Interactive effects of parental age and environmental variation on the breeding performance of Tengmalm’s owls

TONI LAAKSONEN, ERKKI KORPIMÄKI and HARRI HAKKARAINEN

Section of Ecology, Department of Biology, University of Turku, FIN-20014 Turku, Finland

Summary

1. Two main mechanisms have been proposed to account for the changes in breeding performance of long-lived animals with age: progressive appearance or disappearance of different quality individuals within a cohort and within-individual improvements with age.

2. We studied age-related breeding performance of vole-eating Tengmalm’s owls (Aegolius funereus, L.), whose prey populations fluctuate in a cyclic manner in western Finland. In years of low vole abundance, most yearling owls were not able to breed. In years of initially intermediate but increasing vole abundance, clutch size increased with female age and partners of old males initiated egg-laying earlier than those of young males. In years of initially high but decreasing vole abundance, the differences in laying dates were still detectable, whereas age-related differences in clutch size of females tended to disappear.

3. Within-cohort analyses did not indicate quality differences between surviving and dying males of the same age in years of increasing vole abundance, whereas in years of decreasing vole abundance early breeding males were more likely to survive than late-breeding males. This novel finding indicates that quality differences between individuals may induce observed age-related differences in only some years, and especially that differential mortality may occur in a different year when the difference in breeding performance is detectable.

4. Within-individual analyses showed that individual males advanced their nest initiation with age, and there was a trend that females laid larger clutches with increasing age. In nests of long-lived males, a significant decline in the clutch size from mid-age (2–4 years) to older age (6–10 years) was found.

5. We conclude that environmental variation may mask age-related differences in breeding performance at the population level, since the differences appeared to emerge more clearly in poor and intermediate food conditions. Some evidence for the differential mortality-hypothesis was found for males, which are mainly responsible for subsisting their families during the entire breeding season. Substantial improvements in competence or increased reproductive effort from 1 to 3 years of age, and deteriorated skills due to senescence at older ages may account for within-individual changes in breeding performance of males.

Key-words: Aegolius funereus, cyclic variation in food abundance, differential mortality, reproductive effort, senescence.


Introduction

An understanding of age-dependent reproductive output of iteroparous animal species is one of the primary aims of the life-history theory (Roff 1992; Stearns 1992). Effects of parental age on breeding performance have been found for many long-lived animal species. In most cases, breeding performance improves with age in the early years of life and reaches a maximum level at the middle age (reviews in Clutton-Brock 1988; Newton 1989; Saether 1990; Forslund & Pärt 1995; Martin 1995). Some long-term studies have also found...
a decline in breeding performance during later years of the breeding span, which is often attributed to senescence (e.g. Lunn, Boyd & Croxall 1994; Newton & Rothery 1998; Packer, Tatar & Collins 1998; Ratcliffe, Furness & Hamer 1998; Möller & De Lope 1999). Four primary hypotheses that are not mutually exclusive and can operate concurrently within a population have been proposed to explain the observed age-related patterns in breeding performance. The differential mortality- and delayed breeding-hypotheses suggest progressive disappearance or appearance of different-quality individuals within an age-cohort at the population level, and the constraint- and restraint-hypotheses consider changes between breeding attempts of an individual (Forslund & Pärt 1995). The differential mortality-hypothesis suggests that individuals performing poorly in breeding are of lower phenotypic quality than better performing individuals and, hence, also more prone to die or disperse before the next breeding season (Smith 1981; Nol & Smith 1987). Thus, when proportionally more poor-quality than high-quality individuals die between breeding seasons, the mean reproductive performance of a cohort improves in successive years because the relative proportion of high-quality individuals in it increases every year. According to the delayed breeding-hypothesis, the mean performance of a cohort at later age increases if high-quality individuals delay their first breeding attempt and, therefore, recruit in the breeding population later than lower-quality individuals (Hamann & Cooke 1987).

