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Reproduction and Survival in a Variable Environment: Ural Owls (*Strix uralensis*) and the Three-Year Vole Cycle

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ABSTRACT.—We analyzed data on 535 Ural Owl (*Strix uralensis*) breeding attempts and consecutive survival of both adults and offspring from 1987–1998 in relation to the regional abundance of the Ural Owl's main prey, voles, which show a cycle of low, increase, and peak phases in their population numbers. Vole abundance varied up to 49×, crashing during spring–summer every three years. The breeding population tracked abundance of voles in the previous autumn with respect to percentage of pairs breeding and their reproductive output (laying date, clutch size), largely irrespective of phase. Survival depended on vole density in the preceding autumn, but was generally highest in the increase phase. There was thus a paradoxical situation in the peak phases, when vole populations crashed; the owls produced large clutches, but those survived poorly. Some adaptive and nonadaptive scenarios of the Ural Owl's life history are discussed.

RESUMEN.—Analizamos datos sobre 535 intentos reproductivos de lechuzas *Strix uralensis* y la supervivencia consiguiente de adultos y crías entre 1987 y 1998 con relación a la abundancia regional de roedores microtinos (i.e., "voles"), que son sus presas principales. Los tamaños poblacionales de los microtinos varían cíclicamente, con fases de baja abundancia, de incremento y de abundancia pico. La abundancia de microtinos varió hasta 49× y la población colapsó cada tres años entre primavera y verano. La población reproductiva de lechuzas siguió la abundancia de los microtinos en el otoño anterior con respecto al porcentaje de parejas que se reprodujeron y su rendimiento reproductivo (fecha de postura, tamaño de la nidada), en gran medida independientemente de la fase. La supervivencia dependió de la densidad de microtinos en el otoño anterior, pero en general fue máxima durante la fase de incremento. Se presentó una situación paradójica en las fases pico, cuando las poblaciones de microtinos colapsaron: las lechuzas produjeron nidadas grandes, pero éstas tuvieron una baja supervivencia. Se discuten algunos escenarios adaptativos y no adaptativos sobre la historia de vida de *S. uralensis*.

Life history is commonly viewed as the "reproductive schedule" of a species (Lessels 1991, Roff 1992, Stearns 1992, Charlesworth 1994). From an evolutionary point of view, life histories can be viewed as being shaped by various kinds of constraints. The amount of energy available to an organism is one obvious ecological constraint (Cody 1966). Food supply can be viewed as the primary factor in limiting amount of energy available to organisms and is, for example, an important determinant of breeding success in birds. Vole-eating raptors (Cavé 1968) and owls (Southern 1970) are classical cases where variations in food supply between years are reflected in numbers of pairs breeding and their reproductive success.

We studied relationships between food supply, reproduction, and survival in the Ural Owl (*Strix uralensis*). At the time of laying, Ural Owls mainly feed on field voles (*Microtus agrestis*) and bank voles (*Clethrionomys glareolus*) (Lundberg 1981, H. Pietiäinen unpubl. data). In Fennoscandia, voles have shown a cyclic pattern in their population numbers for several decades (Hansson and Henttonen 1985, Hanski et al. 1991, Norrdahl 1995), although recently the cyclic periodicity has begun to disappear (Hansson 1999, Henttonen 2000). The variation in vole density is extreme with over 100× increase in density between extreme low and peak densities (Hanski et al. 1991). Although the length of the cycle varies from three years in southern Finland to five years in northern Lapland, it is regionally fixed (Hansson and Henttonen 1985, Hanski et al. 1991).

Cyclic fluctuations in the population numbers are most commonly found in more northern latitudes. In Fennoscandia, several species of voles show synchronous dynamics (Hansson and Henttonen 1985), but vole cycles are also found in central Europe, for example, Scotland (Taylor 1994) and Germany (Schönfeldt and Girbig 1975; for reviews see Norrdahl 1995, Lindström et al. 2001). In Alaska, the snowshoe hare follows a 10 year cycle, closely tracked by several predators (Rohner 1996, O'Donoghue et al. 1997). Such cycles are, most probably, an outcome of predator–prey interactions, although a single predator is not necessarily solely responsible (Korpimäki and Norrdahl 1998), nor can other aspects—such as the prey's food supply—be ignored (e.g. Krebs et al.

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1995). Among the community of predators, the least weasel (*Mustela nivalis*) is thought to drive the Fennoscandian vole cycle (Hanski and Korpimäki 1995). The bird-of-prey community lacks sufficient predation pressure (Hanski et al. 1991). The Ural Owl, a highly site-tenacious bird (Lundberg 1979, Saurola 1987), therefore has to cope with externally induced fluctuations in its main prey.

In our study area, vole abundance fluctuates in a three-year cycle with low, increase, and peak phases (*sensu* Norrdahl 1995). We have previously shown that Ural Owl reproductive success differs between phases (Pietiäinen 1989) and that those phases form an important determinant for life-history aspects like lifetime reproductive success, age at first breeding, and recruitment of offspring (Brommer et al. 1998). The grouping of life-history data into discrete phase-categories is commonly used (e.g. Korpimäki 1988, 1992), although "phase" is just a name given to a certain vole density. In this article, we extend previous work and consider the Ural Owl's life history in relation to the actual vole abundance, exploring both pattern and variability of this predator-prey system.

Materials and Methods.—Ural Owls were studied in an area of 1,500 km² in Päijät-Häme, southern Finland. Data were gathered from 1977 onwards, but the emphasis for this study is on the years 1987–1998 for reasons explained below. All pairs bred in nest boxes ($n = 170$), which were 3–4 km apart. For further details of the study area, see Pietiäinen (1989).

Regional food supply was estimated from the autumn of 1986 onwards by snap-trappings in late September to early October (henceforth "autumn trappings"), and early June (henceforth "summer trappings"). We used the small-quadrate method (Myllymäki et al. 1971, Hanski et al. 1994), where traps baited with rye bread ($n = 300$) were set in 25 quadrates (15 × 15 m) for two consecutive nights. Each quadrate had three traps in each corner, which were set 1–2 m apart. The quadrates were in three separate areas (8 + 9 + 8 quadrates in each area), which were ~5 km apart in the center of the study area. Trappings were made in habitats, which represented the major vole habitats in the study area (spruce dominated forest, field, clearcut). The results of these index-trappings were consistent with trappings made in later years over a larger part of the study area (J. E. Brommer unpubl. data). Trapping times coincided with the first week(s) of the juvenile owls' life outside the nest box (early June) or the first weeks of independent life in the autumn (juvenile Ural Owls depend on their parents for 3–3.5 months after leaving the nest box). After the peak phase, vole populations may crash any time between late winter and early summer, but due to logistic constraints (mainly because of snow cover), we could not trap voles at the peak of the laying period, which would have been an ideal time for estimating spring food

supply. The estimate for vole abundance is expressed as the number of voles per 100 trap nights and combines field and bank vole numbers. Shrew catches were so low that they were not included.

The number of pairs present in the study population was determined by the scrapings which the owls made in the sawdust layer in the nest boxes. The sawdust layer is scraped two to three weeks before laying to promote drying and to form a hollow in which eggs are laid. We visited the nest boxes from late February to early March onwards, and each time the scrapings were leveled. Nonbreeding pairs had fresh scrapings in their boxes even in late April, indicating that the territory was occupied. Unfortunately, we cannot exclude some error in those data, due to the possibility that sometimes pairs chose natural nest sites, mainly unused nests of large raptors, instead of our boxes.

The laying of at least one egg was classified as a breeding attempt. Laying date was determined either by a visit to a nest with an incomplete clutch or by backdating from nestling wing lengths (see Pietiäinen 1989 for more details). Breeding success was based on the number of young fledged. Females were trapped during laying or incubation. Age of a female was determined on the basis of plumage characteristics (Pietiäinen and Kolunen 1986) or when trapped as a bird ringed as a nestling. During the study, most first-breeders were females replacing previous females (see also Pietiäinen 1988).

Survival was estimated using mark-release-recapture software (program MARK; White 2001, Cooch and White 2001), where both recaptures and recoveries were combined to provide an estimate of first-winter survival and of adult survival (Burnham 1993). In this analysis, "recoveries" are birds found dead and reported by the Finnish public and "recaptures" were birds trapped within the study area. Data from 1981 to 2000 was entered in order to minimize bias, which would occur because of truncation to the focal period 1986–1998. We employed a two age-class (yearlings and adults) version, which allows time-dependent estimation of first-winter survival and adult survival (Cooch and White 2001). We considered Burnham's (1993) fidelity and reporting parameters as time-invariant, but allowed for a difference between the age-classes and between birds banded as offspring and adults. The association between juvenile and adult survival and vole density was explored with correlation, where data points were weighted by the number of pairs laying.

Results.—Estimated spring food supply varied dramatically (Fig. 1A). During low vole years, estimates for early summer vole density varied from one to two voles per 100 trap nights. During summer, voles may increase in numbers and, depending on the winter conditions, voles may even be able to reproduce during the winter (Hansson 1984, Hanski and Korpimäki 1995). Consequently, in increase

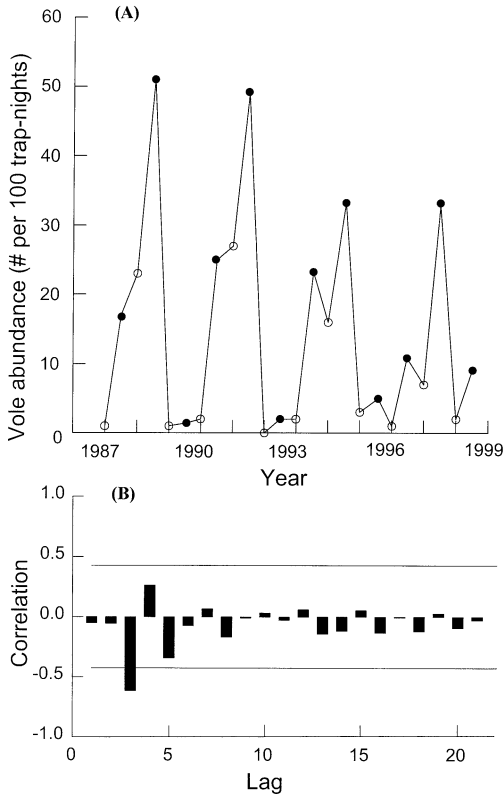


FIG. 1. (A) Vole abundance estimated by biannual snap-trapping for two consecutive nights from 1987 to 1998. Vole abundance in spring is denoted by open circles and vole abundance in autumn by filled circles. Low phases are indicated by "L", increase phases by "I" and peak phases by "P". (B) Partial autocorrelation diagram from the $\ln(x + 1)$ transformed data of panel (A). The horizontal lines indicate the 95% confidence limits. There is a significant negative autocorrelation with a lag of 3.

years the range of early summer vole density estimates was larger, 7 to 27 voles per 100 trap nights. It should be noted, however, that in the last two cycles plotted vole numbers decreased in the transitions from autumnal low to summer increase. Peaks in vole density (both cyclic and seasonal maximums) occurred in the autumn of the increase phase breeding period and were up to 49 \times the lowest density recorded. Nevertheless, also those maximums were substantially lower in the last two cycles as compared to the first two. After the maximum, vole numbers declined over the winter and during the following spring–summer, which is termed here the "peak phase" (see also Norrdahl 1995). Estimates for vole density in the early summer of the peak years indicate that the crash always occurred before June, as

those estimates varied from zero to three voles per 100 trap nights.

Vole abundance in the study area showed a significant negative partial auto-correlation at a lag of three (Fig. 1B). Because we trapped biannually, a lag of three corresponds to ~ 1.5 years, for example the abundance of voles in the summer of a low year is negatively correlated with the abundance in the autumn of the following increase year. There is, however, no positive correlation at lag six, which would be expected. That emphasizes that there is substantial variation between cycles in our study area and that the predictability of the vole cycle may be limited.

The average age of breeding females varied from 4.3 to 10.7 years. Breeding females were younger in years of good food supply than in low vole years (Fig. 1; Table 1; $r_p = -0.70$, $P = 0.012$), when older and presumably more experienced females were breeding. That may also be due to large numbers of first-breeders in the increase and peak phases (76.2% of female Ural Owls started to breed by their third year; Brommer et al. 1998). Thus, the more first-breeders there are in the population, the younger is the mean age of breeding females (Table 1; $r_p = -0.75$, $P = 0.005$).

Variation in food supply led to a pronounced variation in the proportion of pairs breeding (Table 1, Fig. 2). The percentage of breeding pairs was positively related to abundance of voles in the preceding autumn (Fig. 2; $r_s = 0.88$, $P < 0.001$). The proportion of pairs breeding grew with increasing vole abundance, but leveled off rapidly at $\sim 80\%$ of pairs breeding. After peak breeding season, mortality of females was higher than in other years (Brommer et al. 1998), leading to temporal decreases in breeding population size. When vole numbers increased, more pairs also were able to establish themselves, which led to the growth of the breeding population. In other words, Ural Owls had a clear numerical response to food supply.

