

# Predation risk and longevity influence variation in fitness of female roe deer (*Capreolus capreolus* L.)

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**We studied the effects of population density, red fox predation risk, individual body mass and longevity on female fitness in a free-ranging roe deer population. During the study, population density varied from 9.3 to 36.1 deer km<sup>-2</sup>, and red fox abundance varied strongly over years owing to a sarcoptic mange outbreak. In support of our predictions, long-lived females had higher fitness than short-lived ones. Further, fortunate female roe deer that gave birth in years of low red fox abundance attained much higher fitness than those that gave birth in years of high red fox abundance. Longevity and predation risk explained more than half the variation in fitness observed among roe deer females. As a possible effect of small sample size, we found no effect of female body mass or population density at birth. Our study demonstrates that predation risk, a component of environmental stochasticity, may prevent directional selection even when phenotypic quality influences individual fitness.**

**Keywords:** demographic tactic; phenotypic quality; environmental stochasticity; reproductive success; ungulate

## 1. INTRODUCTION

The ultimate measure of an individual's biological success is its fitness, often indexed by its lifetime reproductive success (LRS; Clutton-Brock 1988). In most vertebrate populations, fitness variation among females generally depends on offspring survival and female longevity (Clutton-Brock 1988; Newton 1989). Indeed long-lived animals may encounter a variety of conditions during their lifetime that are likely to influence offspring survival and longevity (Beckerman *et al.* (2002); see Gaillard *et al.* (2000a) for a review on ungulates). Only a few previous studies have quantified the causes of variation in individual fitness of large herbivores (Clutton-Brock *et al.* (1988) on red deer, *Cervus elaphus*; Berger (1986) on wild horse,

*Equus caballus*; Byers (1997) on pronghorn, *Antilocapra americana*). Moreover, all previous studies used LRS as a proxy for fitness. We present a study of female roe deer, *Capreolus capreolus* L., in Sweden where we quantified the relative importance of predation risk by red fox *Vulpes vulpes* L., deer population density, individual body mass and lifespan on fitness variation. We measured fitness as an individual  $\lambda$  (McGraw & Caswell 1996). Both population density and predation risk by red fox were highly variable over the study period. We predicted that individual fitness of female roe deer should increase with individual female longevity (Gaillard *et al.* 2000b) and body mass (Gaillard *et al.* 2000a) and should decrease with increasing population density (Clutton-Brock *et al.* 1988) and increasing frequency of years with high predation risk during the reproductive career of females (Kjellander & Nordström 2003).

## 2. MATERIAL AND METHODS

The study was performed during 1988–2002 at Bogesund, a 1200 ha research area located a few kilometres north of Stockholm (59°23' N, 18°15' E), in the hemi-boreal zone of east central Sweden. The main predator on neonate roe deer in our study area is the red fox.

Roe deer fawns were either caught by hand as newborns during early summer ( $n = 152$ ) or captured during winter using trap boxes ( $n = 389$ ) and nets ( $n = 4$ ). They were individually marked and weighed. We only analysed data from radio-marked females of known age that had reached age at first reproduction (2 years) to measure individual fitness ( $n = 23$ ). Adult females (2 years or older) were weighed during the trapping period from December to March. Population density was estimated from the resightings of radio-marked animals by using the Petersen–Lincoln method (Caughley 1977). Roe deer density increased from  $9.3 \pm 2.3$  (s.e.) deer km<sup>-2</sup> in September 1989, to  $36.1 \pm 5.2$  (s.e.) deer km<sup>-2</sup> 3 years later in September 1992 after a period with no hunting in the study area. In October 1992, an experimental reduction of roe deer was initiated and by April 1994 the population had been reduced to  $8.2 \pm 0.8$  (s.e.) deer km<sup>-2</sup>. Roe deer numbers remained at a low level until 1998. In absence of an accurate density estimate in 1988 (i.e. we can only assess that roe deer density was less than 12 deer km<sup>-2</sup> that year), roe deer females were classified as 'born at high density' (mean estimate of 29.0 deer km<sup>-2</sup>,  $n = 10$ ) or 'born at low density' (mean estimate of 11.6 deer km<sup>-2</sup>,  $n = 13$ ). As an index of red fox density, we used fox-hunting bag records expressed as the number of foxes killed per hunter day in the study area recorded over the same period (1989–2002). In addition, we used official county statistics for the total fox-hunting bag (Swedish Association for Hunting and Wildlife Management, Wildlife Surveillance) to identify the period when fox numbers were low owing to an epizootic outbreak of sarcoptic mange (see Lindström *et al.* 1994; Kjellander & Nordström 2003). Fox densities were thus categorized as 'low' or 'high' for a given year. For each roe deer female, we then determined the proportion of her reproductive career when she was exposed to high fox predation. This was done by dividing the number of reproductive seasons that the female was exposed to high fox predation risk by the total number of reproductive events in her life. We therefore used a continuous measure of fox predation risk in our analysis.

