A quest for the role of habitat quality in nature conservation
Klok, C.

Citation for published version (APA):
5 How birds of prey cope with fluctuating prey: conservation of the barn owl *Tyto alba*

Abstract

Many predator species feed on prey that fluctuate in abundance from year to year. Birds of prey 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. Therefore, conservation directed at preservation of endangered predator populations should consider the impact of fluctuations in food abundance.

The barn owl, as a cosmopolitan 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 (the mean, amplitude, period and regularity) on the barn owl indicates that its population persistence is especially influenced by years with low vole abundance. Although peak vole densities increase the number of owls in the population, the lows bring their numbers down to such levels that the population cannot benefit from the ensuing peak vole years. These results are also relevant for the conservation of other birds of prey.

Introduction

Many species suffer from decreases in population densities as is exemplified by the long lists of endangered species in Red Data Books. Conservation actions to abate this decline should be guided by insight in which factors have the largest impact on improving population performance. 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 & De Roos 1998). Improvement of habitat quality, however, is not easy to realise 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 & Gutierrez 1990; Miller et al. 1997).

Of all habitat quality factors, food abundance is likely to be of overruling
importance on the population dynamics. With low food abundance effects of other habitat quality aspects can become more important, e.g. effects of xenobiotics under low food abundance (Kooijman 2000).

Food shortage is suggested an important cause of the decline of the barn owl Tyto alba, one of the most extensively studied bird of prey species. The densities of this cosmopolite species have declined in parts of its distribution area. The species shows distinct fluctuations in the number of breeding pairs and these are correlated with changes in the density of voles, its major prey species (Schönfeld & Girbig 1975; Kaus 1977; De Bruijn 1994; Taylor 1994). In this paper the impact of fluctuations in vole abundance (the mean, amplitude, period and regularity) on the persistence and population density of the barn owl are analysed.

The barn owl

The barn owl Tyto alba is widely distributed on most continents (Cramp 1985; Snow & Perrins 1998; Del Hoyo et al. 1999). The species seems restricted to areas where the mean temperature in January is above 0 °C (Del Hoyo et al. 1999). 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) whereas North America is inhabited by Tyto alba pratincola. The barn owl is a resident of lowland agricultural habitats. The species prefers open habitat with hedgerows and woodland edges (Glutz von Blotzheim & Bauer 1980; Cramp 1985; De Bruijn 1994; Del Hoyo et al. 1999).

In the sixties the barn owl showed a rapid decline in range and numbers in western Europe and North America (Glutz von Blotzheim & Bauer 1980; Cramp 1985; Del Hoyo et al. 1999). This decline was attributed to intensification of agriculture and urbanisation leading to loss of habitat, nesting facilities, and food supply. In addition, severe winters, pesticide use, persecution, and road traffic kills reduced barn owl populations (Sharrock & Sharrock 1976; Cramp 1985; Cayford 1990; De Bruijn 1994; Snow & Perrins 1998). To abate the decline conservation continues to increase the number of nesting sites and to protect and re-establish foraging habitat (Taylor et al. 1992; De Bruijn 1994; Taylor 1994; Del Hoyo et al. 1999). This has resulted in an increase in the number of barn owls in both Great Britain and The Netherlands. However, population densities are still lower than at the start of the last century (De Bruijn 1994; Shawyer 1997). Nowadays especially food scarcity is claimed to keep owl densities at low levels (De Bruijn 1994; Taylor 1994).
**Food relations**

Barn owls mainly prey on small mammals, their most important prey species are voles, rats, shrews, and mice. Birds, amphibians, fish, and insects have a minor share in the diet (Schönfeld & Girbig 1975; Marti 1988; 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, and *Microtus montanus* and *pennsylvanicus* in North America, make up large quantities of the diet (Marti 1988; De Bruijn 1994; Taylor 1994). Vole densities can fluctuate profoundly from year to year. Within the range of the barn owl most fluctuations have a periodicity of three to four years (Krebs & Myers 1974; Hansson & Henttonen 1988; Mackin-Rogalska & Nabaglo 1990; Jędrzejewski & Jędrzejewska 1996).