Median laying dates varied from 19 March to 19 April with annual mean clutch size from 2.1 to 4.1 eggs (Table 1). Average yearly brood sizes varied from 1.8 to 3.5 young with large clutches producing large broods (Table 1; $r_p = 0.96$, $P < 0.001$). Ural Owls laid earlier when voles were more abundant the previous autumn (Fig. 3). Although the phases clearly group in Figure 3, there was substantial variation in vole density of the preceding autumn within each phase. Differences in preceding autumn vole density explained more variation in laying date than phase (phase, $SS = 38.6$, $df = 2$, $F = 0.85$, $P = 0.47$; vole density in preceding autumn, $SS = 167.1$, $df = 1$, $F = 7.4$, $P = 0.04$; interaction [phase \times vole density], $SS = 278.3$, $df = 2$, $F = 6.1$, $P = 0.05$; error, $SS = 136.2$, $df = 6$; $R^2 = 0.82$).

A higher abundance of voles facilitated the survival of breeding females (Fig. 4A; $r_p = 0.61$, $P = 0.03$).

TABLE 1. Summary data on the reproductive output of the population studied from 1987 to 1998. Note some new nest boxes were added in the initial years 1987–1990 such that the data on the number of pairs is not strictly comparable. Sample sizes over which averages could be calculated are given between parentheses.

| Year | Phase of the vole cycle | Total number of pairs | Laying pairs | Percentage first-breeders | Mean age (<i>n</i>) | Median laying date (<i>n</i>) | Mean clutch size (<i>n</i>) | Mean brood size (<i>n</i>) |
|------|-------------------------|-----------------------|--------------|---------------------------|-----------------------|---------------------------------|-------------------------------|------------------------------|
| 1987 | Low | 62 | 10 | 0 | 10.7 (3) | 17 April (9) | 2.1 (10) | 1.8 (10) |
| 1988 | Increase | 72 | 52 | 37 | 5.1 (24) | 5 April (48) | 3.5 (51) | 2.8 (51) |
| 1989 | Peak | 96 | 83 | 31 | 4.3 (39) | 19 March (66) | 4.1 (79) | 2.6 (79) |
| 1990 | Low | 79 | 37 | 3 | 6.8 (17) | 1 April (26) | 2.4 (36) | 1.4 (36) |
| 1991 | Increase | 102 | 81 | 30 | 5.5 (39) | 31 March (73) | 3.4 (80) | 2.6 (81) |
| 1992 | Peak | 106 | 74 | 18 | 5.2 (31) | 29 March (62) | 2.7 (71) | 2.0 (74) |
| 1993 | Low | 78 | 10 | 33 | 6.4 (5) | 3 April (5) | 2.5 (10) | 1.4 (10) |
| 1994 | Increase | 111 | 85 | 44 | 5.1 (45) | 1 April (76) | 3.6 (83) | 2.7 (83) |
| 1995 | Peak | 106 | 63 | 12 | 6.3 (24) | 31 March (48) | 2.8 (55) | 1.3 (57) |
| 1996 | Low | 83 | 7 | 0 | 8.3 (3) | 19 April (6) | 2.0 (6) | 1.7 (6) |
| 1997 | Increase | 93 | 66 | 43 | 5.1 (34) | 25 March (64) | 4.0 (64) | 3.0 (64) |
| 1998 | Peak | 90 | 65 | 18 | 5.9 (35) | 30 March (59) | 3.2 (64) | 2.4 (65) |

Peak phases with low autumnal vole abundance were characterized by low adult survival. Relationship between first-winter survival and the abundance of voles was less clear (Fig. 4B; $r_p = 0.47$, $P = 0.11$). Variation in first-winter survival was substantial, with estimates varying from 0 to 79%. The two lowest estimates, however, stem from the low phases in 1990 and 1996 with only a limited number of breeding pairs (Table 1). In addition, survival of breeding females and their offspring was not correlated ($r_s = 0.32$, $P = 0.3$).