At the within-individual level, the constraint-hypothesis (Curio 1983) suggests that some abilities or skills affecting breeding performance may improve with maturation or learning by experience. Popular explanations for better performance at older age are increasing foraging efficiency with experience (Desrochers 1992; Derocher & Stirling 1994; De Forest & Gaston 1996; Catry & Furness 1999), and accumulating breeding experience increases reproductive effort and future reproduction, and predicts that reproductive effort increases with age as the residual reproductive value (Williams 1966) decreases, which improves breeding performance with age (Curio 1983). Without a specific experimental design it is difficult to discern between constraint and restraint in wild animal populations, and therefore most researchers have only been able to find out whether age-related differences are detectable at the within-cohort or within-individual levels (Forslund & Pärt 1995; Martin 1995; Espeset al. 2000).

An important aspect that has been considered in only a few studies is the effect of environmental variation on the occurrence of age-related differences in breeding performance. The prediction is that age will affect breeding success less in good and more in poor environmental conditions (Sydeman et al. 1991; Wheelwright & Schultz 1994; Ratcliffe et al. 1998). Apart from that, in a fluctuating environment favourable conditions during birth and growth could result in some cohorts to be of better quality than others, which can last for a lifetime (Desrochers & Magrath 1993; Rose, Clutton-Brock & Guinness 1998).

We studied age-related breeding performance of Tengmalm’s owls (Aegolius funereus), a small nocturnal bird of prey that nests in tree-holes and nest-boxes in the northern coniferous forests (Mikkola 1983). Tengmalm’s owls have distinct intersexual duties during the breeding season: while females stay at the nest until the mid-nesting stage, males provide food for their mates and offspring throughout the breeding season (Korpimäki 1981). Most females change breeding site each year (Korpimäki, Lagerström & Saurola 1987; Korpimäki 1993), whereas males stay resident at the site after their first breeding attempt, and their lifetime breeding success can be estimated (Korpimäki 1988c, 1992). An earlier study indicated differences in breeding performance between age classes of Tengmalm’s owls at the population level (Korpimäki 1988b), but the mechanisms leading to age-related differences remained unclear. Here we investigate whether temporally varying levels of natural food abundance determine the occurrence of age-related differences in breeding performance. We use long-term data on laying dates and clutch sizes to investigate age-related changes in breeding performance. We first compare individuals of different ages cross-sectionally at the population level, then examine within-cohort variation between individuals of the same age and finally, investigate consecutive breeding attempts of individuals. Specifically, the following questions were addressed: (1) do the effects of parental age on breeding performance differ at varying levels of natural food? (2) Are age-related differences in performance due to within-cohort changes in the quality of breeding individuals or within-individual changes in competence or reproductive effort? (3) Does the breeding performance of long-lived individuals decline in later years of life?

Methods

The data were collected in the Kauhava region (c. 63°N and 23°E), western Finland, during 1984–99. The study area covers c. 1300 km² and has c. 500 nest boxes and 30 known natural cavities suitable for Tengmalm’s owls. Methods for finding nests and determining laying dates and clutch sizes are given by Korpimäki (1987). Annually 70–90% of parent owls were trapped from their nests in the early nestling period (Hakkarainen et al. 1996) and aged to four age classes: 1-, 2-, 3- and 4+3-year-old individuals (Table 1). Age determination was based on recaptures of ringed individuals or on the moulting pattern of the primary feathers (see details on the method in Glutz von Blotzheim & Bauer 1980; Hörnfeldt, Carlsson & Nordström 1988). The real age
Age-related breeding performance of Tengmalm’s owl

The breeding density and breeding success of Tengmalm’s owls are strongly dependent on the population fluctuations of their main prey (Table 1, see also Korpimäki 1988a; Korpimäki & Hakkarainen 1991), which is common also for other birds of prey (e.g. Korpimäki & Norrdahl 1991; Taylor 1994; Rohner 1996; Petty & Fawkes 1997; Brommer, Pietiäinen & Kolunen 1998).

