at FZS. Finally, we thank Elizabeth Boakes, and Jean-Michel Gaillard for improving the manuscript by providing detailed comments on a previous version.

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Received 14 November 2006; accepted 24 April 2007

### Supplementary material

The following supplementary material is available for this article.

**Appendix S1.** Estimating the theoretical variance in reproductive success for a given average number of cubs produced over 5 years.

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/full/10.1111/j.1365-2656.2007.01266.x>

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