

# Effects of vole fluctuations on the population dynamics of the barn owl *Tyto alba*

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**Abstract** Many predator species feed on prey that fluctuates in abundance from year to year. Birds of prey can face large fluctuations in food abundance i.e. small mammals, especially voles. These annual changes in prey abundance strongly affect the reproductive success and mortality of the individual predators and thus can be expected to influence their population dynamics and persistence. The barn owl, for example, shows large fluctuations in breeding success that correlate with the dynamics in voles, their main prey species. Analysis of the impact of fluctuations in vole abundance (their amplitude, peaks and lows, cycle length and regularity) with a simple predator prey model parameterized with literature data indicates population persistence is especially affected by years with low vole abundance. In these years the population can decline to low owl numbers such that the ensuing peak vole years cannot be exploited. This result is independent of the length and regularity of vole fluctuations. The relevance of this result for conservation of the barn owl and other birds of prey that show a numerical response to fluctuating prey species is discussed.

**Keywords** Predator–prey model · CONTENT · Habitat quality · Conservation · Birds of prey

## 1 Introduction

The current rate of species extinction by far exceeds historical rates (Pimm et al. 1995), and suggests that we are at the brink of a major biodiversity crisis (Thomas

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et al. 2004). Conservation actions to abate this decline should be guided by insight in which factors have the largest impact on improving population performance (Caswell 2001). Apart from overkill, impact of introduced species and chains of extinction, reductions in habitat quality and size are the main factors that endanger populations (Diamond 1989). These reductions are most apparent in small populations due to demographic stochasticity (Shaffer 1981; Lande 1993). Model studies have revealed that the impact of demographic stochasticity on the likelihood of extinction is countered more effectively by improvement of habitat quality than by that of habitat size (Klok and De Roos 1998). Also Hanski (2005) argues that time to extinction is increased more by increases in habitat quality than size; however, in practice it may be more feasible to increase habitat size. Improvement of habitat quality is not easy to realize since it depends on the specific requirements of the species under consideration and thus needs thorough ecological knowledge (e.g. conservation of the spotted owl; Carey et al. 1990; Solis and Gutierrez 1990; Miller et al. 1997). Food abundance is an important habitat quality factor which has a strong influence on the population dynamics of species. Food abundance may also modify the impact of other habitat quality factors such as effects of xenobiotics which become more apparent under low food abundance (Kooijman 2000).

Loss of suitable hunting habitat and consequently a reduction in food availability is suggested as an important cause of the population decline in the barn owl *Tyto alba* in Western Europe in the last century (De Bruijn 1994; Toms 1994). Western Europe is inhabited by the subspecies *Tyto alba alba*, and *Tyto alba guttata* (*alba* in Great Britain and southern Europe, *guttata* in central Europe). The species prefers open habitat with hedgerows and woodland edges (Glutz von Blotzheim and Bauer 1980; Cramp 1985; De Bruijn 1994; Del Hoyo et al. 1999). In the 1960s the Barn owl showed a rapid decline in range and numbers in Western Europe (Glutz von Blotzheim and Bauer 1980; Cramp 1985; Del Hoyo et al. 1999). This decline was attributed to intensification of agriculture and urbanization leading to loss of habitat, nesting facilities, and food supply. In addition, severe winters, pesticide use, hunting, and road traffic kills reduced barn owl populations (Sharrock and Sharrock 1976; Cramp 1985; Cayford 1990; De Bruijn 1994; Snow and Perrins 1998). To abate the decline conservation actions were directed at an increase in the number of nesting sites by protection of existing sites and placement of nest-boxes, and habitat protection and re-establishment (Taylor et al. 1992; De Bruijn 1994; Taylor 1994; Del Hoyo et al. 1999). These actions halted the population decline (Toms et al. 2001). Nowadays road traffic kills seem the most important cause of death detected in barn owls, road traffic kills increased from 6% in the period 1910–1954 to 50% in the period 1991–1996 in Britain (Newton et al. 1997).

Barn owl populations show distinct fluctuations in the number of breeding pairs which are correlated with changes in the density of voles, its major prey species (Altwegg et al. 2003; Schönfeld and Girbig 1975; Kaus 1977; De Bruijn 1994; Taylor 1994). Also the demographic processes annual adult and juvenile mortality and fecundity are strongly correlated with vole abundance (Taylor 1994), which obviously influence the long term population growth rate as illustrated by (Hone and Sibly 2002) who showed that this rate was significantly positively related to vole abundance. However, since voles can show large fluctuations in abundance over the

years the fluctuations (e.g. their amplitude) may also influence the population viability.

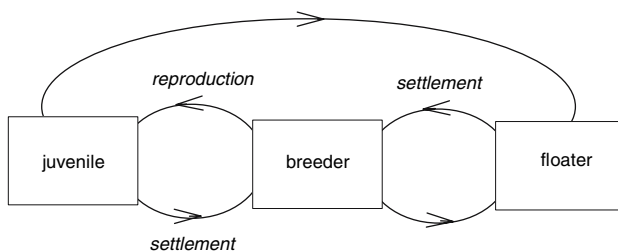
In this paper the impact of fluctuations in vole abundance (their amplitude, peaks and lows, cycle length and regularity) on the population persistence of the barn owl was analyzed with a simple predator prey model parameterized with literature data. Starting with the mathematically simplest case of regular cycles, the influence of the amplitude, peaks and lows and length of the cycle was studied. Since in the range of the barn owl irregularly fluctuating vole populations seem more prevalent than cyclic the influence of randomly fluctuations in vole abundance has been analyzed.

## 2 Methods

### 2.1 Life History of The Barn Owl

The life history of the barn owl was divided into three distinct stages: juvenile, breeder and floater. Juveniles are fledged young and breeders are adult birds that occupy a breeding site which they defend. Although barn owls are not considered territorial since home-ranges of individuals may overlap, breeding barn owls do defend the direct surroundings of their nest sites (Taylor 1994). For simplicity the defended breeding site is described as a breeding territory in this study. Floaters are non-breeding adults that do not occupy a breeding territory. Figure 1 shows a flow diagram of the barn owl life cycle in which survival is implicit. Individuals in the juvenile stage, that survive their first winter, can become breeders if they succeed in occupying a breeding territory. If they fail, they become floaters. Breeders that survived the winter and retain their breeding territories, stay in the breeder stage. If they lose their breeding territory they become floaters. Individuals in the floater stage can remain in that stage the subsequent year, or move to the breeder stage when they succeed in occupying a breeding territory.

Survival and reproduction in barn owls is strongly linked to vole abundance (Taylor 1994). Survival is depressed in winter resulting from low densities of voles; in case of snow cover also availability of voles may decrease (De Bruijn 1994). In Western Europe the breeding season starts around April, May (Snow and Perrins 1998; Del Hoyo et al. 1999). Depending on vole abundance one to two broods are raised each year (Snow and Perrins 1998). Two broods are very uncommon in the



**Fig. 1** The life cycle graph of the barn owl

UK (Taylor 1994) but prevalent in the rest of Europe. In central Europe up to 64% of the pairs raise a second brood in years of high vole abundance (Schönfeld and Girbig 1975). Also the number of barn owls that start to breed and occupy and defend a nest-site varies with vole abundance (Schönfeld and Girbig 1975; Kaus 1977; De Bruijn 1994; Taylor 1994), therefore we assumed that the number of available breeding territories also depends on vole abundance.

## 2.2 Food Relations

Barn owls mainly prey on small mammals, their most important prey species are voles, shrews, and mice. Birds, amphibians, fish, and insects have a minor share in the diet (Schönfeld and Girbig 1975; De Bruijn 1994; Taylor 1994; Del Hoyo et al. 1999). Pellet analyses have indicated that vole species, *Microtus agrestis* in Great Britain, *Microtus arvalis* in continental Europe, make up large quantities of the diet (De Bruijn 1994; Taylor 1994). Vole densities can show strong changes in abundance over the years. Within the range of the barn owl in Europe most irregular vole fluctuations have a mean periodicity of 3–4 years (Krebs and Myers 1974; Hansson and Henttonen 1988; Mackin-Rogalska and Nabagło 1990; Jędrzejewski and Jędrzejewska 1996).

## 2.3 Model Formulation

### 2.3.1 Predator–Prey Relation

The numerical effect of barn owl predation on voles seems negligible. In Great Britain, predation by barn owls is only 1% of the total predation on the field vole, *Microtus agrestis* (Dyczkowski and Yalden 1998). Because of this small effect the vole dynamics is described by an autonomous function, independent of owl density.

Figure 2 displays three empirical vole time series from Western Europe, based on spring density estimates reported in literature. The general pattern emerging from these data is a peak year followed by a sequence of years with low vole abundance. This pattern can be summarized by the mean and amplitude of the vole abundance:

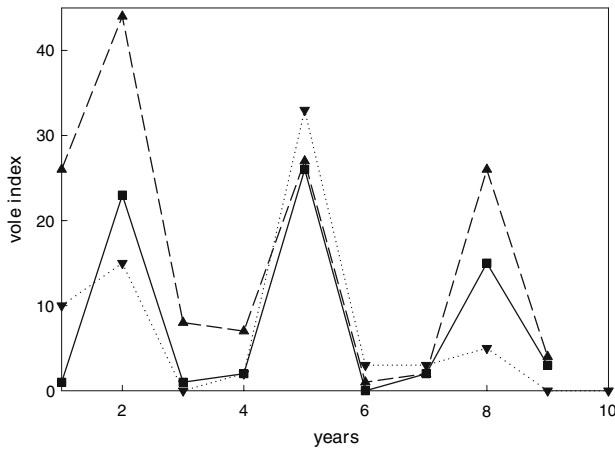
$$\text{mean}(\text{peak}, \text{low}, n) = \frac{\text{peak}}{n} + \frac{(n-1) \cdot \text{low}}{n} \quad (1a)$$

$$\text{amplitude}(\text{peak}, \text{low}, n) = \text{peak} - \text{low} \quad (1b)$$

where  $\frac{1}{n}$  equals the frequency of peak years.

### 2.3.2 The Barn Owl Population Model

A discrete time model with a time step of one year is used to analyze the barn owl population dynamics. The model calculates the number of barn owls each year in spring, just before the onset of breeding. At this time of the year the owl population consists of breeders and floaters only, since juveniles born the preceding year have already matured. Only female barn owls are modeled, assuming a 1:1 sex ratio and



**Fig. 2** Fluctuating vole abundance (index) in Western Europe based on spring census. *Solid line*: vole index in southern Finland (61° NL) over period 1977–1995 (Brommer et al. 1998), *dashed line*: vole index in Scotland (54° NL) over period 1979–1988 (Taylor 1994) and *dotted line*: vole index in Sweden (52° NL) over period 1973–1983 (Lindström 1994)

mortality independent of sex. The population model is based on Fig. 1. Survival, reproduction and the number of available breeding sites are modeled as functions of the vole density. The model assumptions are (1) all vacant breeding territories will become occupied if there are sufficient adult birds, (2) the number of breeding territories is only limited by vole abundance, implying that the number of nest sites is not limiting, and (3) the barn owl population is closed (immigration and emigration do not play a role). The year-to-year dynamics of the total number of adult female birds ( $U_t$ ) is given by Eq. (2).

$$U_{t+1} = S(v_t)\{B(v_t) + z \cdot [U_t - B(v_t) + F(v_t) \cdot B(v_t)]\} \quad \text{if } U_t \geq B(v_t) \quad (2a)$$

$$U_{t+1} = S(v_t) \cdot U_t\{1 + z \cdot F(v_t)\} \quad \text{otherwise} \quad (2b)$$

where  $v_t$  equals the vole abundance in year  $t$ ,  $B(v_t)$  the number of available breeding territories,  $F(v_t)$  the number of female fledglings produced per breeding female and  $S(v_t)$  the survival of breeders. The factor  $z$  symbolizes an amplified mortality risk for juveniles and floaters compared to breeders.

#### 2.4 Parameterization and Model Analysis

Although the population dynamics of the barn owl are closely related to those of the voles (Schönfeld and Girbig 1975; Kaus 1977; De Bruijn 1994; Taylor 1994; Snow and Perrins 1998; Altwegg et al. 2003), quantitative data relating survival and reproduction in the barn owl to vole density are scarce in literature. An exception is a study on an isolated barn owl population in Scotland (Taylor 1994). The number of nest sites (natural sites and nest boxes) in this population exceeded the number of owl pairs in all years of the study, implying that nesting facilities were not limiting.