The main prey of Tengmalm’s owls are voles of the genera Microtus and Clethrionomys, whose populations have fluctuated in a cyclic manner in periods of 3–4 years in the study area (Fig. 1; see also Korpimäki & Norrdahl 1989), although the amplitude of the cycle has been low in 1994–99 (Fig. 1, see also Korpimäki & Wiehn 1998). Based on biannual vole-trappings the years from 1984 to 1993 can be classified as years of low, increasing and decreasing vole abundance (Fig. 1, Table 1). In the low years, vole densities were low during the whole breeding season of owls (March–June), but began to increase in the late summer. In the increase years, vole densities were at intermediate level in the early breeding season of owls, but increased during the summer. Vole densities peaked in the following autumn or winter and began to decline, being still high to intermediate in the beginning of the next breeding season (the decrease years), but reaching low levels in the following autumn. (Hakkarainen & Korpimäki 1993; Hakkarainen, Koivunen & Korpimäki 1997; Korpimäki & Wiehn 1998).

Territory quality for most nest sites was graded from 1 to 5 based on the number of breeding attempts at the site during a 10-year period (1977–86 for 133 territories and 1980–89 for 28 territories) (Korpimäki 1992). The proportion of poor habitats is higher and the abundance of main food (voles) and alternative prey (small birds) is lower on low-quality territories than on high-quality territories of Tengmalm’s owls (Korpimäki 1988c; Hakkarainen et al. 1997).

Table 1. The number of Tengmalm’s owl nests from which at least one parent was trapped, and the number of different aged parent owls trapped at these nests during 1984–99. Phases of the 3-year vole cycle are presented during 1984–93, after which they have been less clear and have not been classified (see Material and methods)

<table>
<thead>
<tr>
<th>Year</th>
<th>Nests</th>
<th>Cycle phase</th>
<th>Female age</th>
<th>Male age</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>1984</td>
<td>10</td>
<td>low</td>
<td>1</td>
<td>5</td>
</tr>
<tr>
<td>1985</td>
<td>37</td>
<td>inc</td>
<td>8</td>
<td>10</td>
</tr>
<tr>
<td>1986</td>
<td>82</td>
<td>dec</td>
<td>44</td>
<td>20</td>
</tr>
<tr>
<td>1987</td>
<td>12</td>
<td>low</td>
<td>–</td>
<td>5</td>
</tr>
<tr>
<td>1988</td>
<td>95</td>
<td>inc</td>
<td>23</td>
<td>23</td>
</tr>
<tr>
<td>1989</td>
<td>136</td>
<td>dec</td>
<td>80</td>
<td>23</td>
</tr>
<tr>
<td>1990</td>
<td>16</td>
<td>low</td>
<td>1</td>
<td>9</td>
</tr>
<tr>
<td>1991</td>
<td>99</td>
<td>inc</td>
<td>14</td>
<td>31</td>
</tr>
<tr>
<td>1992</td>
<td>127</td>
<td>dec</td>
<td>71</td>
<td>16</td>
</tr>
<tr>
<td>1993</td>
<td>14</td>
<td>low</td>
<td>3</td>
<td>5</td>
</tr>
<tr>
<td>1994</td>
<td>44</td>
<td></td>
<td>8</td>
<td>9</td>
</tr>
<tr>
<td>1995</td>
<td>28</td>
<td></td>
<td>10</td>
<td>3</td>
</tr>
<tr>
<td>1996</td>
<td>39</td>
<td></td>
<td>21</td>
<td>7</td>
</tr>
<tr>
<td>1997</td>
<td>18</td>
<td></td>
<td>9</td>
<td>4</td>
</tr>
<tr>
<td>1998</td>
<td>3</td>
<td></td>
<td>–</td>
<td>1</td>
</tr>
<tr>
<td>1999</td>
<td>24</td>
<td></td>
<td>5</td>
<td>4</td>
</tr>
<tr>
<td>Σ</td>
<td>784</td>
<td></td>
<td>298</td>
<td>175</td>
</tr>
</tbody>
</table>

Fig. 1. Fluctuations in density indices of voles (yearly mean) and breeding densities of Tengmalm’s owls in the study area during 1977–99. D, Microtus voles; O, bank voles; ●, no. of owl nests.
from the parameter value and dividing this value with the standard deviation. Negative standardized values for laying date mean that laying began before the annual mean and positive values indicate laying after the mean date. For clutch size, negative values indicate lower and positive values higher than the annual mean performance. In low vole years, no yearling males and only few yearling females were nesting, whereas in years of decreasing vole abundance they formed the majority of breeders (Table 1). This means that the standardized values will be calculated with means derived from old birds in low vole years and with means mainly derived from yearling birds in the decrease vole years. Considering the possible existence of age-related differences in performance this could lead to an over- or underestimation in the standardized values of older birds when comparing between years with or without yearling breeders. Furthermore, the reproductive effort of parent owls may differ according to the phase of the vole cycle (Hakkarainen & Korpimäki 1993, 1994). For these reasons, the cross-sectional analyses were done separately for each phase of the vole cycle.