**Life history of the barn owl**

The barn owl has a large reproductive capacity, female barn owls can produce up to seven fledglings per year (Schönfeld & Girbig 1975). Juveniles mature in their first year and are capable of breeding in their second year of life. Mortality rates in the barn owl are high. The mean life span of barn owls equals about 1.5 years (Stewart 1952; Schifferli 1957; De Bruijn 1994; Del Hoyo et al. 1999). Maximum ages of 18 to 21 years can be reached (Henny 1969; Del Hoyo et al. 1999) but are very uncommon.

Breeding barn owls are territorial. Floaters, adult birds that do not occupy a breeding territory, have home ranges that may overlap with those of breeders (Taylor

---

![Figure 5.1](image-url)

*Figure 5.1*

The life cycle graph of the barn owl.
1994). The life history of the barn owl can be divided into three distinct stages; juveniles, breeders and floaters. Juveniles are young that survived up to fledglings, breeders are adult birds that occupy a breeding territory, and floaters are non-territorial adults. Figure 5.1 shows a flow diagram of the barn owl life cycle. Survival is implicit in the diagram. Individuals in the juvenile stage, that survive their first winter, become breeders if they settle into breeding territories. If they fail to settle, they become floaters. Breeders that survived the winter and retain their breeding territories, stay in the breeder stage. If they lose their 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, settlement and reproduction seem to be linked with vole abundance. Survival is depressed in winter resulting from low densities and or low availability (snow cover) of voles (De Bruijn 1994; Marti 1994; Taylor 1994). Mortality in juveniles is higher than in adults; juveniles have a probability of 47-54% to reach their second year of life whereas adults have a survival of 65-79% (Schönfeld 1974; Glutz von Blotzheim & Bauer 1980; De Bruijn 1994). The number of breeders and thus the number of breeding territories vary with vole abundance (Schönfeld & Girbig 1975; Kaus 1977; De Bruijn 1994; Taylor 1994). Therefore, settlement is likely to depend on vole abundance as well. The breeding season starts around April, May (Snow & Perrins 1998; Del Hoyo et al. 1999). Depending on vole abundance one to two broods are raised each year (Snow & Perrins 1998). Two broods are very uncommon in northern regions (Marti 1994; Taylor 1994) but prevalent in more southern areas. In central Europe up to 64% of the pairs raise a second brood in years of high vole abundance (Schönfeld & Girbig 1975).

**Model formulation**

**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 & Yalden 1998). Because of this small effect of predation by barn owls the vole dynamics are described by an autonomous function, independent of owl density.

Figure 5.2 displays three empirical vole time series, based on spring density estimates. The general pattern emerging from these data is a year where the vole abundance peaks followed by a sequence of years with low vole densities. This pattern is captured by the mean and amplitude of the vole abundance:
Figure 5.2

\[
\text{mean(peak,low,}n) = \frac{\text{peak}}{n} + \frac{(n-1)\cdot\text{low}}{n} 
\]

\[
\text{amplitude(peak,low,}n) = \text{peak} - \text{low} 
\]

where \( \frac{1}{n} \) equals the frequency of peak years. Equation 5.1 is used to analyse both periodic and non-periodic vole fluctuations.

The barn owl population model

A discrete-time model with a time step of one year is used to describe the barn owl population dynamics. The number of barn owls is assessed each year in spring, just before the onset of breeding, just as in the field census on voles. At that time of the year, the owl population consists only of breeders and floaters, since juveniles born the preceding year have already matured. Only female barn owls are modelled, assuming a 1:1 sex ratio and mortality to be independent of sex. The population model is based on Figure 5.1. The life history processes are strongly dependent on vole abundance and are therefore modelled as functions of the vole density. It is assumed that (1) all vacant
breeding territories will become occupied if the number of adult birds in the population is equal to or larger than the number of breeding territories, and that (2) the number of breeding territories is only limited by vole abundance and not by other factors such as shortage of nesting sites, and that (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 equation 5.2.

\[
U_{t+1} = S(v_t)\left\{B(v_t) + z\left[U_t - B(v_t) + F(v_t)\cdot B(v_t)\right]\right\} \quad \text{if} \quad U_t \geq B(v_t) \quad (5.2a)
\]

\[
U_{t+1} = S(v_t)\cdot U_t\left\{1 + z\cdot F(v_t)\right\} \quad \text{otherwise} \quad (5.2b)
\]

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 \( z \) models the increased mortality risk for juveniles and floaters.

### Parameterisation of life history processes

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

The life history functions \( S(v_t), B(v_t), F(v_t) \) (see equation 5.2) are parameterised with data given in Taylor 1994. The empirical data on mortality are fitted with an exponential function (Fig. 5.3a). The exponential function in Figure 5.3a indicates that at high vole densities owl survival is approximately 70%, which is in agreement with empirical data (see section Life history of the barn owl). Data on the number of breeding pairs are fitted by a saturating response curve (Fig. 5.3b). This relationship implies that the total number of breeding pairs cannot increase perpetually. Although the size of the breeding territories changes with vole density (Cramp 1985) there must be a minimum size for a territory to be suitable for breeding. Therefore, the actual size of the area, occupied by the barn owl population, restricts the number of breeding territories. Data on the number of fledglings produced are also fitted by a saturating response curve (Fig. 5.3c).
**Results**

**Periodic three-year vole fluctuations, with equal survival in all stages**

Figure 5.4 depicts simulation results of two owl populations in response to three-year vole cycles. Both simulated populations start with 20 adult females and live at the same mean vole abundance of 10. They differ in the amplitude of vole abundance (difference between peaks and lows) which equals 6 in the left panels and 18 in the right ones. Figures 5.4a and b show the total number of adult owls and the vole abundance index. With the same average vole abundance, dependent on the amplitude of the fluctuations, the barn owl population increases (Fig. 5.4a) or declines in number (Fig. 5.4b). A growing population (Fig. 5.4a) will reach a maximum since the number of available breeding territories is limited (see Fig. 5.3b). The declining barn owl population shown in Figure 5.4b becomes extinct within 110 years (not shown). Figures 5.4a and b indicate that owl density peaks with a time delay of one year compared with voles. The composition of the owl populations in breeders and floaters is given in Figures 5.4c and d. In the surviving population (Fig. 5.4c), the number of breeders peaks in vole peak years and floaters respond with a time delay of one year. In the declining population (Fig. 5.4d), breeders peak with a time delay of one year and floaters are absent from year 5 onwards. Why floaters disappear in vole peak years in Figure 5.4c and are absent from the population in Figure 5.4d is explained by Figures
5.4e and f with breeders and the number of available breeding territories in the surviving and declining population, respectively. The number of available breeding territories fluctuates in synchrony with voles (see equation 5.3b). Figure 5.4e indicates that in the low vole years all available breeding territories are occupied whereas in good years some remain vacant. In the declining population (Fig. 5.4f) there are less owls in the population than breeding territories in all years of the cycle with the exception of
the first three years after a peak in vole abundance (years 1, 4 and 7). Under the vole abundance regime given in the left panels of Figure 5.4, the owl population reaches its maximum density in the years after voles peak, resulting from the high number of owls born the previous year. In these years floaters peak since there are more owls than available breeding territories (see Fig. 5.4e). In the subsequent bad vole years of the cycle, the total number of owls decreases resulting from low reproduction and survival, and reaches a minimum in the peak vole year. In the peak vole years the available breeding territories outnumber the owls (see Fig. 5.4e) leading to settlement by all owls and therefore floaters are absent in those years. The owl population living under the vole abundance regime given in the right panels of Figure 5.4 also reaches its minimum in a good year and its maximum in the ensuing bad year. However, under this vole abundance regime, the number of owls decreases and is lower than the number of available breeding territories in all years of the cycle (Fig. 5.4f) so that floaters are absent. As in the case of a persisting barn owl population (left panels Fig. 5.4), also for a declining population (right panels Fig. 5.4) the good vole years are important to increase the number of birds in the population. However, in the declining population the bad years decrease the number of barn owls to such levels where production of juveniles in the good years cannot compensate for the loss.

To analyse the role of the peaks and lows of the vole cycle in the density and persistence of the barn owl population an equilibrium analysis has been carried out using Content (Kuznetsov 1995), a numerical software package for dynamical system analysis. First the influence of the bad years on the equilibrium owl density is analysed given a constant peak vole abundance. Figure 5.5 shows the equilibrium barn owl density (total number of owls) as a function of the vole index in low years. Every point on the curve in Figure 5.5 represents the equilibrium barn owl density of a population living at a peak vole abundance of 14 and a low indicated by the value on the x-axis. The equilibrium owl density is computed in a peak vole year after the population has become independent of the initial condition. The curve in Figure 5.5 indicates that the equilibrium barn owl density increases approximately linearly with the vole index in low years. For this index smaller than 5.25, the equilibrium owl density drops to zero. For values of the index above this threshold owl populations can persist (they have a positive equilibrium).

