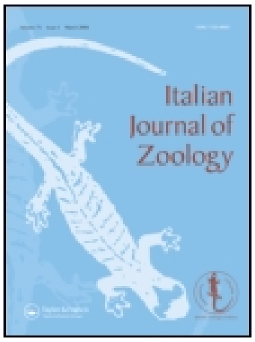

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Investigation of the mortality of a local barn owl population using key factor analysis

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ABSTRACT

The mortality of barn owls breeding in nestboxes between 1995 and 2001 in Baranya county, southern Hungary was investigated using modified key factor analysis. Total mortality and the mortality rates of different stages of the breeding cycle were determined. The mortality rate between the autumn and breeding spring population size was applied as key factor (k_4). Mortality rates, except for k_4, were calculated for both first and second nestings: they differed from each other in the trends of mortality factors, but when comparing the values of mortality rates between the two nesting periods no significant difference was found. Possible relationships between various k-values and the environmental variables behind mortality factors (precipitation, snow depth, temperature, mean small mammal biomass) were tested in three cases (k_1 of first and second breeding, k_4), it was found that some months had observable effects in the development of the actual mortality factors. Significant negative correlation was found between k_1-factor and precipitation in August during the second nesting, although k_1 was expected to be closely correlated with mean small mammal biomass. Significant correlation with the key factor was observed only in the case of snow depth. Partial correlation confirmed that snow depth in itself can determine mortality in winter.

KEY WORDS: *Tyto alba* - Key factor - Mortality - Environmental variables.

ACKNOWLEDGMENTS

We would like to thank László Bank, coordinator of the Baranya Group of Bird Life, Hungary (MME), for letting us use their nestbox data, and wish to express our sincere thanks to members of the same organisation: their work facilitated not only the analysis of data on breeding biology, but also contributed to effective barn owl conservation. We are also grateful to the anonymous referee whose valuable comments improved on earlier version of the manuscript.

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INTRODUCTION

Many studies have investigated barn owl's (*Tyto alba* Scopoli, 1769) mortality (e.g. Frylestam, 1972; Juillard & Beuret, 1983; Percival, 1992; Taylor, 1994; Mátics, 2000), using ringing data to examine the mortality rates in the post-fledged age-classes of the species. According to Taylor (1994), temperate climate barn owl populations show 65-75% mortality in the first year after fledging, 40-60% in the second year, and 30-40% in the third. Hungarian data suggest that mortality rates in the first year of life fall between 50 and 70% (Mátics, 2000). However, by analysing ringing data we can gain information only about a specific part of the population, because the rate of recapture is not independent of the birds' age, the cause of death and the place of finding, in addition these investigations do not provide information about mortality occurring during the time of nesting.

Several studies have already dealt with determining the mortality rates of young owls during the breeding period, some by using k-factor analysis (e.g. Exo, 1992; Percival, 1992). Percival (1992) examined the mortality factors in the barn owl and the tawny owl (*Strix aluco* Linnaeus, 1758) from 1976 to 1987, and found that the most determinative was the post-fledging juvenile mortality during the annual cycle. Exo (1992) also investigated mortality rates in the little owl (*Athene noctua* Scopoli, 1769) using key factor analysis, but mainly concentrated on the effect of winter mortality as the key factor in population density. But as a general conclusion, most examinations established that the most threatened age-class is the fledged, juvenile owls, and the highest mortality rate occurs in their first winter, whether these studies used key factor analysis or not.

The high mortality rate during the highly unfavourable winter period can be explained mostly by weather conditions. The barn owl has adapted primarily to warm climates, its neutral zone in terms of temperature being in the range of 25-33 °C (W. D. Johnson, 1974, M.Sc. thesis, California State University; Edwards, 1987), i.e., the temperature optimum for this species coincides with the Mediterranean climate zone. So the most serious limiting factor is permanent cold and, especially, rain frozen on the snow layer, because these pose great difficulties to the catching of prey (Dobinson & Richards, 1964; Glue, 1973; Marti & Wagner, 1985; Shawyer, 1987). Also, as Ritter & Görner (1977) claimed, extended rainy periods are also unfavourable from the aspect of hunting.

