**Ornis Fennica 82:97–106. 2005**

# Breeding of the Tawny Owl *Strix aluco* in Finland: responses of a southern colonist to the highly variable environment of the North

Tapio Solonen

*Solonen, T., Luontotutkimus Solonen Oy, Neitsytsaarentie 7b B 147, FI-00960 Helsinki, Finland. tapio.solonen@pp.inet.fi*

*Received 11 February 2005, accepted 25 April 2005*

Large-scale patterns and variations in the occurrence and breeding of the Tawny Owl *Strix aluco* in Finland was studied in relation to the availability of small voles and wintering birds as well as to general weather conditions of the preceding winter. In 1986–2000, pronounced three-year cycles in the numbers of occupied territories as well as nesting attempts recorded were less regular near the southern coast than elsewhere in Finland. On average, 64.7 ± 6.8 (SD)% of the Tawny Owl territories recorded were annually found to be occupied by breeding birds. The annual mean of the clutch size averaged 3.67 ± 0.46 (SD), and that of the fledglings produced per nesting attempt 2.73 ± 0.37 (SD). The annual mean fledgling production per occupied territory was significantly lower in the southern coastal region than elsewhere in Finland. The average long-term fledgling production of Finnish Tawny Owls was high, but not consistently higher compared to that of more southern populations. The clutch size and fledgling production followed mainly the cyclically fluctuating levels of small voles. High numbers of wintering birds seemed to have favourable effects on breeding, while benign weather conditions of the preceding winter tended to increase the number and proportion of breeding birds.

## 1. Introduction

The distribution and abundance of bird species are largely determined by the availability of essential resources and their tolerance of prevailing climatic conditions (Lack 1954, Newton 1998). The responses of birds to environmental variation emerge in their reproduction and numbers. The growth potential of populations is largely determined by the relationship between fecundity and mortality (Ricklefs 1973). In heterogeneous habitats and peripheral parts of species' range, the most suitable localities are, in general, occupied first (Fretwell & Lucas 1970, Fretwell 1972). When conditions get worse, only they may provide resources enough for breeding. This means that when breeding conditions and the numbers of breeding pairs vary, the average clutch size and fledgling production show relatively minor variations (Solonen *et al*. 1991).

The Tawny Owl *Strix aluco* is a resident generalist predator whose present distribution area covers most of Europe, ranging up to the southern parts of Fennoscandia in the north (Mikkola 1983, Cramp 1985). Large variation in population densities between the central and peripheral northern parts of the range in Europe (40–600 pairs/100 $km^2$; Southern 1970, Wallin 1988, Ranazzi *et al.*

2002, and 5–40 pairs/100 $km^2$; Solonen 1993, 1994, Saurola 1995, respectively) suggest that there are considerable local and regional differences in food supply. Near the northern limit of the species' range, Tawny Owls are confronted with more variable environmental conditions than in the more southern areas (e.g., Linkola & Myllymäki 1969, Francis & Saurola 2004). In the central parts of range, the relatively abundant and stable food availability is from time to time broken by the mass occurrence of small rodents due to the peaks in the mast production (Southern 1970, Jędrzejewska & Jędrzejewski 1998, Lithner & Jönsson 2002). In the north, the food availability of owls is largely governed by the pronounced cyclic fluctuations of their staple prey, small microtine voles (Kalela 1962, Hansson & Henttonen 1985, Hanski *et al.* 1991, Stenseth 1999, Korpimäki *et al*. 2002, Sundell *et al*. 2004).

Consequently, owls are regularly confronted with fluctuating foraging conditions covering large geographical areas and long periods of time. In general, Tawny Owls and other resident generalist predators respond to these kinds of challenges by modifying their food intake and reproduction (Southern 1970, Brommer *et al*. 2002, Solonen & Karhunen 2002). Their numerical response lags behind increases in prey densities (e.g., Korpimäki & Krebs 1996).

Besides fluctuations in the food supply, the life of owls in the north is also influenced by harsh and both seasonally and annually highly variable weather conditions. In spite of the ongoing general long-term warming in climate, extremely cold winters still occur (Watkinson *et al*. 2004). The range expansion of the temperate Tawny Owl to the north has probably been induced by climate warming (cf. Kalela 1949, Crick 2004) in combination with a population increase in more southern areas (Mikkola 1983, Cramp 1985) as well as human-induced habitat changes in northern Europe (Järvinen *et al*. 1977, Väisänen *et al*. 1998, Sunde *et al*. 2001).

In Finland the species has been a resident for only slightly more than a hundred years (von Haartman *et al*. 1963–1972, Mikkola 1983, Saurola 1995, Väisänen *et al*. 1998). It occurs mostly near fields and wetlands in rural and urban habitats of the southernmost parts of the country, where proper nest sites (at present mainly nest boxes, to a lesser extent natural holes) and suitable food is better available than elsewhere.

During the recent decades, the general level of the Finnish Tawny Owl population seems to have remained largely unchanged (Mikkola 1983, Saurola 1995, Väisänen *et al*. 1998, Hannula *et al*. 2002, Francis & Saurola 2004, Saurola & Francis 2004). This stability, the relatively high capacity for reproduction (Linkola & Myllymäki 1969, Mikkola 1983, Solonen & Karhunen 2002), and the behavioural adaptability of the species (Sunde *et al*. 2001) suggest that the Tawny Owl manages rather well near the northern border of its range. However, food shortages, especially in combination with hard winters, seem to have limited the distribution and abundance of the species in Finland (Saurola 1995, Väisänen *et al*. 1998). It could be expected that recent mild winters (Finnish Meteorological Institute 2002) have been favourable to Finnish Tawny Owls. However, also the mildness of winters may deteriorate living conditions of vole-eating birds of prey by affecting negatively their food supply (Solonen & Karhunen 2002, Solonen 2004, 2005). In mild winters frequent alternate wetting and freezing of wintering holes may be disastrous to voles. At present, such circumstances seem to be common, especially in the lowland areas near the southern coast of Finland.

In this paper, long-term data are used to assess how general environmental factors, such as regional food availability and large-scale weather conditions, affect the breeding of Finnish Tawny Owls. Effects of the population density and reproduction of preceding breeding seasons are considered as well. As the southern coastal birds are expected to experience a less favourable environment than the inland ones (Solonen 2004), these two subpopulations (Fig. 1) are compared. Further, the expected higher reproductive potential of birds in the north as compared to that in more southern parts of the species' range (Linkola & Myllymäki 1969, Mikkola 1983, Overskaug & Bolstad 1998) is examined.

## 2. Material and methods

Nationwide data on the abundance and breeding of Finnish birds of prey have been gathered systematically and published annually since the early 1980s

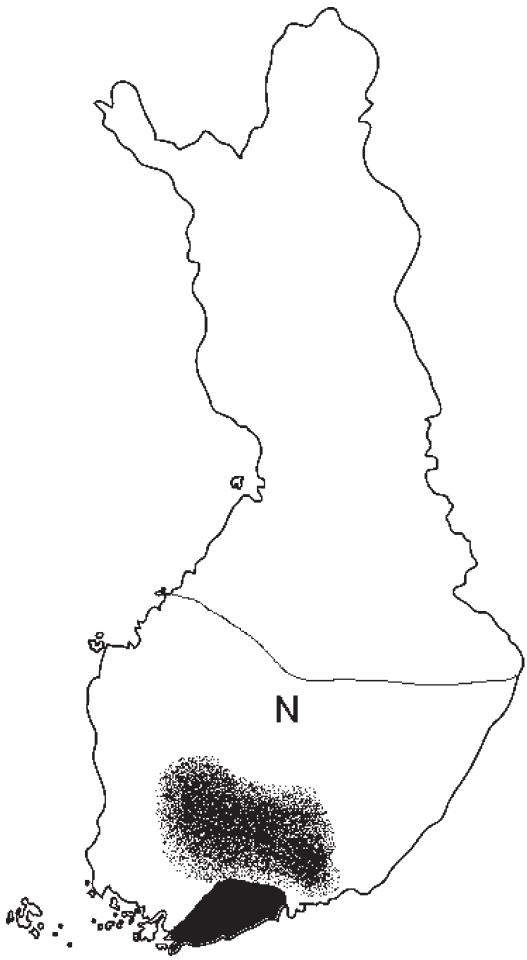


Fig. 1. The division of the Finnish Tawny Owl population used in this study: the southern coastal population is defined as the uniform black-coloured area. The remaining part is the more northern "inland" population, the approximate northern limit of which is denoted by N. Most of the inland data are derived from the black-sprayed area.

(Saurola 1985, Saurola & Francis 2004). The data used in this study were derived from these annual reports (see Solonen 2004, 2005, and references therein), as well as from a regional report (Solonen 2002).

The breeding data were collected annually from hundreds of territories using standard methods (see Saurola & Francis 2004, Solonen 2005). About a third of the total Finnish Tawny Owl population of some 2,000 pairs (Saurola 1985) was included in this study. The number of territories, i.e. locations recorded as occupied by nesting and/or calling individuals was used as a rough estimate of the population size. The breeding activity of the population was characterized by the proportion of nesting attempts to the total number of occupied territories (minimum breeding proportion). The measure of the reproductive output was the mean clutch size, i.e. the number of eggs laid per nesting attempt. The mean fledgling production was measured as the number of nearly fledged (ringed) young per nesting attempt. This is a commonly available measure that is not considerably higher than the actual number of fledglings (Southern 1970, Wallin 1988, own obs.). Breeding success was indicated by the mean fledgling production per mean clutch size. Recent data on fledgling production from other European countries made available to the author were used for comparison.

The general availability of voles was estimated indirectly by the breeding frequency (the recorded number of nests) of Tengmalm's Owl *Aegolius funereus*. This species is intensively monitored over the species' Finnish range (Saurola 1995) and is closely associated with the abundance of small voles (e.g., Korpimäki 1985, Korpimäki & Norrdahl 1989, Hanski *et al.* 1991, Solonen 2005). The well-monitored populations of vole-eaters probably reflect the regional fluctuations in vole abundance more precisely than do the direct vole trapping samples of relatively restricted spatial scale (Solonen 2004, Sundell *et al.* 2004).

The fluctuations in the availability of alternative winter food for Tawny Owls were indicated by the abundance indices of the Fieldfare *Turdus pilaris* from the Finnish late winter bird censuses (individuals/km census route; Väisänen & Solonen 1997, R. A. Väisänen unpubl.). This measure characterizes fluctuations in the numbers of wintering birds in general and those of frugivorous species in particular. It showed pronounced three-year cycles largely opposite to those of small voles and the breeding frequency of owls (Solonen 2005). Thrush-sized birds are important alternative prey for Finnish Tawny Owls during the breeding season (Solonen & Karhunen 2002).

The general weather conditions of winters were characterized by the winter NAO index (Hurrell 1995, Hurrell *et al.* 2001). This index is defined as the difference between the normalized sea-level pressures at the Azores and Iceland averaged over the period December–March, describing the meteorological situation in winter and early spring. Positive NAO indices correspond to stronger winds from the west, which bring higher temperatures and higher levels of precipitation from the Atlantic Ocean to northwest Europe. In contrast, negative values, with weaker west winds, indicate a stronger influence of the continental winter high.

Spearman correlation, linear regression and t-test (Sokal & Rohlf 1981, Fowler & Cohen 1986) were used in general statistical analyses (SigmaStat 3.1 software). Cyclicity in the parameters was determined using autocorrelation analysis (Wessa 2005). To analyse how food availability, weather conditions, and some demographic factors affect the breeding of owls, backward stepwise multiple regression analyses (Sokal & Rohlf 1981) were performed (SigmaStat 3.1 software). Coefficients of determination were adjusted ($R^2_{adj}$), taking into account the number of independent variables, which reflects the degrees of freedom.

## 3. Results

### 3.1. Patterns and variations in breeding parameters

Breeding parameters of Finnish Tawny Owls showed considerable variations (Table 1). Fluctuations in the numbers of occupied territories and nesting attempts recorded were similar both within and between regional populations ($0.59 < r^S < 0.97$, $P \leq 0.02$). Pronounced three-year cycles (Fig. 2) were less regular near the southern coast (autocorrelation function ACF = 0.27–0.49, t = 1.0–1.8, P > 0.05) than elsewhere in Finland (ACF = 0.56–0.72, t = 2.0–2.6, P < 0.01). On average, 64.7 ± 6.8 (SD)% of the Tawny Owl territories recorded were annually found to be occupied by breeding birds.

The annual mean of the clutch size averaged 3.67 ± 0.46 (SD), and that of the fledglings produced per nesting attempt 2.73 ± 0.37 (SD). Clutch size and fledgling production per nesting attempt did not differ between the populations ($t_{28} = 0.18$ and $t_{28} = -0.65$, respectively) (Table 1). Fluctuations in the clutch size and fledgling production were correlated, both within populations and between regions ($0.65 < r^S < 0.87$, $P \leq 0.008$) (Fig. 3). In the total Finnish population, the annual mean fledgling production per occupied territory averaged 1.78 ± 0.36 (SD). This value was significantly lower in the southern coastal region (1.42 ± 0.34 SD) than elsewhere in Finland (1.94 ± 0.39 SD) ($t_{28} = -3.87$, $P < 0.001$). The average long-term fledgling production of Finnish Tawny Owls was comparatively high, but no consistent latitudinal gradient was found in the European Tawny Owl populations studied (linear regression, $F_{1,6} = 0.46$, $P > 0.05$) (Table 2).

Table 1. Means (± SD), coefficients of variation (CV), and ranges in the number of occupied territories and nesting attempts, as well as in the annual means of the clutch size and fledgling production per nesting attempt in the Tawny Owl *Strix aluco* recorded near the southernmost coast (upper figures) and elsewhere (lower figures) in Finland in 1986–2000 (n = 15).

| | Mean | SD | CV% | Range |
|---|---|---|---|---|
| Territories | 186.1 | 46.7 | 25.1 | 102–262 |
| | 404.1 | 95.7 | 23.7 | 179–535 |
| Nesting attempts | 100.5 | 30.7 | 30.5 | 37–152 |
| | 285.5 | 83.0 | 29.1 | 104–396 |
| Clutch size | 3.7 | 0.5 | 14.8 | 3.0–4.8 |
| | 3.6 | 0.4 | 11.8 | 2.9–4.4 |
| Fledgling production | 2.7 | 0.5 | 17.9 | 2.1–3.5 |
| | 2.8 | 0.4 | 13.6 | 2.1–3.3 |


Fig. 2. Fluctuations in the numbers of occupied territories (Ter) and nesting attempts (Nes) of Tawny Owls recorded near the southernmost coast (S) and elsewhere (N) in Finland as well as in the whole country (F) in 1986–2000.

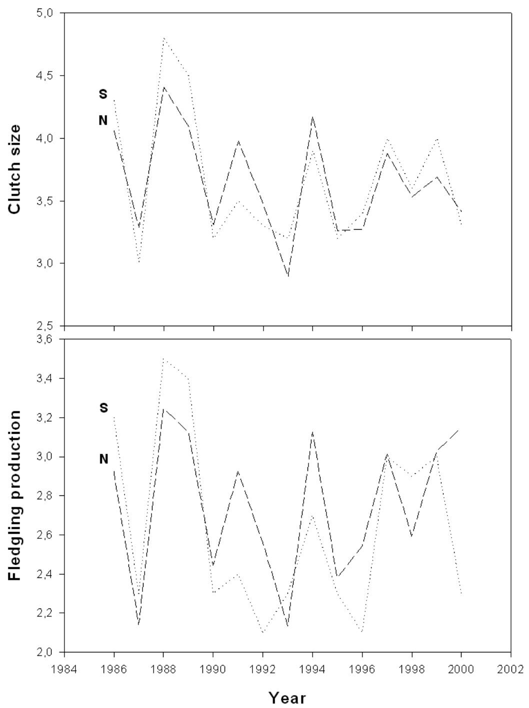


Fig. 3. Fluctuations in the mean clutch size and fledgling production of the Tawny Owl near the southernmost coast (S) and elsewhere (N) in Finland in 1986–2000.