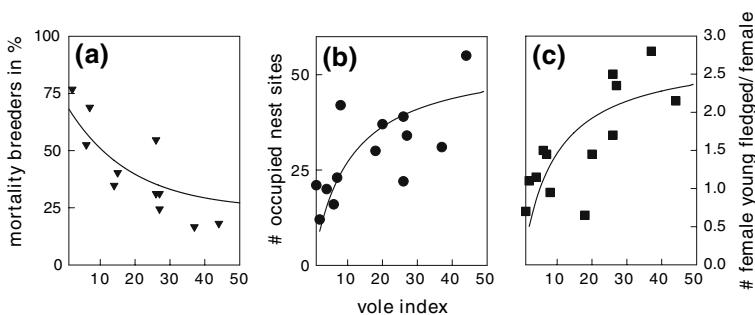
This study was used to parameterize the functions  $S(v_t)$ ,  $B(v_t)$ ,  $F(v_t)$  (see Eq. 2). Empirical data on mortality were fitted with an exponential function (Fig. 3a). The exponential function in Fig. 3a indicates that at high vole densities owl survival is approximately 70%, which is in agreement with other empirical data (Altwegg et al. 2003; De Bruijn 1994; Taylor 1994). Data on the number of breeding pairs were fitted by a saturating response curve (Fig. 3b). This relationship implies that the total number of breeding pairs cannot increase perpetually. Data on the number of fledglings produced are also fitted by a saturating response curve (Fig. 3c). The functions  $S(v_t)$ ,  $B(v_t)$ ,  $F(v_t)$  were fitted to the data by least squares estimation. The factor  $z$  was varied from 1, 0.75 to 0.5, which implies that survival in juveniles and floaters can be up to a factor 2 lower than in adults. This corresponds to literature on mean yearly survival which equaled 0.294 and 0.570 in juveniles and adults respectively in a Swiss barn owl population (Altwegg et al. 2003, 2006). Data on floater survival, however, was virtually absent in literature. Since floaters usually occupy habitat of lesser quality compared to breeders, we assumed their survival to be lower than that of breeders, but higher than that of inexperienced juvenile birds. As a conservative estimate we set the unknown floater survival equal to juvenile survival.

The numerical software package for dynamical system analysis CONTENT 1.5 (Kuznetsov 1995) was used to analyze the model (Eq. 2) by equilibrium analysis. Model output was only generated for the range of measurement data on vole abundance to which the functions  $S(v_t)$ ,  $B(v_t)$ ,  $F(v_t)$  were fitted (interpolation).

### 3 Results

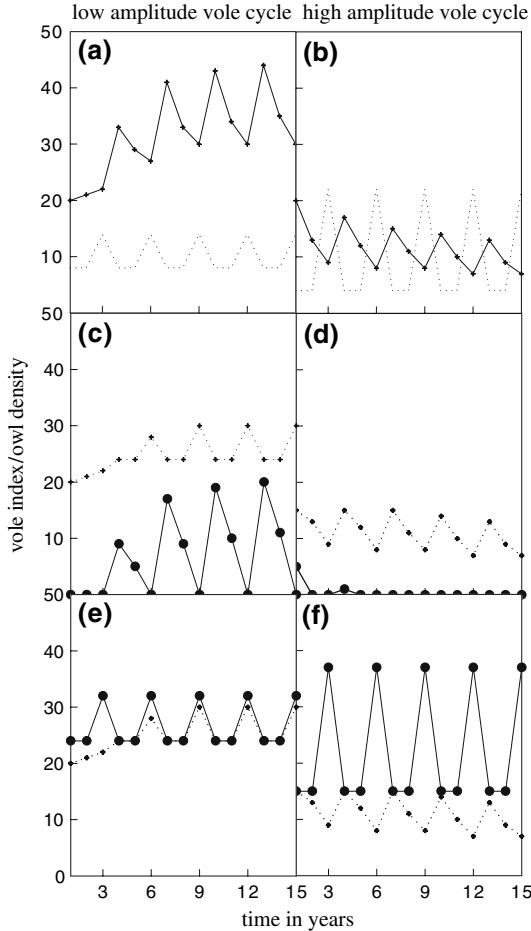
#### 3.1 Periodic Vole Fluctuations (3-Year Cycle) with Equal Survival in all Stages; Influence of Amplitude

Figure 4 depicts simulation results of two owl populations in response to vole cycles with a periodicity of 3 years. The two simulated populations started with 20 adult



**Fig. 3** Breeder survival (a), available breeding territories (b) and reproduction (c) in the barn owl as function of vole density. Symbols in figures empirical data (Taylor 1994). Solid lines in (a): exponential curve, (b) and (c): saturating response curve.  $S(v_t)$ ,  $B(v_t)$ ,  $F(v_t)$ : equations of curves fitted to breeder survival, available breeding territories and reproduction data, respectively

**Fig. 4** Total number of barn owls (solid line) and vole abundance (dotted line) (a, b), the number of floaters (solid line) and breeders (dotted line) (c, d), and the number of available breeding territories (solid line) and breeders (dotted line) (e, f) as a function of a three-year vole cycle. Left panels (a, c, e) vole cycle: mean = 10, low = 8, and peak = 14, right panels (b, d, f) mean = 10, low = 4, and peak = 22, respectively. Survival in all stages equivalent ( $z = 1$ ), populations starts in year one with 20 barn owls



females. The mean vole abundance of 10 for both populations and the amplitude of vole abundance (difference between peaks and lows) equaled 6 in the left panels and 18 in the right. Figure 4a and b shows that owl density peaked with a time delay of one year compared to the voles. In case of the low amplitude of six the barn owl population sustains (Fig. 4a) and reached stable dynamics after 12 years (Fig. 4a) whereas with the high amplitude of 18 (Fig. 4b) the population went extinct for the given parameter values within 110 years (result not shown). The composition of the owl populations in breeders and floaters is given in Fig. 4c and d. In the low amplitude case the number of breeders peaked in vole peak years and floaters responded with a time delay of 1 year (Fig. 4c), whereas with the high vole amplitude breeders peaked with a time delay of 1 year and floaters were absent from year 5 onwards (Fig. 4d). Why floaters disappeared in vole peak years in Fig. 4c and are absent from the population in Fig. 4d is explained by Fig. 4e and f which shows the number of breeders and available breeding territories. The number of breeding territories fluctuated in synchrony with voles (see Eq. 3b). Figure 4e indicates that in

the years with low vole density all available breeding territories were occupied whereas in good years with high vole abundance some remained vacant. In the high amplitude case (Fig. 4f) breeding territories outnumbered owls in all years of the cycle with the exception of the first 3 years after a peak in vole abundance (years 1, 4 and 7). Under the vole abundance regime given in the left panels of Fig. 4, the owl population reached its maximum density in the years after voles peaked, resulting from the high number of owls born in peak years. In the year following a peak year the number of floaters peaked since there were more owls than available breeding territories (see Fig. 4e). In the subsequent bad vole year of the cycle, the total number of owls decreased resulting from low reproduction and survival, and reached a minimum in the ensuing peak vole year. In the peak vole years the available breeding territories outnumber the owls (see Fig. 4e) leading to settlement by all owls and therefore floaters were absent in these years. The owl population living under the vole abundance regime given in the right panels of Fig. 4 also reached its minimum in a good year and its maximum in the ensuing bad year. However, under this vole abundance regime, the number of owls was lower than the number of available breeding territories in all years of the cycle (Fig. 4f) resulting in the absence of floaters. As in the case of the persisting barn owl population (left panels Fig. 4), also for the population that goes extinct (right panels Fig. 4) the good vole years were important to increase the number of birds in the population. However, in the last population the bad years decreased the number of barn owls to such low levels where production of juveniles in the good years could not compensate for the loss.

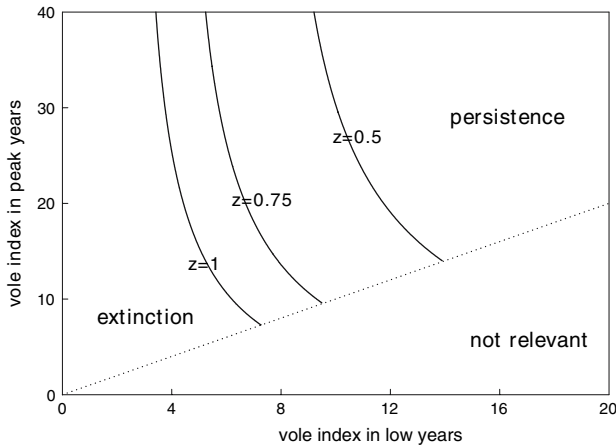
### 3.2 Periodic Vole Fluctuations (3-Year Cycle) Influence of Peaks and Lows, Variation in Survival of Juveniles and Floaters