Despite the mentioned studies, there are still unknown aspects of mortality occurring in the barn owl's nesting. In the case of earlier papers, the breeding cycle is not subdivided, and in turn, the values of the mortality factors calculated during the first and second nesting, and also their background can be very dissimilar. Furthermore, the correlation of the mortality rates and the possible environmental factors behind them have not been quantitatively examined yet. Therefore, in the present study based on nestbox data, we (i) determined the mortality rates of different age classes of the barn owl during the first and second nesting, (ii) looked for the key factor in mortality, as well as (iii) analysed the effects of environmental variables behind mortality factors.

MATERIALS AND METHODS

Our investigations were performed in Baranya county, southern Hungary, where we gained data from barn owl nestboxes put in place by the Baranya Group, Bird Life, Hungary (MME) between 1995 and 2001. The nestboxes were controlled by volunteers in pre-established intervals, which allowed us to create an accurate database of nesting parameters. More and more nestboxes were set up continuously from 1987, after a survey in 1985-86, which revealed that the decline of the barn owl population in the region was caused mostly by the absence of acceptable nesting places (Bank, 1990). Although, through the nestboxes provided, the population increased in the region, the collected data indicate that on occasions the population regressed because of some environmental factors. We have frequent and reliable information only about the barn owls breeding in nestboxes, so our analysis and conclusions relate solely to that population. The survey of freely nesting pairs was also started on by the Department of Zootaxonomy and Synzoology, University of Pécs in 1996.

Key factor analysis introduced by Varley & Gradwell (1960) was applied for the investigations. This has great practical use in ecology, but it is also known to have conceptional errors in its statistical analysis (Manly, 1990; Royama, 1992). Nevertheless, it is still used (e.g. Exo, 1992; Percival, 1992; Lens & Wauters, 1995; Kirsch, 1996), primarily because the collected data can be easily processed with key factor analysis, and the conclusions drawn from it do not differ considerably from those generated by mathematically more precise but much more sophisticated calculations (Sibly & Smith, 1998). Our calculations of k-values were made based on the study of great tits by Krebs (1970), modified by our use of natural logarithm (Sibly & Smith, 1998).

Our basic equation is as follows:

$$k_i = \ln\frac{\textit{(population size at the start of the investigations)}}{\textit{(population size at the end of the investigations)}},$$

this formula being used in each period of the nesting, throughout the entire year. The figures inside the parentheses are always the mean values of the number of the studied age-class, whereas +2 stands for the parent birds and N represents the number of nesting pairs. For calculating k_1-values we considered the largest potential clutch size to be 11 (Witt, 1992).

$$k_1 = \ln\left[\frac{\textit{(largest potential clutch size} + 2)\,N}{\textit{(actual number of eggs in a nest} + 2)\,N}\right],$$

$$k_2 = \ln\left[\frac{\textit{(number of eggs laid} + 2)\,N}{\textit{(number of chicks hatched} + 2)\,N}\right],$$

$$k_3 = \ln\left[\frac{\textit{(number of chicks hatched} + 2)\,N}{\textit{(number of chicks fledged} + 2)\,N}\right],$$

$$k_4 = \ln\left[\frac{\textit{(number of chicks fledged} + 2)\,N}{\textit{(number of birds in the nesting population of following year)}}\right].$$

The total decrease rate of the examined population from one nesting to the other was calculated as $K = k_1+k_2+k_3+k_4$. To establish which k is the key factor, regression analysis was performed between K total mortality and each of the k-values.

Having determined and analysed the mortality factors for both first and second nesting separately, we also investigated which environmental variables had a crucial effect on their values. However, to investigate the relationship between environmental variables behind mortality factors and the k-values of the nestings is problematic. This is because mortality rates have to be bound to months, since meteorological and small mammal trapping data are available in monthly periods. Therefore, we examined only those k-values (k_1 and k_4) that could be correlated to certain periods of the year, to avoid distorted results and to prove statistically the limiting effect of environmental factors on the barn owl population.

Weather data (temperature, precipitation, snow depth) were obtained from the National Institute of Meteorology, whereas small mammal information from the studied area in the form of live trapping data was provided by the Department of Zootaxonomy and Synzoology, University of Pécs. Regression analysis was used to test for correlation between k-values and environmental variables. Nevertheless, these environmental factors are not effective consistently and independent, so in order to examine clearly the impact of a single variable, a correlation matrix was created from the Pearson correlation coefficient values of examined k-factors and each of the environmental variables, and this was further used for partial correlation testing (Zar, 1996).

RESULTS

Calculating annual mortality values, determining the key factor

During the key-factor analysis, calculations were based on nestings occurring in artificial nestboxes in the studied years. As Figure 1 shows, the number of available nestboxes grew continuously in this period, but the size of the barn owl population was determined not only by the availability of nesting sites, but, in particular strikingly so during the spring of 1996-1997, also by other environmental variables. The number of breeding pairs dropped considerably in these years, then from 1998 the breeding population gradually grew.

To analyse annual mortality rates, total mortality (K) calculated for each year and different k-values were charted, to reveal which mortality factor showed similarity to the trend of K (Fig. 2.). According to the assumption, we found that k_4 was the most determining mortality factor, as it represented the greatest proportion of the total annual loss.

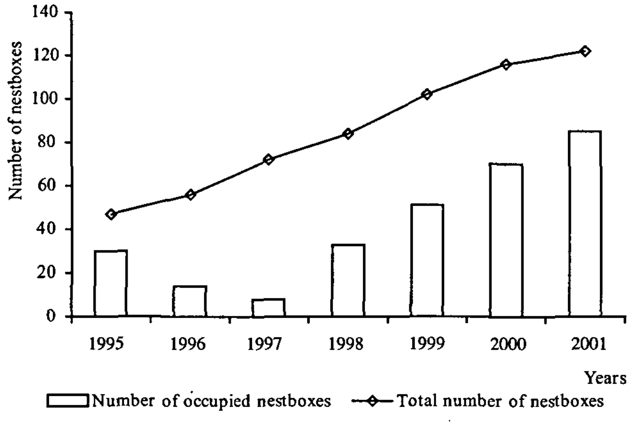

Fig. 1 - Basic data of investigated nestboxes between 1995 and 2001.

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Regression analysis between k-values and total mortality (K) proved unequivocally that only k_4 had significant linear regression with total mortality (k_1, k_2 and k_3: $r = 0.051$-0.249, NS; k_4: $r = 0.978$, $P < 0.001$) and the value of the correlation coefficient clearly showed that the key factor in the particular study period was k_4, i.e., the mortality rate between autumn and spring population sizes.

Mortality factors of the first and second nestings

The first and second nestings were also analysed separately, with regard to the k_1-k_3 factors. It was found that the first and second breedings differed from each other in the mortality factor trends. At the first breeding, mortality rates decreased continuously as the brood advanced, the k_1 factor had the highest value of all the mortality factors in the years and chick loss never exceeded incubation loss (Fig. 2.). Both k_2 and k_3 factors had a two-peak graph during the studied years, and showed similarity.

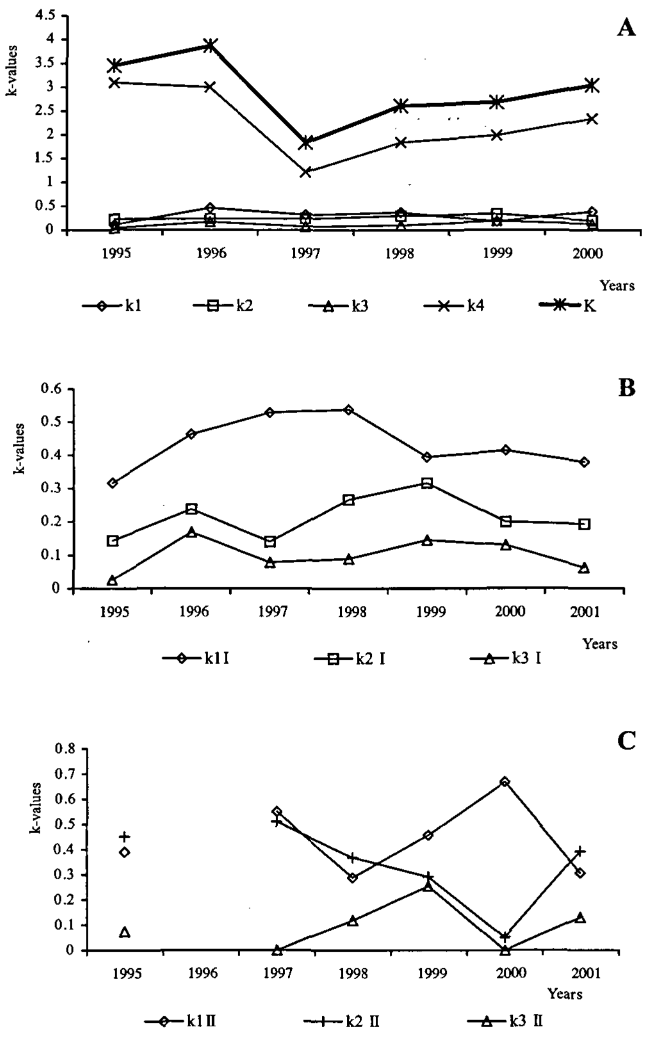

Fig. 2 - Values of mortality factors in the studied years. **A**, total mortality (K) and various k-values. **B**, mortality factors of the first nesting. **C**, mortality factors of the second nesting (no breeding occurred in 1996).

In the case of second nesting, the mortality rates displayed quite a different pattern (Fig. 2.). The reason is that they showed a more intensive fluctuation, and the order between mortality factors, which was constant at the first breeding, did not fully fit with this period. Namely, the k_2 factor, which means incubation loss, more than once exceeded the value of k_1 mortality factor. However, the k_3 mortality rate was constantly the lowest of all the factors just as during the first breeding, but at the second breeding it reached zero value twice during the years. Nevertheless, when comparing the values of the different k-factors between the two nesting periods, no significant difference was found (paired--samples t-test, k_1, k_2 and k_3: $t = 0.201$-1.656, NS).

Analysis of correlation between k-factors and environmental variables

In our investigations, the values of k_1 factors for the first breedings were compared with the April mean temperature, rainfall and biomass data, while in the case of second nesting, k_1 was looked at together with mean values of August weather and biomass data (Table I). In both cases, these months represented the start of the breeding period (Taylor, 1994), so environmental variables may have had crucial effects in that time.

Possible correlation between the mortality factors and environmental variables were tested for using linear regression analysis. Pearson's correlation coefficient values are also shown in Table I, revealing only one significant negative correlation ($r = -0.987$, $P < 0.001$), i.e., between k_1 mortality of the second nesting and August precipitation. This indicates that precipitation may have had a considerable impact on the start of the breeding when the second nesting period occurred.

In the key-factor analysis and the environmental variables having an effect on it, data from the period between November to March were used, whereas biomass data used referred to periods of between September and March. By performing regression analysis between the background variables and the key factor, the intensity of their correlation was tested. When looking at the relationship between temperature and the key factor, non--significant negative correlation was revealed ($r = -0.463$, NS). At the same time, significant positive linear regression was found between mean snow depth and the key factor ($r = 0.892$, $P < 0.02$) and positive linear regression between k_4 and the months in which snow occurred ($r = 0.851$, $P < 0.02$). The results mean that the thickness and even the presence of snow in winter greatly influenced the rate of mortality. No significant correlation was found between the key factor and small mammal biomass in the examined period ($r = -0.322$, NS), and a non-significant result was obtained in the case of k_4 and precipitation in the winter months, too ($r = 0.379$, NS).

To reveal further details in the effects of environmental parameters, the strength of the relationship between pairs of the quantitative variables was tested, on the assumption that other quantitative variables could influ-

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TABLE I - *Values of environmental variables, k_1 factors and correlation coefficients.*

	Temperature (°C)		Precipitation (mm)		Biomass (g)		k_1	
	I nesting	II nesting	I nesting	II nesting	I nesting	II nesting	I nesting	II nesting
1995	10.9	20.6	48.6	69.2	277.78	987.65	0.3172	0.3902
1996	11.3	19.9	38.7	61.0	46.30	268.52	0.4630	-
1997	7.4	20.8	48.3	47.4	628.10	1586.78	0.5281	0.5501
1998	11.8	21.5	78.0	86.0	280.10	950.41	0.5380	0.2877
1999	12.0	20.3	73.6	66.4	28.93	432.23	0.3951	0.4571
2000	14.0	23.6	60.6	22.6	181.82	565.29	0.4144	0.6678
k_1 of the first nesting	-0.3779	-	0.1603	-	0.4339	-	-	-
k_1 of the second nesting	-	0.5765	-	0.9869[a]	-	0.0812	-	-

[a], P < 0.001

ence this relationship. The latter influence can be eliminated by considering it as constant (Zar, 1996). For calculating such partial correlation coefficients, first the coefficients among mortality factor k_4 and the environmental variables had to be determined (Table II).

Partial correlation coefficient values between k_4 and the various environmental variables were then calculated, with one variable always regarded as constant, so that its influence was filtered off. However, eliminating the effects of more than one variable would provide questionable results (Zar, 1996). In all cases significant correlation was revealed in the test: whether biomass, temperature or precipitation values were regarded as constant, we found significant correlation between the key factor and snow depth ($r_{15.4} = 0.961$, $P < 0.01$; $r_{15.2} = 0.896$, $P < 0.05$; $r_{15.3} = 0.889$, $P < 0.05$).

DISCUSSION

The Baranya Group of Bird Life Hungary (MME) has aided the settling of barn owls by providing nestboxes since 1987. As a result of the continuous project with nestboxes, a precise database was established, allowing further investigations in breeding biology (L. Bank *et al.*, 2003, *Abstract* in VI world conference on birds of prey and owls, Budapest). Due to the fact that we had frequent and reliable information only about barn owls breeding in nestboxes, our analysis and conclusions refer solely to that population.

First of all, we determined mortality rates using modified key-factor analysis and, as a result, found that the k-value calculated from the difference between autumn and spring population size (k_4) can be considered the key factor – similarly to other studies (e.g. Percival, 1992). Not surprisingly, this confirms that the greatest mortality occurs during the winter period and the most threatened age-class is that of the post-fledging juveniles (Taylor, 1994; Mátics, 2000; Altwegg *et al.*, 2003).

Using key factor analysis to assess density dependence in time series is flawed, as is pointed out by, e.g., Ito (1972), Kuno (1973) and Bulmer (1975). It is because there is a serial correlation between populations in a series of years, that k-values and N cannot be inde-

TABLE II - *Pearson's correlation coefficients between the various variables.*

	k_4	Biomass	Precipitation	Temperature	Snow depth
k_4	-				
Biomass	-0.322	-			
Precipitation	0.379	-0.732	-		
Temperature	-0.463	0.149	-0.127	-	
Snow depth	0.937[a]	-0.081	0.159	-0.859[b]	-

[a], P < 0.01; [b], P < 0.05

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pendent. Besides, population size is estimated and the errors of the estimation are not equal for all life stages. Nevertheless, there are other studies (e.g. Krebs, 1970; Exo, 1992) that use key-factor analysis as a standard method to examine population regulation and to determine density dependence. In this paper, we did not analyse the density dependence of the key factor, because the sample size was not large enough to carry out such an investigation properly, and it would have been difficult to interpret its results since our data are confined to nestbox-breeding pairs.

During the investigation, first and second nestings were also differentiated and k_1, k_2 and k_3 mortalities were determined for the two nesting periods. It was found that the first and second breedings differed from each other in the trends of mortality factors, and the 'regular' ranking between the mortality rates during the second breeding changed. However, comparing the values of the different k-factors between the two nesting periods no significant difference was found. Second broods often occurred in temperate regions, but during second nesting the individual differences of breeding pairs had greater influence on breeding success, and environmental factors, mostly the amount of available prey, were more determinant (Taylor, 1994). Because of that, the process of second breeding is more inordinate than in the case of the first nesting period, which is indicated also by the calculated mortality rates.

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With the investigation of mortality rates and the different environmental variables that may play an important role in their development, we have to be very careful. That is because we examined a relatively short period (n = 6), so our data set was not appropriate for analysing each mortality factor – environmental element correlation in detail, or for detecting every slight consistency. Besides, weather data were available as monthly average values, which would also have made the investigation problematic. For that reason, we analysed the correlation of mortality factors and environmental variables only in three cases (k_1 of first and second breeding, k_4), when we expected that some months would have had observable effects on the development of the actual mortality factor. Because of the assumed close relationship, the number of studied years may be acceptable for these analyses.

According to the assumption, k_1 was expected to be closely correlated with mean small mammal biomass, since the amount of reserves the female bird can accumulate for egg-laying depends on the amount of available prey (Taylor, 1994). Another assumption was that k_1 may have close correlation with mean precipitation, since extended rainy periods are unfavourable from the standpoint of hunting (Ritter & Görner, 1977). However, we found significant negative correlation only between k_1-factor and precipitation in August during the second nesting. In the case of k_1 in the first breeding period, we did not find any significant relationship between the mortality rate and the examined environmental variables.

The non-significant correlations in the case of k_1 during the first nesting and weather parameters can be explained by the fact that unfavourable conditions rather delay the onset of egg laying (Marti, 1994), which results in second nesting perhaps not occurring or even being delayed, thus leading to a reducing effect on breeding success. However, the ability to rear a second brood depends greatly on the timing of the first brood, so it is advantageous for barn owls in temperate regions to start breeding as early as possible, i.e., late March or April (Taylor, 1994). Although the results suggest that April weather parameters by themselves do not primarily determine the number of clutch laid, variability in the severity of winter weather has a strong influence on reproductive success through adult mortality, reduction in clutch size and in the likelihood of producing two broods in one season (Marti, 1997). The close relationship between k_1 during the second nesting and August precipitation cannot be easily interpreted by weather conditions. August is generally the driest month in the year and higher precipitation values may indicate a more favourable season for small mammals, which may contribute to lower k_1-values. However, that relationship is not confirmed by our investigation. On the other hand, the timing of second breeding is greatly influenced by spring weather parameters, as mentioned above, so comparing August data with the k_1 mortality factor of the second brood may not be adequate every year.

Our results cannot prove the presumed close correlation between any of the examined mortality factors (k_1 and k_4 factors) and mean small mammal biomass, although annual adult and juvenile mortality has been reported to be correlated with vole abundance (Hone & Sibly, 2002; Taylor, 1994). That strengthens the conclusion of other studies claiming that the composition and amount of available prey for barn owls can differ significantly from small mammal populations estimated by live trapping (e.g. Derting & Cranford, 1989; Dickman *et al.*, 1991) and pellet analysis may offer a much more suitable method for investigating prey abundance.

Among variables behind the key factor, it was mean snow depth and the number of months in which snow occurred that showed significant correlation with the studied factor. This result statistically confirms that the greatest difficulty the owls face in the winter period is snow cover, and especially breaking through the deep snow and the icy crust forming on top of it, which are serious obstacles to catching prey (Marti & Wagner, 1985; Shawyer, 1987). Due to hostile conditions, barn owls cannot build up considerable reserves in the form of fat, and thus starvation may last for one week (Handrich *et al.*, 1993). At the same time, we did not find any close relationship between winter temperature and the key factor. Although this cannot be confirmed by our investigation, the high cost of regulatory thermogenesis and limited hypothermia during fasting may also contribute to the high mortality of barn owls during winter periods (Thouzeau *et al.*, 1999). To reveal further details in the effects of each environmental parameter, partial correlation coefficients were calculated, with the influence of one variable always filtered off (Zar, 1996). As a result, significant correlations were found to exist between the k_4 factor and snow depth, when values of biomass, temperature or precipitation were regarded as constant. From this, it follows that winter snow depth in itself can determine mortality in winter and has the greatest influence on the key factor.

It is not necessarily only mortality resulting from unfavourable environmental conditions that can be behind k_4-factor, but migration can also play a role in creating changes of population size. However, to detect the impact of migration, a detailed analysis is needed (e.g. to determine the ratio of ringed vs. unringed individuals in the population each year); but no substantial amount of ringing data was available about the barn owl population breeding in nestboxes. Besides, a comprehensive investigation cannot be limited to research on nestbox breedings. For that reason, further studies are required to examine the whole population in the region, and continuous information also has to be gained about 'free-nesting' barn owls.

REFERENCES

Altwegg R., Roulin A., Kestenholz M., Jenni L., 2003 - Variation and covariation in survival, dispersal, and population size in barn owls, *Tyto alba*. J. Anim. Ecol., 72: 391-399.

Bank L., 1990 - Az 1985-86 évi gyöngybagoly- (*Tyto alba* Scop.) felmérés eredményei Baranya megyében. Aquila, 96-97: 113-126.

Bulmer M. G., 1975 - The statistical analysis of density dependence. Biometrics, 31: 901-911.

Derting T. L., Cranford J. A., 1989 - Physical and behavioural correlates of prey vulnerability to barn owl (*Tyto alba*) predation. Am. Midl. Nat., 121: 11-20.

Dickman C. R., Predavec M., Lynam A. J., 1991 - Differential predation of size and sex classes of mice by the barn owl, *Tyto alba*. Oikos, 62: 67-76.

Dobinson H. M., Richards A. J., 1964 - The effects of the severe winter of 1962/1963 on birds in Britain. Br. Birds, 57: 373-434.

Edwards T. C., 1987 - