Lifetime reproduction of a forest-dwelling owl increases with age and area of forests

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Loss and alteration of habitats by human actions are the largest worldwide hazard to biodiversity and viability of populations. In boreal forests of Eurasia and North America the natural habitat is changing, mainly because of forestry practices and agriculture. Although there is evidence that the diversity and abundance of animal species are lower in intensively managed than in natural forests, very little is known about how the changes in habitat composition affect reproduction and survival. The best available measure of individual performance in the wild is lifetime reproductive success (LRS), the number of offspring produced during a lifetime, because it combines both survival and reproductive success to a single measure. We show that the LRS of forest-dwelling Tengmalm's owls (*Aegolius funereus*) increases with the proportion of old forest in the territory because of a higher number of breeding attempts, whereas it decreases with the proportion of agricultural land because of declining fledging success in years when prey populations crashed during owl breeding. These unique results provide an interesting insight into how human influence on the landscape can affect life-history traits of animals through various pathways.

Keywords: forest management; habitat loss; habitat quality; nature conservation; reproduction; wildlife management

1. INTRODUCTION

Loss and alteration of habitats are the largest worldwide hazard to biodiversity and viability of populations (Hanski *et al.* 1995; Fahrig 2003). In the boreal forests of Eurasia and North America the natural habitat is changing, mainly because of forestry practices and agriculture (Hansson 1992). Although there is evidence that the diversity and abundance of animal species are lower in intensively managed than in natural forests (Hansen *et al.* 1991; Schmiegelow & Mönkkönen 2002), very little is known about how the changes in habitat composition affect reproduction and survival at the level of individuals. The best available measure of individual performance in the wild is lifetime reproductive success (LRS), the number of offspring produced during a lifetime, because it combines both survival

and reproductive success to a single measure (Clutton-Brock 1988; Newton 1989).

Tengmalm's owl (*Aegolius funereus*) is a small, nocturnal, hole-nesting bird of prey living in the boreal forests of Eurasia (Mikkola 1983) and North America (Hayward & Hayward 1993). Male Tengmalm's owls are faithful to their breeding territory after their first breeding attempt, which makes it possible to estimate their LRS (Korpimäki 1992). By contrast, the females disperse widely after each breeding attempt and a pair breeds together only once (Korpimäki 1993).

The population dynamics of Tengmalm's owls depends strongly on the population fluctuations of their main prey, *Microtus* and *Clethrionomys* voles (Laaksonen *et al.* 2002). Populations of these voles in our study area in western Finland fluctuate in a cyclic manner in 3 year periods (Korpimäki *et al.* 2002). In low vole years, vole densities are low during the breeding season of the owls. In increase vole years, vole densities increase during the owl breeding season and peak in the following autumn. In decrease vole years, the vole densities are still high to intermediate at the beginning of the owl breeding season, but crash during the summer. The size of the breeding population and reproductive output of Tengmalm's owls depend on the vole cycle, so that they are low in the low vole years, intermediate and high in the increase years, and high and intermediate in the decrease years, respectively (Laaksonen *et al.* 2002). The LRS is higher for males that breed for the first time in an increase year than for those first breeding in a decrease year (Korpimäki 1992). We examined how the habitat composition of the territory was associated with the LRS of male Tengmalm's owls in a landscape that is typically a mosaic of different aged forests and agricultural land (Hakkarainen *et al.* 2003).

2. MATERIAL AND METHODS

The data on LRS were collected in a long-term population study on Tengmalm's owls in the Kauhava region in western Finland (approximately 63° N, 23° E; 1300 km²). Breeding data were combined with land-use and forest-resource data using GIS. Land-use and forest-resource data were obtained from Landsat TM 5 images, classified by the National Land Survey (NLS) of Finland (Vuorela 1997). In digital maps, landscape is differentiated between different habitat classes at a pixel level (25 m × 25 m). Initially, NLS classification includes several land use and forest classes, but we reduced the amount of examined habitat classes to the five most relevant for the study species (Hakkarainen *et al.* 2003; table 1).

We included only males that began their breeding career during 1987–1992 because the landscape satellite data on the land use and forest resources were recorded in 1991. Annually, 70–90% of male owls breeding in the study area were captured. Only three of the males first bred in a low year of the vole cycle; these males were combined with those that had first bred in the increase phase (Korpimäki 1992). Males breeding closer than 5 km to the edge of the study area were excluded, because these males could also have bred outside the study area (Korpimäki 1993). Because in some nest-sites different males had used the same site in consecutive years, we randomly chose only one male for each nest-site, resulting in 209 males that had been using different nest-sites. The population study continues; the last observation from one of these males was from 1996.