Figure 5 depicts the influence of low (x-axis) and peak (y-axis) vole abundance on the population persistence for three different values of mortality in floaters and juveniles ( $z$ ). The graphs in Fig. 5 indicate that an increase in the value of the vole index in low years can bring the population from extinction to persistence irrespective of the peak vole index, whereas an increase in the good years does have that effect only for a small range of values. This implies that the persistence of the population is more sensitive to changes in the low years than to changes in the peaks. This result remains unchanged for lower survival values of floaters and juveniles ( $z = 0.75$  and  $0.5$ ), however, with this lower survival populations can only sustain with higher vole abundance (lines in graph shifted to the right).

### 3.3 Variation in Cycle Length

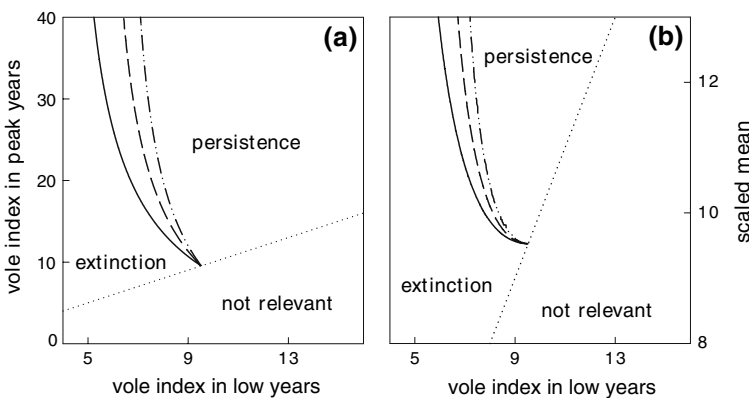
Figure 6a presents the region where barn owls can persist as a function of the vole index in low and peak years for a 3-, 4-, and 5-year cycle, which consist of a single peak year followed by a sequence of years with low vole abundance, and survival in juveniles and floaters reduced by 25% ( $z = 0.75$ ). Similar to Fig. 5, Fig. 6a indicates that, also with increased cycle length, the persistence of the owl population is more sensitive to changes in the value of the vole index in bad years than in good ones.





**Fig. 5** Parameter space of combinations of low and peak vole abundance indicating regions where the population persists. Periodic fluctuations in vole abundance with a period of 3 years for three values of survival of juveniles and floaters reduced by 0% ( $z = 1$ ), 25% ( $z = 0.75$ ) and 50% ( $z = 0.5$ ) compared to breeders floater survival. *Dotted line*: constant vole abundance

Moreover, Fig. 6a shows that with longer cycle length the region where barn owls can persist shrank, implying that population survival becomes even more sensitive to the years of low vole abundance. However, the comparison of the three cycles given in Fig. 6a poses some methodological difficulties since the peak and low vole values lead, for different cycle lengths, to unequal mean vole densities (see Eq. 1a). To achieve a more precise comparison of the cycles, the mean and low vole abundance was fixed whereas the peaks were varied as is shown in Fig. 6b. This figure depicts the regions where the population can persist for the different vole cycles where the low and mean vole densities are comparable for all cycles.



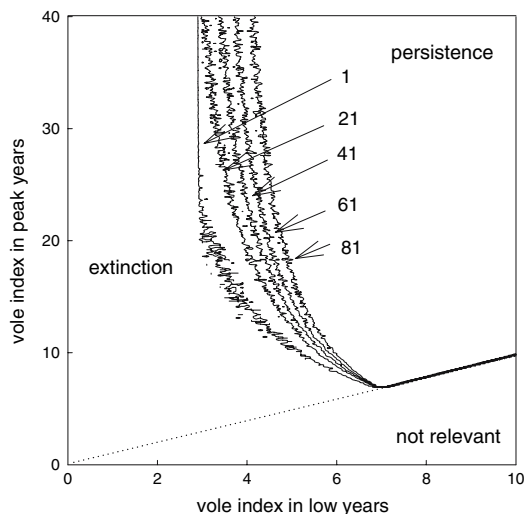
**Fig. 6** Parameter space of combinations of low and peak vole abundance where the barn owl population can persist. Survival of juveniles and floaters reduced by 25% compared to breeders ( $z = 0.75$ ). *Solid line*: three-, dashed: four-, and dash-dotted five-year vole cycle, respectively. Curves in graph separate extinction from persistence region. (a): not scaled, (b): scaled for mean vole abundance

Figure 6b indicates that also in terms of scaled mean vole densities the region where the population can persist decreases when the cycle length increases. Moreover Fig. 6b confirms the large influence of the low vole years.

### 3.4 Non-Periodic Vole Fluctuations

The main result of the analyses with periodic fluctuating voles is that vole abundance especially in low years has a drastic effect on the population persistence and density in the barn owl. However, in the distribution area of the barn owl non-periodic vole fluctuations are more prevalent than periodic (Hansson and Henttonen 1988). Other authors, however, document cycles with a period of 3–4 years in Europe (Mackin-Rogalska and Nabagło 1990; Jędrzejewski and Jędrzejewska 1996). To assess the influence of non-periodic vole fluctuations the model was re-analyzed with random fluctuations in vole abundance. Figure 7 shows the regions where barn owl populations become extinct or persist as a function of the vole index in low (x-axis) and peak (y-axis) years with random vole fluctuations and owl survival equal in all stages. For each combination of low and peak vole abundance the number of simulated owl populations out of 100 that persist for a period of 100 years was calculated. In these simulations the sequence of vole peaks and lows was chosen randomly and peak vole years were encountered with a probability of one third. The contours in Fig. 7 connect low and peak vole values where an equivalent number of simulated owl populations persisted over 100 years. Figure 7 indicates that again low vole years have a high impact on the survival of the owl population. As in case of periodic vole fluctuations the persistence of the owl population turns out to be especially sensitive to changes in years with bad food conditions whereas changes in years with peak vole numbers have virtually no effect.

**Fig. 7** Contour graph depicting combinations of low and peak vole abundance where the barn owl population can persist. The sequence in vole peak and low years is random and the frequency of peaks 0.33. Survival in all stages equivalent. *Dotted line*: constant vole abundance. Contours indicate the number of barn owl populations out of one 100 (shown by the numbers in the graph) that persist for a period of 100 years



## 4 Discussion

### 4.1 Model Results

In this paper we demonstrate that the persistence of a barn owl population that preys on fluctuating voles is more sensitive to years with low vole abundance than to those with high. Although years with peak vole abundance are important to increase the number of owls in the population, the years with low vole abundance determine to what extent the owl population can benefit from the years that voles peak. This result is irrespective of cycle length and regularity of the fluctuations in vole abundance.

The impact of fluctuations in prey abundance on owl persistence is analyzed with a deterministic model assuming a closed population. Stochastic events, e.g. a sequence of years with no reproduction, however, can bring populations to extinction, especially when small (Shaffer 1981; Lande 1993; Lande et al. 2003). The low vole years reduce the number of barn owls in the population to levels where stochastic events may cause extinction, such that inclusion of stochastic events is expected to make the population even more sensitive to the years with low vole abundance. Under the condition that the population is closed, and due to low reproduction and survival in the bad vole years, the number of owls can decrease to levels too small to exploit vole abundance in the ensuing peak years. If the population is not closed, immigrants could fill up vacant breeding territories in peak years and hence increase in this way the exploitation of food. This will make population survival less sensitive to the lows. However, in Western Europe years of high vole abundance were often followed by massive emigration of mainly juvenile barn owls over large areas (Sauter 1956; Honer 1963) which suggests synchrony in vole abundance over these areas.

The model is parameterized with data from a barn owl population at the edge of the species geographical range (Shawyer 1987). More in the center of its range the number of fledglings produced is usually higher, resulting from second broods (Schönfeld and Girbig 1975; Cramp 1985). However, it is not clear whether this higher reproductive output and survival result from elevated vole densities or from other factors since data on these life history processes are not collected together with data on vole densities. If the conservative assumption is made that in the center of the species range barn owls have a higher reproductive output and survival for given vole densities, it can be assumed that owl densities in both peak and low vole years will increase. Thus, compared to the edge of the species range, in the center barn owl populations can be expected to sustain at lower vole abundance in both peak and low years. This implies that the curves in Figs. 6 and 7 move in the direction of the origin. However, the shape of the curves will not change and so the main result will hold that especially the low vole years have a major impact on the persistence of the barn owl population.

The functions describing the relations between the number of fledglings produced  $F(v_t)$  and the number of available breeding territories  $B(v_t)$  were fitted by saturating response curves. To assess the influence of these non-linear relations on the main result, the functions  $F(v_t)$  and  $B(v_t)$  were also fitted with linear relations

$B(v_t) = 0.794 v_t + 11.27$  ( $R^2 = 0.72$ ) and  $F(v_t) = 0.039 v_t + 0.91$  ( $R^2 = 0.60$ ). With linear relations the owl population can increase infinitely but its persistence remains more sensitive to the low than the peak vole years (results not shown).

Furthermore, we assumed equal survival rates for adults irrespective of sex. A recent study on a Swiss barn owl population (Altwegg et al. 2007) indicates that survival in males tend to be higher than in females respectively 0.720 ( $\pm 0.097$ ) for males and 0.658 ( $\pm 0.108$ ) for females. With higher survival rates for males, and under the assumption that reproduction is not biased to one of the sexes, male floaters are expected to outnumber female floaters. This may reduce the stabilizing effect of floaters making the population viability more sensitive to the years with low vole abundance.

#### 4.2 Implications for Conservation of The Barn Owl

Conservation of the barn owl in The Netherlands and Great Britain has been directed at increasing the number of nesting sites, and decreasing its mortality by putting a ban on hunting and deliberate killing. Further actions are directed at protecting and restoring the preferred habitat of the barn owl, mosaic-like landscapes with rough grasslands and hedges (Del Hoyo et al. 1999; Toms et al. 2001). The actions to improve barn owl habitat have the ultimate aim to increase the prey abundance. In this paper it is indicated that in regions where barn owls depend on fluctuating voles, the prey abundance in the low prey years restricts the persistence of the barn owl populations. Therefore, conservation actions should aim to increase the prey abundance in such a way that especially in low vole years the number of voles is increased. This may be achieved by improvement of prey habitat, specifically mosaic-like landscapes which reduce the amplitude of vole variation (Delattre et al. 1999) or supplementary feeding in low prey years.

#### 4.3 Implications for Conservation of Predators Showing a Numerical Response to Fluctuating Prey

Predators that show a numerical response (Solomon 1949) on fluctuating prey are faced with the problem how to track changes in their food abundance. This study shows that if the level of the main prey species in some years is too low, decreased survival and reproduction lead to such a decline in the number of resident predators that the population cannot benefit optimally from the good years and ultimately cannot maintain itself. Therefore, the food level in the bad compared with the good vole years has a much higher impact on the persistence of the population. This result holds for the barn owl, a resident species that responds numerically to changes in vole density with a time delay of 1 year, since individuals mature within the year of birth. It is expected that population persistence is also more sensitive to the low food years than to the peaks in other resident predator species showing a numerical response to their main prey. Examples are the hen harrier *Circus cyaneus*, buzzard *Buteo buto*, and the kestrel *Falco tinnunculus* in Western Europe (Cramp 1985; Del Hoyo et al. 1994, 1999) and Montagu's harrier *Circus pygargus* (Salamolard et al. 2000). Therefore, conservation of these species may also benefit from management

aiming to improve habitat in such a way that years with low vole density are avoided. Obviously, if these predators have a substantial impact on their prey dynamics improvement of habitat to increase prey levels at low prey years will become more complex.

Whereas resident predators have to track changes in food abundance in time, nomadic species are expected not to depend strongly on the abundance of one specific local prey species. However, nomadic species such as the short-eared owl *Asio flammeus* and the long-eared owl *Asio otus*, respond numerically to voles, since their reproductive output is strongly correlated with vole density (Korpimäki and Norrdahl 1991). If voles do fluctuate in synchrony over extensive regions (Mackin-Rogalska and Nabagło 1990; Norrdahl and Korpimäki 1996; Korpimäki and Krebs 1996), it can be expected that the population density of these nomadic species also depends more on the low vole years than on the peaks. Therefore, improvement of vole habitat, with the aim to increase the vole abundance in the low vole years, in general can be considered a conservation strategy that will improve the persistence of not only the barn owl but also other resident and nomadic predators that depend on voles or numerically respond to their abundance.

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