Discussion.—We have provided a description of the reproductive performance and survival of the Ural Owl in relation to variations in its main prey. Ural Owls start to lay in late March to early April when voles are practically the only accessible source of food and climatic conditions unfavorable (average snow depth in March is 40 cm, average temperature in March is -5°C ; Alalammi 1987). Thus, hunting may be difficult and energy demands may be high. It is only later in the season that migrant birds arrive in Finland and water voles (*Arvicola terrestris*) become available as alternative prey (H. Pietiäinen unpubl. data). In general, birds are thought to time their

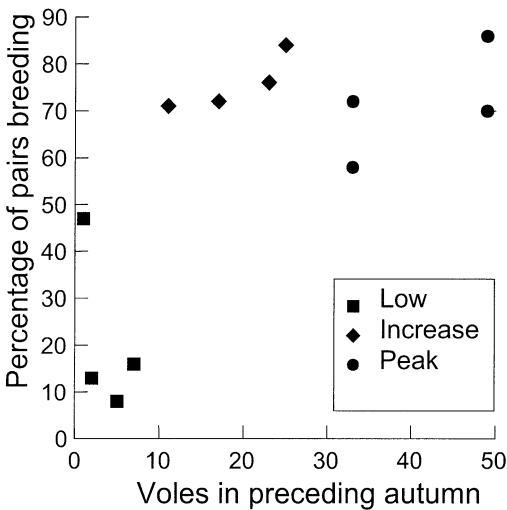


FIG. 2. Percentage of pairs breeding, as calculated from Table 1, plotted against vole abundance in the preceding autumn. Peak vole years are denoted by a filled circle, increase vole years by a diamond, and low vole years by a square. A higher percentage of Ural Owls bred when voles were more abundant ($r_s = 0.88$, $P < 0.001$).

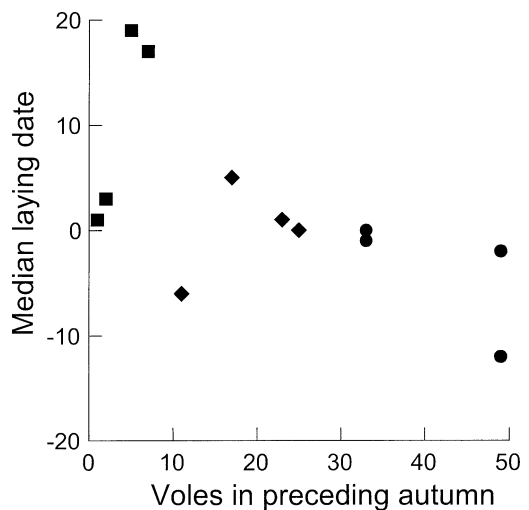


FIG. 3. The median laying dates for 1987–1998 in relation to regional vole abundance in the preceding autumn. Ural Owls reproduced earlier when there were more voles ($r_s = -0.70$; $P = 0.01$). Symbols as in Figure 2.

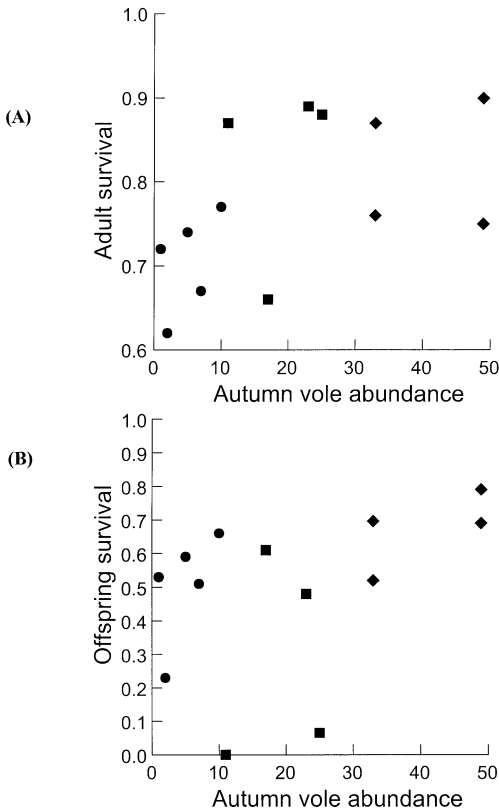


FIG. 4. Survival of breeding females (A) and offspring (B) for 1986 to 1998 plotted against vole density in autumn. Survival estimates are derived from a mark–release–recapture model. Symbols are as in Figure 2. Adult survival was clearly facilitated by a higher vole abundance ($r_p = 0.61$, $P = 0.03$), but first-winter survival was not ($r_p = 0.47$, $P = 0.11$).

breeding such that peak demand for food during the nestling period coincides with high food availability (Perrins 1991, van Noordwijk et al. 1995). Nevertheless, breeding earlier in the season than the time of maximum food abundance may be advantageous if early hatched offspring are of higher fitness value (Daan and Tinbergen 1997). Furthermore, Ural Owls face an extensive period of parental care, because young disperse from their natal territories five to six months after laying started and that places a clear upper limit on time of breeding.