Figure 5.6a depicts the influence of both the lows (x-axis) and peaks (y-axis) in vole abundance on the population persistence of the barn owl. The solid line borders the parameter space where the population goes extinct. The dotted line indicates the absence of fluctuations (equal vole densities in peak and low years). Figure 5.6a shows that with constant vole density the owl population survives given a vole density of at least 7.3. The graph also indicates that the persistence of the population is more sensitive to changes in the low years than to changes in the peaks. Whereas increasing the value of the vole index in low years can bring the population from extinction to
Figure 5.5
Equilibrium barn owl density (total number of owls) as function of vole abundance in the low years. Peak vole abundance fixed at 14, periodic fluctuations in vole abundance with a period of three years, survival in all stages equivalent (z=1).

Persistence irrespective of the peak vole index, increase in the good years does have that effect only for a small range of values. Moreover, below certain values of the bad years the barn owl population cannot survive irrespective of the values of the peaks. This is depicted in Figure 5.6a for values of lows smaller than 3.5. With values of the vole index in the low years smaller than 3.5 increased survival and reproduction in good years cannot compensate for the decrease in number of owls in low vole years. The effect of the vole abundance in low and peak years on the barn owl densities is illustrated in Figure 5.6b. Owl densities are sampled in a peak vole year after their transient dynamics have been discarded. The contours in the plot indicate equivalent owl densities. As in Figure 5.6a, Figure 5.6b shows that the increase in vole abundance in bad years has a high impact on the population density whereas the increase in good years has virtually no effect.

**Periodic three-year vole fluctuations, reduced survival of juveniles and floaters**

Given the lack of data, it is assumed in the above analyses that survival of juveniles and floaters is equivalent to survival in breeders. However, since juveniles and floaters can
Figure 5.6a
Parameters space of combinations of low (x-axis) and peak (y-axis) vole abundance indicating the region where the owl population persists. Periodic fluctuations in vole abundance with a period of three years, survival in all stages equivalent (z=1). Dotted line: constant vole abundance. Solid line: combinations of low and peak vole abundance where the owl population can just maintain itself.

Figure 5.6b
Contour graph showing barn owl population densities in peak vole year after transient dynamics have been discarded. Periodic fluctuations in vole abundance with a period of three years, survival of all stages equivalent (z=1). Dotted line: constant vole abundance. Contours connect equivalent owl densities as indicated by the figures in the graph.
Figure 5.7a
Parameter space of combinations of low and peak vole abundance indicating regions where the owl population persists. Periodic fluctuations in vole abundance with a period of three years. Solid line: survival of all stages equivalent (z=1). Dashed line: survival of juveniles and floaters reduced by 25% compared to breeders (z=0.75). Dash-dotted line: survival of juveniles and floaters reduced by 50% compared to breeders (z=0.5). Dotted line: constant vole abundance.

have less reliable food resources than breeders, the effect of decreases in their survival on the persistence and density of the owl population is studied. Figure 5.7a represents the region where the population persists as a function of the vole index in low (x-axis) and peak (y-axis) years for a three-year cycle when \( z \) (the ratio of juvenile/floater to breeder survival, see equation 5.2) is equal to 1, 0.75, and 0.5, respectively. As in Figure 5.6a, also with \( z<1 \) population persistence is more sensitive to changes in vole abundance in low years than in peak years. Figure 5.7a indicates that with a constant vole abundance and decreased juvenile and floater survival (\( z=0.75 \) and 0.5) owl populations can persist if the vole abundance increases from \( \geq 7.3 \) to \( \geq 9.6 \), and \( \geq 13.9 \), respectively. With periodic fluctuating vole abundance and \( z<1 \) the region where the population can attain positive equilibrium densities moves to the right (Fig. 5.7a), which implies that with decreased survival in juveniles and floaters the owl population needs higher vole abundance to maintain itself. The effect of the vole abundance in bad and good years on barn owl density is given in Figure 5.7b where survival of juveniles and floaters is reduced by 50% compared to breeders (\( z=0.5 \)). The owl densities are sampled in a peak vole year after their transient dynamics have been discarded. The contours in the plot indicate equivalent owl densities. The contour plot (Fig. 5.7b) indicates that with \( z=0.5 \) the number of owls in the population decreases drastically; compared with Figure 5.6b this number declines by more than 50%.
Figure 5.7b
Contour graph showing barn owl population densities in peak vole years after transient dynamics have been discarded as function of low and peak vole densities. Periodic fluctuations in vole abundance with a period of three years, survival of juveniles and floaters reduced by 50% compared to breeders ($z=0.5$). Dotted line: constant vole abundance. Contours connect equivalent owl densities as indicated by the figures in the graph.