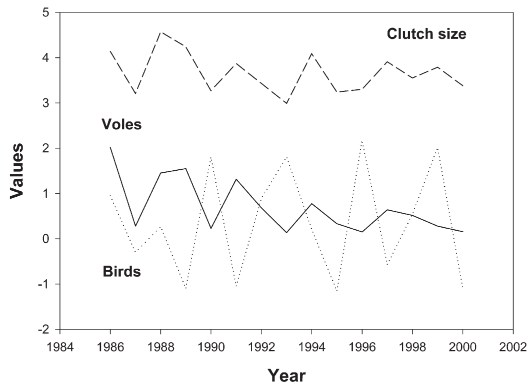


Fig. 4. Fluctuations in the annual mean clutch size of the Tawny Owl as well as in the abundance indices of voles and wintering birds (logarithmic scale) in Finland in 1986–2000.

### 3.2. Effects of food supply, weather and demographic factors

The major variations in the breeding of Tawny Owls were explained by vole abundance (Tables 3 and 4, Fig. 4). Near the southern coast, the number of wintering birds offered an additional contribution to the reproductive output (Table 3). Mild winters indicated by the NAO index tended to increase the number and proportion of breeding birds.

The fledgling production of the three preceding breeding seasons, corresponding to the length of the vole cycles, reflected positively in the population size (Table 4). The contribution of the fledgling production three years earlier was positive but that of the preceding year negative to the breeding proportion of owls. Breeding success was negatively affected by the vole abundance and the population size of the preceding year.

## 4. Discussion

Finnish Tawny Owls seem to in general produce more eggs and fledglings per nesting attempt than

Table 2. Mean fledgling production per nesting attempt in the Tawny Owl in various parts of the species' European range.

| Locality | Latitude | Period | Mean | n | Data source |
|---|---|---|---|---|---|
| Finland | 61 | 1986–2000 | 2.76 | 5159 | Present study |
| Estonia | 58 | 1994–2003 | 1.99 | 154 | Lõhmus (1999, 2004) |
| Holland | 52 | 1986–2000 | 1.12 | 199 | F. Koning (pers. comm.) |
| Germany | 50 | 1976–2000 | 2.30 | 1752 | Mammen (2002) |
| Hungary | 47 | 1992–2000 | 2.32 | 117 | Sasvári & Hegyi (2002) |
| Switzerland | 46 | 1987–2000 | 2.73 | 544 | Roulin *et al*. (2003) |
| Spain | 43 | 1993–1998 | 1.63 | 89 | Zuberogoitia (2002) |
| Italy | 41 | 1986–1999 | 1.78 | 311 | Ranazzi *et al*. (2000) |

Table 3. Effects of food supply and winter weather on the Finnish Tawny Owls in the two regional populations in 1986–2000: a summary of the results of the backward stepwise multiple regression analyses conducted.

| | Coastal population | | | | Inland population | | | |
|---|---|---|---|---|---|---|---|---|
| Dependent variable | Vars | $R^2_{adj}$ | F | P | Vars | $R^2_{adj}$ | F | P |
| Population size | Vole | 19.6 | 4.4 | 0.056 | None | | | |
| Breeding proportion | NAO | 42.1 | 11.2 | 0.005 | Vole | | | 0.008 |
| | | | | | NAO | | | 0.020 |
| | | | | | Total | 54.0 | 9.2 | 0.004 |
| Reproductive output | Vole | 71.0 | 35.3 | <0.001 | Vole | 68.4 | 31.4 | <0.001 |
| | Bird | | | 0.017 | | | | |
| | Total | 80.7 | 30.4 | <0.001 | | | | |
| Breeding success | None | | | | None | | | |

The independent variables included were 1) the spring vole abundance index (Vole), 2) the abundance index of wintering birds (Bird), and 3) the index of weather conditions of the preceding winter (NAO). Explaining variables included in the models (Vars), adjusted $R^2$ (%) as well as F and P of the variance analyses are given. "None" means that all variables were eliminated from the model.

Table 4. Effects of food supply, winter weather and some demographic factors on the Finnish Tawny Owl population in 1989–2000: a summary of the results of the backward stepwise multiple regression analyses conducted.

| Dependent variable | Independent variables | $R^2_{adj}$ | F | P |
|---|---|---|---|---|
| Population size | Production 3 yrs earlier | | | 0.009 |
| | Production 2 yrs earlier | | | 0.022 |
| | Vole abundance | | | 0.024 |
| | Preceding yr production | | | 0.025 |
| | Winter NAO index | | | 0.029 |
| | Total | 64.3 | 5.0 | 0.038 |
| Breeding proportion | Winter NAO index | | | 0.002 |
| | Production 3 yrs earlier | | | 0.060 |
| | Preceding yr production – | | | 0.038 |
| | Total | 77.1 | 13.4 | 0.002 |
| Reproductive output | Vole abundance | | | 0.013 |
| | Preceding yr production – | | | 0.054 |
| | Total | 72.5 | 15.5 | 0.001 |
| Breeding success | Vole abundance – | | | 0.021 |
| | Preceding yr population – | | | 0.023 |
| | Total | 40.1 | 4.7 | 0.040 |

The independent variables included in relevant combinations in the analyses were 1) the fledgling production of the population three years earlier , 2) the fledgling production of the population two years earlier, 3) the fledgling production of the preceding breeding season, 4) the population size of the preceding breeding season, 5) the population size of the current breeding season, 6) the spring vole abundance, 7) the winter bird abundance, and 8) the weather conditions of the preceding winter (NAO index). Explaining variables included in the models, adjusted $R^2$ (%) as well as F and P of the variance analyses are given. Negative effects are denoted by minus (–).

do birds in the more southern parts of the species' range. The breeding of Tawny Owls in Finland is largely governed by the fluctuating availability of small voles. The southern coastal population seems to be more sensitive to both the alternative food supply and the fluctuations in the winter weather compared to inland birds.

### 4.1. Trends in the clutch size and fledgling production

The mean clutch size and fledgling production over the period 1986–2000 of this study (3.67 and 2.73, respectively) were similar to those presented earlier for the years 1952–1966 (3.68 and 2.77;

Linkola & Myllymäki 1969). The annual fledgling production fluctuates but its general level has remained stable over years (Saurola & Francis 2004).

The Finnish Tawny Owl population seems to fit well the general large-scale pattern of significantly increasing trend in the mean clutch size from south to north and from west to east documented in birds in Europe (Lack 1947, Linkola & Myllymäki 1969, Mikkola 1983, Overskaug & Bolstad 1998). It is suggested that a periodically high abundance of prey and less inter- and intra-specific competition in the Nordic environments may explain the higher mean clutch size in the Tawny Owl towards the northernmost part of its range (Overskaug & Bolstad 1998). Cycles in the numbers of small voles are, in general, most marked in the north, and become progressively less pronounced southwards, ranging from high-amplitude cycles of five years to low non-cyclic annual variations (Kalela 1962, Erlinge *et al.* 1984, Hansson & Henttonen 1985, Hanski *et al.* 1991, Norrdahl 1995, Sundell *et al.* 2004). These cycles are most probably due to the combined effect of primary productivity (the availability of winter food for voles) and predation (e.g., Hansson 2002, Korpimäki *et al.* 2002, Huitu *et al.* 2003).

During a concurrent period, the long-term average of fledgling production of Tawny Owls in Europe showed no increase from south to north, differing from the pattern reported earlier for the clutch size and brood size of the species (Mikkola 1983). The recent data show large and irregular regional variations, suggesting that a larger sample of populations is needed for a more rigorous comparison.

### 4.2. Responses to the environmental factors

The major variations in the breeding of Tawny Owls were explained by the direct effects of the vole abundance. When the demographic factors reflecting the vole abundance of preceding years were included, the explanatory power of the models considerably increased. The significant negative effects of the vole abundance and the population size of the preceding year suggest the influence of the vole crash during breeding, and that breeding attempts affect the capacity of birds to reproduce in the next year (cf. Brommer *et al.* 2002).

This study showed no signs of declining trends to correspond to the suggested decline in the Finnish vole populations (cf. Solonen & Karhunen 2002, Solonen 2004, Sundell *et al.* 2004). However, the more exact population monitoring of the Finnish raptor grid study plots (Saurola 1986) revealed a recent levelling off in fluctuations in the numbers of Tawny Owl territories and nests (Hannula *et al.* 2002).

The difference in the fledgling production between the regional Tawny Owl populations suggests that the breeding conditions were less favourable near the southern coast than elsewhere in Finland. The regional differences revealed may be at least partly due to differences in the homogeneity of the data. The southern coastal area is small and relatively uniform compared to the large and heterogeneous more peripheral part of the Finnish range. On the other hand, the densities of wintering birds are higher in the south than elsewhere in Finland (Väisänen 2003), possibly explaining the regional differences in the effect of this alternative food resource. Correspondingly, the effects of mild winters can be expected to be more pronounced in coastal areas than in more continental ones (Hörnfeldt 2004, Solonen 2004). The present results suggest these effects to be positive. The negative effects of mild winters on owls, via decreasing the abundance of voles by the “frost seesaw effect” (Solonen 2001), frequently wetting and freezing their wintering holes, are probably mainly seen in secondary habitats and in years of good vole supply (Solonen & Karhunen 2002, Solonen 2004). In the light of the present study, the negative effects of mild winters may be compensated by the availability of prey alternatives to voles.

The availability of voles as well as other prey may also have improved due to benign wintering conditions. The mildness of winters may therefore have opposite effects that somewhat offset each other (cf. Solonen 2004, 2005). For example, in contrast to the probable negative effects of mild winters on voles, the opportunities of resident owls to prey upon microtines may have increased with decreasing snow cover (cf. Sonerud 1986, Jędrzejewski *et al.* 1994, Solonen & Karhunen 2002), increasing the winter survival of owls

(Francis & Saurola 2004). When plenty of food is available, mild winters allow early breeding, which is, in general, considered a favourable trait (e.g., Southern 1970).