For analyses of senescence in males and within-individual changes in breeding performance of individual females, longitudinal data from all study years was used and standardized values were calculated with means and deviations derived from older than 1-year-old birds. This was performed to minimize the variation caused by varying proportions of yearling breeders (see Table 1). On the other hand, this value is calculated from a smaller number of nests and is more prone to random error.

The data were divided into two parts for a population level analysis: a cyclic period during 1984–93 consisting of four low, three increase and three decrease years according to the direction of change in local vole abundance during the breeding season of owls, and a weakly cyclic period from 1994 to 1999 (Fig. 1 and Table 1). Cross-sectional analyses were performed in the cyclic period separately for different phases of the cycle by combining data from years in the same cycle (version 9·0 SPSS Inc., Chicago, Il, USA) statistical software.

Results

POPULATION-LEVEL DIFFERENCES

Because only few yearling females and no yearling males were capable of breeding in the low phase of the vole cycle (Table 1), most of the population level analyses were performed for the data from the increase and decrease phases of the vole cycle. In the increase and decrease phases of the vole cycle, the partners of yearling males had the latest and the partners of 3-year-old males the earliest laying date when the age of the female was controlled for ($F_{1,195} = 3.90$, $P = 0.01$ (Bonferroni-corrected $6 \times$ contrasts: $P > 0.006$) in the increase phase and $F_{2,326} = 2.64$, $P = 0.05$ in the decrease phase, no
interactions with female age, Fig. 2). Male age was not associated with the laying date of their partners in the low phase of the vole cycle ($F_{1,13} = 0.56$, $P = 0.58$, Fig. 2) or during the weakly cyclic period ($F_{1,19} = 1.19$, $P = 0.32$). Laying date was not related to female age ($F_{1,13} = 1.00$), $P = 0.40$ in the low, $F_{1,13} = 0.39$, $P = 0.76$ in the increase, $F_{2,156} = 0.81$, $P = 0.49$ in the decrease and $F_{1,13} = 0.16$, $P = 0.92$ in the weakly cyclic phase of the vole cycle). Territory quality did not have obvious effect on laying date when it was added into the ANOVA model as a factor (for territory quality, $F_{1,122} = 0.99$, $P = 0.42$ in the increase phase and $F_{3,148} = 1.46$, $P = 0.22$ in the decrease phase, no interaction with male or female age).

Three-year-old females had the largest and 1-year-old females the smallest relative clutch size in the increase phase of the vole cycle ($F_{1,14} = 4.05$, $P = 0.008$ (Bonferroni-corrected d.f for contrasts $P = 0.006$), but not in the low and decrease phases ($F_{1,12} = 0.24$, $P = 0.86$ and $F_{2,136} = 0.79$, $P = 0.50$, respectively, Fig. 3) or during the weakly cyclic period ($F_{1,13} = 0.61$, $P = 0.61$).

In the decrease phase of the vole cycle, laying date predicted survival significantly (logistic regression: $B = -0.84$, Wald statistic $= 10.83$, d.f. = 1, $N = 266$, $P = 0.001$) in all age classes (interaction $P = 0.13$). The partners of surviving males appeared to initiate their egg-laying earlier than partners of dying males, as survival decreased with later laying date (Fig. 4). There was no obvious difference in clutch sizes between these males ($B = 0.18$, Wald statistic $= 0.09$, d.f. = 1, $N = 256$, $P = 0.53$, no interaction with male age). In the increase phase of the vole cycle, none of the entered variables was associated with male survival (logistic regression: total model $\chi^2 = 8.47$, d.f. = 11, $N = 162$, $P = 0.67$, all interactions and single variables in reduced models $P > 0.3$). There were no obvious differences in the performance between males with different breeding experience (Table 2).