Figure 5.8
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.
Variation in cycle period

To assess the influence of the vole cycle period on the owl persistence four- and five-year vole cycles are analysed. The cycles consist of a single peak year followed by a sequence of three or four years with low vole abundance. Figure 5.8a presents the region where barn owls can persist as a function of the vole index in low and peak years for a three-, four-, and five-year cycle with survival in juveniles and floaters reduced by 25% (z=0.75). Similar to Figures 5.6a and 5.7a, Figure 5.8a 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. Moreover, Figure 5.8a shows that with longer cycle periods the region where barn owls can persist shrinks, implying that population survival becomes even more sensitive to the bad years. However, the comparison of the three cycles given in Figure 5.8a poses some methodological difficulties since the peak and low vole values lead, for different cycle lengths, to unequal mean vole densities (see equation 5.1a). To achieve a more precise comparison of the cycles, the mean and low vole abundance were fixed whereas the peaks were varied as is shown in Figure 5.8b. 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. Figure 5.8b indicates that also in terms of scaled mean vole densities the region where the population can persist decreases when the cycle length increases. Moreover, Figure 5.8b confirms the large influence of the low vole years.

Non-periodic vole fluctuations

The main result of the analyses with periodic fluctuating voles is that especially vole abundance 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 both periodic and non-periodic vole fluctuations occur. According to Hansson & Henttonen (1988) most vole populations in northwestern Europe, with the exception of northern populations, are non-periodic. Other authors, however, document cycles with a period of three to four years in Europe (Mackin-Rogalska & Nabaglo 1990; Jędrzejewski & Jędrzejewska 1996). In North America both periodic and non-periodic vole populations are common (Taitt & Krebs 1985). To assess the influence of non-periodic vole fluctuations the model was re-analysed with random fluctuations in vole abundance. Figure 5.9 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 is calculated. In these simulations the sequence of vole peaks and
Figure 5.9
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 owls populations out of one 100 that persist for a period of 100 years.

Lows is chosen randomly and peak vole years are encountered with a probability of one third. The contours in Figure 5.9 connect low and peak vole values where an equivalent number of simulated owl populations persisted over 100 years. Figure 5.9 indicates that again low vole years have a high impact on the survival of the owl population. As in case of periodic vole fluctuations (Figure 5.6a) 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.
Discussion

This paper demonstrates that the density and persistence in barn owl populations that prey on fluctuating voles are more sensitive to the abundance of voles in low years than in peak years. Although years with peak vole abundance are important to increase the number of owls in the population (Fig. 5.4), the level of the vole abundance in bad years determines whether the owl population can benefit from the years that voles peak. Therefore, vole abundance in low years have a higher impact on the population survival and density than peak abundance (see Fig. 5.6a, b). This result is irrespective of periodicity or randomness of the dynamics in vole abundance (see Fig. 5.9). Analysis of the model with lower values of survival in juveniles and floaters shows that the owl population can only persist when vole levels increase (Fig. 5.7a). Whereas with a longer cycle length of the prey, population persistence becomes more sensitive to the low vole years (Fig. 5.8).

The impact of fluctuations in prey abundance on owl persistence is analysed with a deterministic model. However, stochastic events, e.g. a sequence of years with no reproduction, can bring populations to extinction, especially in small populations (Shaffer 1981; Lande 1993). The low vole years reduce the number of barn owls in the population to levels where stochastic events may cause extinction. Inclusion of stochastic events therefore is expected to make the population even more sensitive to the bad years.