We estimated female individual fitness by using the dominant eigenvalue ( $\lambda$ ) of Leslie matrices built on individual females, as recommended by McGraw & Caswell (1996) and used by Gaillard *et al.* (2000b). Individual  $\lambda$  were calculated using S-PLUS software (Venables & Ripley 1994). The total number of females used after excluding females that died from human-related causes (including culling and road kills) was 23. Total lifespan was measured by radio tracking, but for most females, reproductive success was not known for all years of their lives. Individual annual reproductive success was measured as the number of fawns surviving to weaning by a given female. This measure was directly assessed through fawn–doe observations after radio tracking or occasional observations during autumn, before winter (i.e. 20 December; see Gaillard *et al.* (2000b) for further details). We only retained females for which data from more than half of their lifespan had been obtained. We then estimated the missing values by using the mean reproductive success measured in years when that female was monitored (Gaillard *et al.* 2000b). On average, we had data from 83.8% of the years concerned. We found all covariates to be independent ( $R^2 < 0.035$ ,  $p > 0.39$  in all cases). Owing to the small sample size ( $n = 23$ ), we did not test for

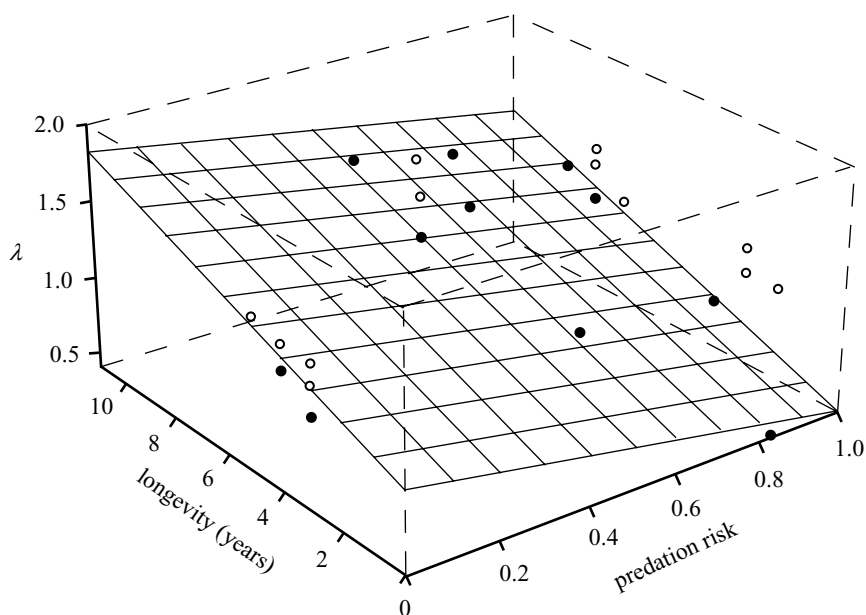


Figure 1. Fitness in 23 female adult roe deer measured as individual  $\lambda$  in relation to longevity and fox predation risk during 1989–2002 at Bogesund, Sweden. Both open and filled circles indicate observed values and the plane indicates the expected relationship from the retained model. Open circles are above the plane and filled circles are beneath it.

interaction among factors. However, based on previous work that suggests changing effects of fox predation at different levels of population density (Kjellander 2000), we tested for the interaction between density and predation risk.

### 3. RESULTS

The most general model included thus additive effects of population density, body mass, longevity and predation risk on individual  $\lambda$ . From this model and contrary to our expectation, we did not find any significant influence of density ( $F_{1,18} = 0.106$ ,  $p > 0.7$ ) or body mass ( $F_{1,18} = 0.149$ ,  $p > 0.7$ ) on individual fitness. Likewise, we did not find any support for an interaction effect between density and predation risk ( $F_{1,18} = 0.018$ ,  $p > 0.8$ ). However, both longevity ( $F_{1,18} = 14.567$ ,  $p = 0.0013$ ) and predation risk ( $F_{1,18} = 9.112$ ,  $p = 0.0074$ ) had marked effects on  $\lambda$ . As expected,  $\lambda$  increased with longevity (slope  $\pm 1$  s.e. =  $0.0826 \pm 0.0213$ ) and decreased with predation risk (slope  $\pm 1$  s.e. =  $-0.4875 \pm 0.1529$ ; figure 1). The selected model accounted for 52.5% of the observed variation in  $\lambda$ .

Two females had  $\lambda$  equal to 0. However, whether we discarded or retained these two females did not affect the results (mean  $\lambda_{n=21} = 1.169$ , s.e.  $\pm 0.046$ ; mean  $\lambda_{n=23} = 1.067$ , s.e.  $\pm 0.082$ ). We therefore chose to include them in the above presentation of the results.