**Fig. 2.** Standardized mean (± SE) laying dates of partners of different-aged males in the increase, decrease and low phases of the vole cycle. Negative values indicate earlier and positive values later than yearly average laying date of the population ($N =$ number of clutches).

**Fig. 3.** Standardized mean (± SE) clutch sizes of different-aged females in the increase, decrease and low phases of the vole cycle. Negative values indicate smaller and positive values larger clutch than yearly average of the population ($N =$ number of clutches).

**Fig. 4.** Standardized mean (± SE) laying dates of partners of males known to survive and to die after their breeding in the increase and decrease phases of the vole cycle. Negative values indicate earlier and positive values later than yearly average laying date of the population ($N =$ number of clutches). ●, Dying; ○, surviving.

There were no differences in clutch sizes between the partners of different-aged males ($F_{1,13} = 0.53$, $P = 0.60$ in the low, $F_{1,14} = 0.41$, $P = 0.74$ in the increase, $F_{2,136} = 0.09$, $P = 0.96$ in the decrease and $F_{1,13} = 0.13$, $P = 0.94$ in the weakly cyclic phase of the vole cycle). Territory quality had no obvious effect on the clutch size in the increase phase (for territory quality $F_{1,118} = 1.65$, $P = 0.17$, no interaction with male and female age).

**Between-individual differences**

In the decrease phase of the vole cycle, laying date predicted survival significantly (logistic regression: $B = -0.84$, Wald statistic $= 10.83$, d.f. = 1, $N = 266$, $P = 0.001$) in all age classes (interaction $P = 0.13$). The partners of surviving males appeared to initiate their egg-laying earlier than partners of dying males, as survival decreased with later laying date (Fig. 4). There was no obvious difference in clutch sizes of these males ($B = 0.18$, Wald statistic $= 0.09$, d.f. = 1, $N = 256$, $P = 0.53$, no interaction with male age). In the increase phase of the vole cycle, none of the entered variables was associated with male survival (logistic regression: total model $\chi^2 = 8.47$, d.f. = 11, $N = 162$, $P = 0.67$, all interactions and single variables in reduced models $P > 0.3$). There were no obvious differences in the performance between males with different breeding experience (Table 2).

**Within-individual changes**

The males breeding as yearlings in the increase phase and then as 2-year-olds in the decrease phase appeared to advance their nest initiation (paired t-test, $P = 0.05$, Fig. 5), but in other age classes similar advancement was not detected ($P > 0.5$). Clutch sizes of partners of these males did not change from the increase to the decrease phase in any age class (paired t-tests, all $P > 0.5$). There was a marginally significant trend for
females to increase their clutch size with age (Table 3). Long-lived males had smaller clutches in their old days than at middle age (paired $t$-test, $P < 0.01$, Fig. 6), but no obvious change was found in the laying date of their partners ($P > 0.5$, Fig. 6).

**Discussion**

Age-related differences in the breeding performance of Tengmalm’s owls were found in years of low vole abundance when no yearling males and only few females were capable of breeding, and in years of increasing vole abundance when food supply was intermediate at the early stages of breeding and young birds performed poorly compared to older ones. In accordance, the differences either became less clear or tended to disappear in the decrease years when the vole abundance was high to intermediate at the early stages of the breeding season. The few studies that have examined age-related breeding performance in relation to estimated environmental variation have concluded similarly that differences become more evident in demanding and stressful conditions (Hamer & Furness 1991; Sydeman et al. 1991; Ratcliffe et al. 1998).

**Table 2.** Mean (±SE) laying dates and clutch sizes of partners of experienced and inexperienced breeding males. Differences between males with and without breeding experience were analysed with $t$-test or Wilcoxon rank sum-test if the requirements of $t$-test were not fulfilled.