We used a 1000 m radius (314 ha) around the nest-boxes as proxy to the breeding territory because it covers the approximate home range size of Tengmalm's owls (*ca.* 200–500 ha; Hakkarainen *et al.* 2003) and is the most relevant radius for breeding success (Hakkarainen *et al.* 2003). The mean distance between occupied nest-sites was 2700–8800 m depending on the year (Hakkarainen *et al.* 2003), and therefore the potential overlap between habitat measurements of two males with the 1000 m radii circles is very small. For each male we present results with habitat variables from one randomly chosen breeding occasion, but the results were the same when the analyses were performed with habitat data averaged over all nest-sites used by the male (the median distance that the

Table 1. The five habitat classes, the proportions they cover, on average, from the territory of male Tengmalm's owls within a radius of 1000 m around the nest-box, and the eigenvectors of the first two principal components of the habitat variables. (PC1 explained 48.4% of the variation and represented a decreasing proportion of agricultural land with increasing proportions of all three forest types and clear-cut and sapling areas. PC2 explained 35.2% of the variation and represented increasing proportions of old and middle-aged forest, and decreasing proportions of agricultural land, young forest and clear-cut areas.)

habitat variable ($\text{m}^3 \text{ wood ha}^{-1}$)	coverage ($\% \pm \text{s.d.}$)	range (%)	PC1	PC2
old forest (more than 151)	12.36 ± 5.47	35.1	0.089	0.660
middle-aged forest (102–151)	11.90 ± 3.96	21.8	0.309	0.587
young forest (less than 102)	36.97 ± 12.93	57.2	0.582	-0.203
clear-cut and sapling areas	5.26 ± 3.05	17.0	0.417	-0.414
agricultural land	27.50 ± 16.86	78.6	-0.620	-0.081

Table 2. Results of a generalized linear model analysis on LRS (log-link, Poisson distribution). (The models were run with interaction terms that were subsequently removed if not significant according to likelihood-ratio tests. The reduced model presented here fitted the data well (deviance = 328.4, d.f. = 202, dispersion parameter = 1.63).)

independent variable	d.f.	χ^2	<i>p</i> -value
vole cycle phase at first breeding	1	17.09	< 0.0001
age at first breeding	1	0.59	0.4415
number of breeding attempts	1	137.98	< 0.0001
PC1	1	8.38	0.0038
PC2	1	0.35	0.5519
age at first breeding * PC2	1	8.07	0.0045

males move between two breeding attempts is 1300 m; Korpimäki 1993).

We first performed principal component analysis (PCA) on the habitat variables to reduce the number of variables and to create new uncorrelated variables. In the subsequent analyses we used the first two principal components (PCs), which together explained 83.4% of the variation in the habitat variables (PC1 explained 48.2% and PC2 35.2%; table 1). The data on LRS were analysed with generalized linear models (generalized linear model; log-link and Poisson distribution) in which vole cycle phase and age at first breeding were class variables, and number of breeding attempts and the two PCs on habitat composition were quantitative variables. We used the total number of breeding attempts as an explanatory factor for LRS rather than breeding lifespan because 10–20% of boreal owl males are polygynous in good vole years (Korpimäki 1992) and thus the total number of breeding attempts is more relevant for their LRS than breeding lifespan. Because LRS can be affected through reproductive success at any one breeding attempt, or through number of breeding attempts, we also analysed the correlations between the number of breeding attempts and the habitat variables.

3. RESULTS

As found previously (Korpimäki 1992), LRS increased with number of breeding attempts. It was higher for males that first bred in the increase phase of the vole cycle than for those that first bred in the decrease phase (table 2). From the habitat variables LRS increased with PC1 (table 2; figure 1), which represented an increasing proportion of all forest age classes with decreasing proportion of agricultural land (table 1). The relationship between LRS and PC2, which represented an increasing proportion of middle-aged and old forests (table 1), differed with age at first breeding (table 2); LRS had no obvious relationship with PC2 in males that bred for the first time at the age of 1 year ($\chi^2 = 2.45$, $p = 0.11$; figure 2a), but it increased with PC2 in males that first bred at the age of 2 or more years ($\chi^2 = 6.31$, $p = 0.012$; figure 2b). PC1 did not correlate with the number of breeding attempts ($r_s = -0.02$, $p = 0.72$), whereas PC2 did ($r_s = 0.19$, $p = 0.005$).