### 4. DISCUSSION

In this study, we have demonstrated that longevity and predation risk account for most of the observed variation in fitness among female roe deer. By contrast, and contrary to our predictions and as a possible effect of small sample size, the variation in body mass and population density had no detectable influence on individual fitness. Ungulates such as roe deer seem to adopt a bet-hedging tactic involving both a risk-averse and a risk-spreading component (Gaillard & Yoccoz 2003). In such a game, the key component is the number of breeding events. Therefore, females with the largest number of breeding

attempts, i.e. with the longest life, should be selected for. Our results support such an expectation. Further, our study also demonstrates that environmental stochasticity can markedly affect individual fitness. Thus, for a given longevity, fortunate females giving birth in years with low fox abundance, and therefore low neonate predation risk, had a much higher fitness than the unfortunate ones that gave birth in years of high fox abundance. In stochastic environments, a large part of fitness variation among individual females is therefore due to chance alone (i.e. because offspring survival is related to an extrinsic factor such as variable fox abundance). Such a pattern is expected to reduce or even prevent directional selection. In particular, the surprising absence of any effect of female body mass or population density at birth on female fitness could be owing to the high yearly variation in predation risk in our study population. In roe deer, generally, the heaviest individuals survive better (Gaillard *et al.* 2000b), start to reproduce earlier in life (Gaillard *et al.* 1992) and produce a larger number of offspring than lighter conspecifics (Hewison 1996). In predator-free environments where most offspring mortality is care dependent (*sensu* Lycett *et al.* 1998), such differences lead to obvious fitness advantages for heavier individuals. However, when most offspring mortality is care independent (*sensu* Lycett *et al.* 1998), mediated by predation or disease, individual fitness may vary strongly and independently of female phenotypic quality.

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- Beckerman, A., Benton, T. G., Ranta, E., Kaitala, V. & Lundberg, P. 2002 Population dynamic consequences of delayed life-history effects. *Trends Ecol. Evol.* **17**, 263–269.
- Berger, J. 1986 *Wild horses of the Great Basin. Social competition and population size*. University of Chicago Press.
- Byers, J. A. 1997 *American pronghorn. Social adaptations and the ghosts of predators past*. University of Chicago Press.
- Caughley, G. 1977 *Analysis of vertebrate populations*. New York: Wiley.
- Clutton-Brock, T. H. 1988 *Reproductive success*. University of Chicago Press.
- Clutton-Brock, T. H., Albon, S. D. & Guinness, F. E. 1988 Reproductive success in male and female red deer. In *Reproductive success* (ed. T. H. Clutton-Brock), pp. 325–343. University of Chicago Press.
- Gaillard, J.-M. & Yoccoz, N. G. 2003 Temporal variation in survival of mammals: a case of environmental canalization? *Ecology* **84**, 3294–3306.
- Gaillard, J. M., Sempéré, A. J., Boutin, J. M., Van Laere, G. & Boisubert, B. 1992 Effects of age and body weight on the proportion of females breeding in a population of roe deer (*Capreolus capreolus*). *Can. J. Zool.* **70**, 1541–1545.
- Gaillard, J.-M., Festa-Bianchet, M., Yoccoz, N. G., Loison, A. & Toïgo, C. 2000a Temporal variation in fitness components and population dynamics of large herbivores. *A. Rev. Ecol. Syst.* **31**, 367–393.
- Gaillard, J. M., Festa-Bianchet, M., Delorme, D. & Jorgenson, J. 2000b Body mass and individual fitness in female ungulates: bigger is not always better. *Proc. R. Soc. Lond. B* **267**, 471–477. (DOI 10.1098/rspb.2000.1024.)
- Hewison, M. 1996 Variation in the fecundity of roe deer in Britain: effects of age and body weight. *Acta Theriol.* **41**, 187–198.
- Kjellander, P. 2000 Density dependence in roe deer population dynamics. PhD thesis, Grimsö Wildlife Research Station, Swedish University of Agricultural Sciences, Uppsala, Sweden.
- Kjellander, P. & Nordström, J. 2003 Cyclic voles, prey switching in red fox, and roe deer dynamics—a test of the alternative prey hypothesis. *Oikos* **101**, 338–344.
- Lindström, E. R., Andrén, H., Angelstam, P., Cederlund, G., Hörnfeldt, B., Jäderberg, L., Lemnell, P.-A., Martinsson, B., Sköld, K. & Swenson, J. E. 1994 Disease reveals the predator: sarcoptic mange, red fox predation, and prey populations. *Ecology* **75**, 1042–1049.
- Lycett, J. E., Henzi, S. P. & Barrett, L. 1998 Maternal investment in mountain baboons and the hypothesis of reduced care. *Behav. Ecol. Sociobiol.* **42**, 49–56.
- McGraw, J. B. & Caswell, H. 1996 Estimation of individual fitness from life-history data. *Am. Nat.* **147**, 47–64.
- Newton, I. 1989 *Life time reproduction in birds*. London: Academic Press.
- Venables, W. N. & Ripley, B. D. 1994 *Modern applied statistics with S-PLUS*. New York: Springer.