<table>
<thead>
<tr>
<th>Age of males</th>
<th>Year</th>
<th>Laying date</th>
<th>Clutch size</th>
<th>Experience</th>
<th>N</th>
<th>Inexperience</th>
<th>N</th>
<th>Z</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Three-year-olds in the increase phase</td>
<td></td>
<td>-0.24 ± 0.28</td>
<td>0.19 ± 0.25</td>
<td>Experienced</td>
<td>16</td>
<td>-0.16 ± 0.11</td>
<td>43</td>
<td>-0.97</td>
<td>0.33</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Two-year-olds in the decrease phase</td>
<td></td>
<td>0.16 ± 0.22</td>
<td>-0.16 ± 0.22</td>
<td>Experienced</td>
<td>11</td>
<td>-0.13 ± 0.09</td>
<td>44</td>
<td>-1.44</td>
<td>0.15</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Three-year-olds in the decrease phase</td>
<td></td>
<td>-0.33 ± 0.21</td>
<td>0.10 ± 0.28</td>
<td>Experienced</td>
<td>15</td>
<td>-0.48 ± 0.13</td>
<td>14</td>
<td>0.57</td>
<td>0.58</td>
</tr>
</tbody>
</table>

**Table 3.** Within-individual changes in the standardized mean (±SE) laying dates and clutch sizes of females. Data were pooled so that the first breeding attempt includes 1- and 2-year-old females breeding for the first time in the area and the second breeding attempt includes a later attempt of the same individual at the age of 3–5 years. Paired $t$-tests were performed to determine whether the change between two different breeding attempts was significant.

<table>
<thead>
<tr>
<th></th>
<th>First</th>
<th>Second</th>
<th>T</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lay date</td>
<td>18</td>
<td>-0.20 ± 0.14</td>
<td>-0.38 ± 0.14</td>
<td>0.81</td>
</tr>
<tr>
<td>Clutch size</td>
<td>19</td>
<td>-0.24 ± 0.14</td>
<td>0.40 ± 0.24</td>
<td>-1.87</td>
</tr>
</tbody>
</table>

**Fig. 5.** Within-individual changes in the standardized mean (±SE) laying dates of partners of individual males that first bred as yearlings in the increase year and then in the next decrease year of the vole cycle (on the left). The corresponding values for 2-year-old and 3-year-old males in the same phases of the vole cycle are given in the middle and on the right, respectively. The number of males in each group is on the lines.

**Fig. 6.** Mean (±SE) laying dates and clutch sizes of partners of males that were breeding at middle age (2–4 years) and then again at an older age (6–10 years). Negative standardized laying dates mean that egg-laying began before and positive values in turn mean that laying began after the annual mean laying date of the study population. For clutch size, negative values indicate lower and positive values higher than the annual mean performance ($N =$ number of long-lived males). M, Middle age; O, old age.
THE DIFFERENTIAL MORTALITY HYPOTHESIS

The partners of yearling males began to lay eggs later than the partners of older males in the increase phase of the vole cycle, but our analysis did not indicate within-cohort quality differences between surviving and dying males in this phase. Delayed breeding was not the explanation either, as there were no obvious differences in the laying dates of partners of experienced and inexperienced males. Interestingly, there seemed to be differential mortality of early and late breeding males in the decrease phase of the vole cycle. The relatively good conditions at the early stages of breeding in the decrease years may have given a breeding opportunity to most individuals, whereas in poor or intermediate conditions the lower quality individuals were not able to breed or survive. Thus, in intermediate conditions there may not have been detectable selection effects, but there were no quality differences among breeding individuals of the same age. Instead, since the early breeding 3-year-old males in the increase phase could have been selected during two preceding winters of relatively low food abundance, they may on average have been of better quality than the younger individuals in the increase phase. In the discussion above, we consider survival and timing of breeding to be characters measuring the quality of an individual. On the other hand, decreased survival may reflect a direct cost of late breeding. However, this should only emphasize the importance of early breeding in those years and not change the conclusions above.

Some earlier studies have found support for the differential mortality-hypothesis (Nel & Smith 1987; Gehlbach 1989, Wooletter et al. 1990, Espie et al. 2000). However, none of these studies has considered the possible effect of yearly variation in food abundance on the occurrence of selection. Our results indicate that quality differences between individuals may induce observed age-related differences in only some years and, especially, that differential mortality may occur in a different year when the difference in breeding performance is detectable. Nevertheless, as in the earlier studies, we consider that differential mortality alone is not an adequate explanation for age-related differences in the breeding performance of Tengmalm’s owls in the increase phase of the vole cycle.