Low densities and breeding activity as well as high reproductive output in the north suggest that only relatively good (locally best) habitats were occupied and only the most capable individuals of the population, at least in terms of territory occupancy, were engaged in breeding (cf. Fretwell & Lucas 1970, Pietiäinen 1989, Solonen *et al*. 1991). Low densities due to limited resources also explain the large home ranges in northern populations (Sunde *et al*. 2001). In the south, the higher population densities increase possibilities of active encounters and potential competition. Increasing fragmentation of suitable foraging habitats correlate with an increase in territory size and a decrease in territorial conflicts (Redpath 1995).

In Central Europe, feeding conditions seem to be reflected heavily both in the number of breeding pairs of Tawny Owls as well as in their average fledgling production (Southern 1970, Wendland 1984, Roulin *et al*. 2003). In the Finnish populations this relationship is not so clear, suggesting that in poor vole years owls are able to breed only in those locations where territories can provide alternative prey. This seems to be the case regularly only in the relatively few superior habitats near human settlements (pers. obs.). So, Tawny Owls seem to respond to the highly variable environment of the North opportunistically by using such prey that is at any given time best available, and by attempting to breed only when the food supply is sufficient.

*Acknowledgements.* I thank Risto A. Väisänen for providing the winter bird census results for the Fieldfare. Thanks are also due to Fred Koning, Asko Lõhmus, Jose A. Martinez and Lajos Sasvári for data on Tawny Owls. Useful comments came from Mårten Hjernquist, Juha Meriläinen and Hannu Pietiäinen. Marcus Walsh kindly checked the English.

### Lehtopöllön pesintä Suomessa

Lehtopöllön esiintymistä ja pesintää suhteessa myyrien ja talvilintujen saatavuuden sekä talven sääolojen vaihteluihin tutkittiin Suomessa vuosina 1986–2000 kerätyn valtakunnallisen aineiston valossa. Mittava aineisto kattoi noin kolmanneksen koko maan lehtopöllökannasta. Pesyekoon vuosittainen keskiarvo oli keskimäärin 3.67 (± 0.46 SD) ja poikastuotto pesintäyritystä kohti vastaavasti 2.73 (± 0.37 SD) poikasta. Keskimääräinen poikastuotto oli Suomessa korkea, mutta ei johdonmukaisesti suurempi kuin levinneisyysalueen eteläisemmissä osissa. Poikastuotto aloitettua pesintää kohti ei myöskään eronnut eteläisimmän Suomen ja muun maan välillä. Poikastuotto asuttua reviiriä kohti oli kuitenkin etelärannikon tuntumassa pienempi kuin muualla.

Pesyekoko ja pesintätulos vaihtelivat jaksoittain vaihtelevien myyräkantojen mukaan. Talvehtivien marjalintujen suurella määrällä näytti olevan myönteinen vaikutus pöllöjen pesintään. Edellisen talven suotuisat sääolot heijastuivat pesivien lintujen suurempana määränä ja osuutena kannasta. Pohjolan voimakkaasti vaihtelevissa ympäristöoloissa eteläinen lehtopöllö näyttää selviytyvän käyttämällä joustavasti kulloinkin parhaiten saatavilla olevia ravintokohteita ja pesimällä vain silloin, kun ravintoa on riittävästi. Koska sen luontaista pesäpaikkapulaa on meillä paljolti lievitetty pesäpöntöillä, talviravinnon riittävyys on jäänyt pesintää ensisijaisesti määrääväksi tekijäksi.

## References

Brommer, J. E., Pietiäinen, H. & Kolunen, H. 2002: Reproduction and survival in a variable environment: Ural owls and the three-year vole cycle. — Auk 119: 544–550.

Cramp, S. 1985: Handbook of the Birds of Europe, the Middle East and North Africa. The Birds of the Western Palearctic. Vol. IV. — Oxford University Press.

Crick, H. Q. P. 2004: The impact of climate change on birds. — Ibis 146, Suppl. 1: 48–56.

Erlinge, S., Göransson, G., Högstedt, G., Jansson, G., Liberg, O., Loman, J., Nilsson, I., von Schantz, T. & Sylvén, M. 1984: Can vertebrate predators regulate their prey? — American Naturalist 123: 125–133.

Finnish Meteorological Institute 2002: Climatological Statistics of Finland 1971–2000. — Finnish Meteorological Institute, Helsinki.

Fowler, J. & Cohen, L. 1986: Statistics for ornithologists. — BTO Guide 22.