Figure 1. LRS in relation to PC1. LRS is presented as residuals from a model with vole cycle phase, age at first breeding, number of breeding attempts and PC2.

Although the PCA indicated that the proportions of middle-aged and old forests covary in the landscape (table 1), they do not necessarily have equal biological importance to the owls. As we were specifically interested in confirming whether the relationship was due to the amount of old forests, we also analysed the relationship between the life-history traits and these two forest types separately.

The proportion of old forest correlated more strongly with the number of breeding attempts ($r_s = 0.24$, $p = 0.0005$) than the proportion of middle-aged forest ($r_s = 0.12$, $p = 0.07$). Moreover, when the variable for number of breeding attempts was removed from the GLM, and PC2 was replaced either with the proportion

Figure 2. LRS in relation to PC2. LRS is presented as residuals from a model with vole cycle phase, age at first breeding and PC1. LRS had no relationship with PC2 in males breeding for the first time at the age of 1 year (a), but it increased with PC2 in males that first bred at the age of 2 or more years (b).

of old forest or with the proportion of middle-aged forest, LRS increased significantly with the proportion of old forest ($\chi^2 = 6.24$, $p = 0.012$), but not with the proportion of middle-aged forest ($\chi^2 = 1.98$, $p = 0.16$).

4. DISCUSSION

LRS can be affected through reproductive success at any one breeding attempt or through several breeding attempts. The result that PC1 correlated positively with LRS is in accordance with an earlier study on the reproductive success of Tengmalm's owls at single breeding attempts, which showed that in years of decreasing vole abundance, fledging success from eggs to fledglings decreased with an increasing proportion of agricultural land in the territory (Hakkarainen *et al.* 2003). Thus, the positive relationship between LRS and PC1 is most probably explained by the decline in fledging success in the decrease years of the vole cycle, as PC1 did not correlate with the number of breeding attempts. In the decrease years the vole populations crash in spring and summer during the breeding season of the owls. As Tengmalm's owls are sit-and-wait hunters that hunt in forests, the area

of agricultural land is directly away from their hunting grounds in those years when their prey is getting scarcer throughout the season. In addition, it has been suggested that the crash of the vole populations begins earlier at agricultural areas owing to a high predation impact by many predator species on vole populations (Hakkarainen *et al.* 2003). This suggestion is based on the population densities of vole-eating predators being especially high in farmland-predominated areas (Korpimäki & Norrdahl 1991), but the theory remains to be tested directly.

Although no relationships have been detected between reproductive success at single breeding attempts and the proportions of old or middle-aged forest in the territory (Hakkarainen *et al.* 2003), we found that PC2 correlated with the number of breeding attempts. The proportion of old forest correlated more strongly with the number of breeding attempts than the proportion of middle-aged forest. These results indicate that the number of breeding attempts increased in particular with an increasing proportion of old forest within the territory, but it must be remembered that discerning the relationships is difficult because the two habitat types covary in the landscape. It is, as yet, unclear why the relationship between PC2 and LRS depended on age at first breeding. We suggest that those males that begin their breeding career at an older age can better take advantage of their territory because they have had more time to settle there and/or they are more experienced.

In conclusion, our results indicate two different ways that habitat composition is associated with the fitness of male Tengmalm's owls. First, LRS increased with the amount of old forest through a higher number of breeding attempts. Old forests with dense coverage probably offer better refuges against predators, such as larger owls (Hakkarainen & Korpimäki 1996) and goshawks, *Accipiter gentilis* (Sunde *et al.* 2004), than younger forests. In addition, old forests may be better feeding areas for Tengmalm's owls, thus improving the probability of survival or breeding. Second, LRS decreased with an increasing proportion of agricultural land mainly because of decreased fledging success in years of decreasing vole abundance. This effect may have arisen from a reduction in the area suitable for hunting, or because the vole populations, and consequently the fledging success of owls, crashed, particularly in agricultural areas during the owl breeding season (Hakkarainen *et al.* 2003). We emphasize that it is impossible, without experiments, to conclusively distinguish whether habitat composition directly affects the fitness components or individuals differ in phenotypic quality, and good-quality individuals have access to the best territories. However, as experimental studies on this scale are very difficult to conduct, our results from a large dataset in a natural population currently provide one of the best available indications that human-induced changes in the landscape can affect essential life-history traits and subsequently the persistence of vertebrate populations and species through various pathways.

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