HYPOTHESES ON WITHIN-INDIVIDUAL CHANGES

The yearling males beginning late in the increase phase of the vole cycle advanced their clutch initiation to the same level with others in the next breeding season, which shows that they were not late breeders consistently. Female age had a positive association with clutch size in the increase phase of the vole cycle, and there was a within-individual trend for clutch size to increase with female age.

The poor performance of yearling owls of both sexes in the low and increase phases and the within-individual improvements could be explained by constraints in foraging skills. The young males may have had difficulties in providing food for their mates during the courtship period early in the increase years because they were not as efficient in foraging as the older males. The finding that young Tengmalm’s owl males had smaller prey caches in their nests than older males (Korpimäki 1988b) supports this view. In species where males provide food for their mate and brood, male age is expected to be more important than female age in determining breeding success (Newton 1979; Korpimäki & Hakkakainen 1991; Taylor 1994; Korpimäki & Wieln 1998; Ratcliffe et al. 1998). However, clutch size increased with female age independent of male age, indicating that the differences were apparently due to events before the courtship-feeding period. Many studies have shown that maternal condition has an effect on clutch size, and food is probably the restricting factor behind it (e.g. Perrins 1970; Boutin 1990; Korpimäki & Wieln 1998). Tengmalm’s owl females responded to food supplementation by laying larger clutches even when the natural food levels were high during the egg-laying period (Korpimäki 1989a). This lets us suspect that the young females have been in poorer initial body condition because they were less efficient foragers than the old females, and they had not been in plentiful food conditions during their earlier life.

Constraint is hard to discern from restraint, and both could be working simultaneously (Curio 1983; Forslund & Larsson 1992). With the present data we cannot distinguish between constraint- and restraint-hypotheses, as reproductive effort at young age may have costs in terms of future survival and breeding success (e.g. Clinton & Le Boeuf 1993; Lunn et al. 1994). Most of the earlier studies, however, have supported the constraint-hypothesis, and only few have found support for the restraint-hypothesis (reviews in Saether 1990, Forslund & Pärt 1995; Martin 1995). Future work should take an experimental approach to distinguish between restraint- and constraint-hypotheses, possibly by offering food supplements and simultaneously measuring reproductive effort of individuals of different age in years of low or intermediate natural food abundance. Data on age-specific survival is also essential to determine whether restraint-hypothesis could work for Tengmalm’s owls.

SENCENCE

A significant within-individual decline was detected in the clutch size of males from mid-age to older age. This is most probably explained by degenerative senescence (sensu Abrams 1991), which has been demonstrated more often in wild mammals (see Promislow 1991; Millar 1994; Packer et al. 1998) than in wild birds (but see Komdeur 1996; Newton & Rothery 1997; Ratcliffe et al. 1998; Möller & De Lope 1999). The decline in clutch size was not due to later laying date. Possible
conclusions could be that the old males were restricted in their ability to feed the female for egg formation, or that the old males are no longer attractive and can only obtain low-quality females (Møller & De Lope 1999).

acknowledgements

we are grateful to vesa koivunen, petteri ilmonen, mikko hast, timo hyrsky and mikko hänninen for assistance in the collection of these data, and to esa lehikoinen, pia mutikainen, mia rönkä, and two anonymous referees for improving the manuscript with their comments. the academy of finland financially supported this study (grants to e.k. and h.h.).

references


clinton, w.l. & le bœuf, b.j. (1993) sexual selection’s effects on male life history and the pattern of male mortality. ecology, 74, 1884 – 1892.


de forest, l.n. & gaston, a.j. (1996) the effect of age on timing of breeding and reproductive success in the thick-billed murre. ecology, 77, 1501 – 1511.


Derocher, a. (1992) age and foraging success in european blackbirds: variation between and within individuals. animal behaviour, 43, 885 – 894.


Espie, r.h.m., oliphant, l.w., James, p.c., Warkentin, I.G. & liske, D.J. (2000) age-dependent breeding performance in merlins (Falco columbarius). ecology, 81, 3404 – 3415.