Francis, C. M. & Saurola, P. 2004: Estimating components of variance in demographic parameters of Tawny

Owls, Strix aluco. — Animal Biodiversity and Conservation 27: 489–502.
Fretwell S. D. 1972: Populations in a seasonal environment. — Princeton University Press.
Fretwell, S. D. & Lucas, H. L. 1970: On territorial behaviour and other factors influencing habitat distribution in birds. I. Theoretical development. — Acta Biotheoretica 19: 16–36.
von Haartman, L., Hildén, O., Linkola, P., Suomalainen, P. & Tenovuo, R. 1963–1972: Pohjolan linnut värikuvin. — Otava, Helsinki.
Hannula, H., Haapala, J. & Saurola, P. 2002: Breeding and population trends of common raptors and owls in Finland in 2001 – a year with rodents almost absent. — Linnut-vuosikirja 2001: 15–25. (In Finnish with English summary)
Hanski, I., Hansson, L. & Henttonen, H. 1991: Specialist predators, generalist predators, and the microtine rodent cycle. — Journal of Animal Ecology 60: 353–367.
Hansson, L. 2002: Dynamics and trophic interactions of small rodents: landscape and regional effects on spatial variation? — Oecologia 130: 259–266.
Hansson, L. & Henttonen, H. 1985: Gradients in density variations of small rodents: the importance of latitude and snow cover. — Oecologia 67: 394–402.
Huitu, O., Koivula, M., Korpimäki, E., Klemola, T. & Norrdahl, K. 2003: Winter food supply limits growth of northern vole populations in the absence of predation. — Ecology 84: 2108–2118.
Hurrell, J. W. 1995: Decadal trends in the North Atlantic Oscillation: regional temperatures and precipitation. — Science 269: 676–679.
Hurrell, J. W., Kushnir, Y. & Visbeck, M. 2001: The North Atlantic Oscillation. — Science 291: 603–605.
Hörnfeldt, B. 2004: Long-term decline in numbers of cyclic voles in boreal Sweden: analysis and presentation of hypotheses. — Oikos 107: 376–392.
Jędrzejewska, B. & Jędrzejewski, W. 1998: Predation in vertebrate communities. The Białowieża Primeval Forest as a case study. — Springer Verlag, Berlin.
Jędrzejewski, W., Jędrzejewska, B., Zub, K., Ruprecht, A. L. & Bystrowski, C. 1994: Resource use by Tawny Owls Strix aluco in relation to rodent fluctuations in Białowieża National Park, Poland. — Journal of Avian Biology 25: 308–318.
Järvinen, O., Kuusela, K. & Väisänen, R. A. 1977: Effects of modern forestry on the numbers of breeding birds in Finland in 1945–1975. — Silva Fennica 11: 284–294. (In Finnish with English summary)
Kalela, O. 1949: Changes in geographic ranges in the avifauna of Northern and Central Europe in relation to recent changes in climate. — Bird Banding 20: 77–103.
Kalela, O. 1962: On the fluctuations in the numbers of arctic and boreal small rodents as a problem of production biology. — Ann. Acad. Sci. Fenn. Ser. A IV Biol. 66: 1–38.
Korpimäki, E. 1985: Rapid tracking of microtine populations by their avian predators: possible evidence for stabilizing predation. — Oikos 45: 281–284.
Korpimäki, E. & Krebs, C. J. 1996: Predation and population cycles of small mammals. — Bioscience 46: 754–764.
Korpimäki, E. & Norrdahl, K. 1989: Predation of Tengmalm's owls: numerical responses, functional responses and dampening impact on population fluctuations of microtines. — Oikos 54: 154–164.
Korpimäki, E., Norrdahl, K., Klemola, T., Pettersen, T. & Stenseth, N. C. 2002: Dynamic effects of predators on cyclic voles: field experimentation and model extrapolation. — Proceedings of the Royal Society (London) B 269: 991–997.
Lack, D. 1947: The significance of clutch size. — Ibis 89: 302–352.
Lack, D. 1954: The natural regulation of animal numbers. — Oxford University Press.
Linkola, P. & Myllymäki, A. 1969: Der Einfluss der Kleinsäugerfluktuationen auf das Brüten einiger kleinsäugerfressender Vögel im südlichen Häme, Mittelfinnland 1952–1966. — Ornis Fennica 46: 45–78.
Lithner, S. & Jönsson, I. 2002: Abundance of owls and Bramblings Fringilla montifringilla in relation to mast seeding in south-eastern Sweden. — Ornis Svecica 12: 35–45.
Lõhmus, A. 1999: Monitoring of raptors and owls in Estonia, 1994–1998. — Hirundo 12: 19–35. (In Estonian with English summary)
Lõhmus, A. 2004: Monitoring of raptors and owls in Estonia, 1999–2003: decline of the Goshawk and the clockwork of vole-cycles. — Hirundo 17: 3–18.
Mannen, U. 2002: Monitoring Greifvögeln und Eulen. — http://www.biologie.uni-halle.de/zool/vert_ecol/monitoring/salu.html.
Mikkola, H. 1983: Owls of Europe. — Poyser, Calton.
Newton, I. 1998: Population limitation in birds. — Academic Press, San Diego.
Norrdahl, K. 1995: Population cycles in northern small mammals. — Biological Reviews 70: 621–637.
Overskaug, K. & Bolstad, J. P. 1998: Geographical variation in female mass and reproductive effort in the Tawny Owl Strix aluco in Europe. — Fauna Norw. Ser. C 21: 1–6.
Pietiäinen, H. 1989: Seasonal and individual variation in the production of offspring in the Ural Owl Strix uralensis. — Journal of Animal Ecology 58: 905–920.
Ranazzi, L., Manganaro, A. & Salvati, L. 2000: The breeding success of the Tawny Owls (Strix aluco) in a Mediterranean area: a long-term study in urban Rome. — Journal of Raptor Research 34: 322–326.
Ranazzi, L., Manganaro, A. & Salvati, L. 2002: Density fluctuations in an urban population of Tawny Owl Strix aluco: a long-term study in Rome, Italy. — Ornis Svecica 12: 63–67.
Redpath, S. M. 1995: Habitat fragmentation and the individual: Tawny Owls Strix aluco in woodland patches.