A large predatory bird as the Ural Owl is a typical “capital breeder” (Drent and Daan 1980, Jönsson 1997), which gathers energy resources prior to laying. Indeed, higher density of voles in the preceding autumn, presumably closely related to winter abundance of voles, correlates well with earlier laying dates. Thus, breeding seems to be a direct response to vole abundance, where phase is largely ignored.

Such direct reproductive and numerical responses to rodent abundance are commonly found in birds of prey (e.g. Newton and Marquiss 1986, Korpimäki and Norrdahl 1991, Taylor 1994, Jedrzejewski et al. 1996, Rohner 1996).

In the Ural Owl, possibilities for breeding are few during the low phase of the vole cycle. However, due to increasing vole numbers in autumn, survival prospects for the young and adults are may be good. In the increase phase, resources allow most pairs to breed, and both young and adult birds survive well, because vole populations reach their cyclic (and annual) peak in autumn, at the time when the offspring disperse, and vole abundance remains high over the winter. In the peak phase, the variance in clutch size is highest, where both the largest and the smallest clutch sizes can be found (see also Pietiäinen 1989) and a high proportion of birds breed. However, a regular feature of the vole cycle is the crash every third year. The crash occurs during the spring in the so-called peak phase breeding season (*sensu* Norrdahl 1995) and, consequently, young and adult birds have severe difficulties surviving over the following winter. Survival of adults clearly is facilitated by higher vole abundance, and the winter from peak to low phase forms a returning bottle-neck (on average 30% mortality, this article) for the breeding population. Because the Ural Owl is highly site-tenacious (Saurola 1987), mortality is the most common way that territories become vacant. The crash in vole numbers thus creates recruitment possibilities after the peak phase and the breeding population experiences an influx of first breeders.

We have shown that there is substantial variation in abundance of voles within each phase. Nevertheless, there appears to be relatively little overlap between the phases in terms of abundance of voles in the preceding autumn. Offspring survival was generally lower than adult survival and more variable in relation to abundance of voles in autumn. First-winter survival of offspring hatched in the increase phase was higher than survival of offspring hatched in peak phases. Offspring survival probably forms the main factor in determining the vole cycle’s long-term effect on performance of offspring. Both in Tengmalm’s (*Strix tengmalmi*) and in Ural owls peak-hatched offspring have a 2 to 3× lower recruitment probability than those hatched in an increase year (Korpimäki 1992, Brommer et al. 1998). Such differences between the offspring’s survival probabilities may have evolutionary consequences as parents are expected to raise their reproductive effort in years of predictably higher offspring survival (Hirschfield and Tinkle 1975, Carlisle 1982, Lindström 1988, Hakkarainen and Korpimäki 1994).

In the Ural Owl’s life history, the peak breeding season apparently forms a paradoxical situation, where parents respond to the good initial food conditions by producing large clutches, which survive

poorly. It is possible that Ural owl parents respond directly to food availability alone, without consideration of the long-term consequences. In fact, the rigor of a causal chain, where food supply determines laying date, which, in turn, determines clutch size was underlined by experimental work in the Eurasian Kestrel (*Falco tinnunculus*) in The Netherlands (Meijer et al. 1990, but see Aparicio 1994, Korpimäki and Wiehn 1998). On the other hand, our results also underline that the predictability of the vole cycle may be poor. In fact, in certain regions in central Finland, the crash in vole abundance may happen a year later, in which case one distinguishes an additional (decrease) phase (Norrdahl 1995). Parents may therefore face a situation in which bet-hedging their reproduction in peak phases could pay off. Furthermore, fitness costs for the parents, which underlie this reproductive behavior are unknown. Certainly the costs of reproduction may be relatively small in peak phases while food levels are still high. Brommer et al. (2000) considered whether a higher reproductive effort in the increase phase could be adaptive in the Ural Owl system, by modeling a variety of possible costs. They concluded that the observed Ural Owl life history was likely to be in line with a scenario where parents worked proportionally harder in the increase phase when the costs of reproduction were paid in the autumn.

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