One of the assumptions made is that the number of breeding sites is only limited by vole abundance. Even if other factors, such as depletion of nesting sites, restrict the number of breeding territories the general conclusion is expected to hold. Depletion of nesting sites will in particular become apparent in peak vole years, when the demand for nesting sites is high. Therefore, depletion of nesting sites is expected not to affect the sensitivity to the vole abundance in low-density years.

Since data on survival of juveniles and floaters related to vole abundance were virtually absent in literature, it is assumed that survival in these stages is proportional to that of breeders and hence will increase with vole abundance (see Fig. 5.3a). The effect of lower survival of juveniles and floaters is explored (Fig. 5.7), assuming that non-territorial birds have a higher mortality than territorial birds. In addition, literature data show that peak vole years are often followed by massive dispersal of mainly juveniles in autumn, which leads to extreme mortality in winter (Sauter 1956). And data on the Ural owl Strix uralensis (Brommer et al. 1998), Tengmalm's owl Aegolius funereus (Korpimäki 1988), Eurasian kestrel Falco tinnunculus (Korpimäki & Rita 1996) and great horned owl Strix nebulosa (Rohner & Hunter 1996) show that recruitment in the breeding population from hatchlings born in peak prey years is far lower than that of birds born in low prey years. Together these data suggest that the mortality of juveniles is higher in winters following prey peak years than in those
following lows. If the survival of juveniles has indeed decreased in years with high prey levels, recruitment will decrease and thus the benefit of peak vole years. This enhances the sensitivity to the years of low vole density.

As argued before the functions describing the relations between the number of fledglings produced $F(v_t)$, in other words the number of available breeding territories and vole density $B(v_t)$ are fitted by saturating response curves. To assess the influence of these non-linear relations on the main result, these life history processes were also fitted with linear relations: $B(v_t) = 0.794 \cdot v_t + 11.27$, and $F(v_t) = 0.039 \cdot v_t + 0.91$, $R^2 = 0.60$. 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).

The results (Figs. 5.6-9) indicate that in a closed population due to low reproduction and survival under bad food conditions, 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 and density less sensitive to the lows. However, voles can fluctuate in synchrony over extensive geographical ranges (Mackin-Rogalska & Nabaglo 1990; Norr Dahl & Korpimäki 1996; Korpimäki & Krebs 1996) which may lead to synchrony in barn owl populations over large areas. This seems to be illustrated by literature data showing that in western Europe years of high vole abundance are often followed by massive emigration of barn owls over large areas (Sauter 1956; Honer 1963). These literature data do indicate such synchrony. Therefore, it is expected that even for open populations the general result holds.

The model is parameterised with data from a barn owl population at the edge of the species geographical range (Shawyer 1987). More in the centre of its range the number of fledglings produced is usually higher, resulting from second broods (Schönfeld & Girbig 1975; Cramp 1985). Also in North America survival is higher in southern populations than in northern ones (Marti 1997). 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 centre 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 centre barn owl populations can be expected to sustain at lower vole abundance in both peak and low years. This implies that the curves in Figures 5.6a and 5.9 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.
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 persecution. Further actions are directed at protecting and restoring the preferred habitat of the barn owl, that is mosaic-like landscapes with rough grasslands and hedges (Del Hoyo et al. 1999). The actions to improve barn owl habitat have the ultimate aim to increase the prey abundance. In this chapter 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 can be achieved by improvement of prey habitat. When this is not feasible, supplementary feeding in low prey years may be an option.

Implications for conservation of predators showing a numerical response to fluctuating prey

Predators that depend 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, the decreased survival and reproduction lead to such a decline in the number of resident predators that the population cannot benefit from the good years and ultimately cannot maintain itself. Therefore, the food level in the bad compared with the good 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 one year, since individuals mature within the year of birth. It is expected that population persistence in other resident predator species showing a numerical response to their main prey, is also more sensitive to the low food years than to the peaks. Examples are the hen harrier *Circus cyaneus*, buzzard *Buteo buteo*, and the kestrel *Falco tinnunculus* in western Europe (Cramp 1985; Del Hoyo et al. 1994, 1999). Therefore, conservation of these species will also benefit from improvement of habitat in such a way that the years with low vole density are avoided.

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 on voles, since their reproductive output is strongly correlated with vole density (Korpimäki & Norrdahl 1991). If voles do fluctuate in synchrony over extensive regions, it can be expected that the population density of these nomadic species also depends more on the low prey 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.

References