— Journal of Animal Ecology 64: 652–661.
Ricklefs, R. E. 1973: Fecundity, mortality, and avian demography. — In Breeding biology of birds (ed. Farner, D. S.): 366–435. National Academy of Sciences, Washington, D. C.
Roulin, A., Ducret, B., Ravussin, P.-A. & Altwegg, R. 2003: Female colour polymorphism covaries with reproductive strategies in the Tawny Owl Strix aluco. — Journal of Avian Biology 34: 393–401.
Sasvári, L. & Hegyi, Z. 2002: Effects of age composition of pairs and weather condition on the breeding performance of Tawny Owls, Strix aluco. — Folia Zoologica 51: 113–120.
Saurola, P. 1985: Finnish birds of prey: status and population changes. — Ornis Fennica 62: 64–72.
Saurola, P. 1986: The raptor grid: an attempt to monitor Finnish raptors and owls. — Vår Fågelvärld, Suppl. 11: 187–190.
Saurola, P. (ed.) 1995: Owls of Finland. — Kirjayhtymä, Helsinki. (In Finnish with English summary)
Saurola, P. & Francis, C. M. 2004: Estimating population dynamics and dispersal distances of owls from nationally coordinated ringing data in Finland. — Animal Biodiversity and Conservation 27: 403–415.
Sokal, R. R. & Rohlf, F. J. 1981: Biometry. — Freeman, New York.
Solonen, T. 1993: Spacing of birds of prey in southern Finland. — Ornis Fennica 70: 129–143.
Solonen, T. 1994: Factors affecting the structure of Finnish birds of prey communities. — Ornis Fennica 71: 156–169.
Solonen, T. 2001: Has owl prey availability deteriorated due to mild winters in southern Finland? — Linnut 36: 6–9. (In Finnish with English summary)
Solonen, T. 2002: Monitoring of breeding owls in western Uusimaa, southern Finland, until 2000. — Tringa 29: 34–41. (In Finnish with English summary)
Solonen, T. 2004: Are vole-eating owls affected by mild winters in southern Finland? — Ornis Fennica 81: 65–74.
Solonen, T. 2005: Breeding of Finnish birds of prey in relation to variable winter food and weather conditions. — Memoranda Societas Fauna Flora Fennica 81: 19–31.
Solonen, T. & Karhunen, J. 2002: Effects of variable food conditions on the Tawny Owl Strix aluco near the northern limit of its range. — Ornis Fennica 79: 121–131.
Solonen, T., Tiainen, J., Korpimäki, E. & Saurola, P. 1991: Dynamics of Finnish Starling Sturnus vulgaris populations in recent decades. — Ornis Fennica 68: 158–169.
Sonerud, G. A. 1986: Effect of snow cover on seasonal changes in diet, habitat, and regional distribution of raptors that prey on small mammals in boreal zones of Fennoscandia. — Holarctic Ecology 9: 33–47.
Southern, H. N. 1970: The natural control of a population of Tawny Owls (Strix aluco). — Journal of Zoology (London) 126: 197–285.
Stenseth, N. C. 1999: Population cycles in voles and lemmings: density dependence and phase dependence in a stochastic world. — Oikos 87: 427–461.
Sunde, P., Overskaug, K., Bolstad, J. P. & Øien, I. J. 2001: Living at the limit: ecology and behaviour of Tawny Owls Strix aluco in a northern edge population in Central Norway. — Ardea 89: 495–508.
Sundell, J., Huitu, O., Henttonen, H., Kaikusalo, A., Korpimäki, E., Pietiäinen, H., Saurola, P. & Hanski, I. 2004: Large-scale spatial dynamics of vole populations in Finland revealed by the breeding success of vole-eating avian predators. — Journal of Animal Ecology 73: 167–178.
Wallin, K. 1988: Life history evolution and ecology in the Tawny Owl (Strix aluco). — Ph. D. thesis, Department of Zoology, University of Göteborg, Sweden.
Watkinson, A. R., Gill, J. A. & Hulme, M. 2004: Flying in the face of climate change: a review of climate change, past, present and future. — Ibis 146, Suppl. 1: 4–10.
Wendland, V. 1984: The influence of prey fluctuations on the breeding success of the Tawny Owl Strix aluco. — Ibis 126: 284–295.
Wessa, P. 2005: Free statistics and forecasting software. — http://www.wessa.net/wessa.wasp
Väisänen, R. A. 2003: Regional population trends of 33 common bird species in Finland during 27 winters. — Linnut-vuosikirja 2002: 41–62. (In Finnish with English summary)
Väisänen, R. A., Lammi, E. & Koskimies, P. 1998: Distribution, numbers and population changes of Finnish breeding birds. — Otava, Helsinki. (In Finnish with English summary)
Väisänen, R. A. & Solonen, T. 1997: Population trends of 100 winter bird species in Finland in 1957–1996. — Linnut-vuosikirja 1996: 70–97. (In Finnish with English summary)
Zuberogoitia, I. 2002: Eco-etología de la comunidad de rapaces nocturas de Bizkaia. — Ph.D. thesis, Bask Country University, Leioa.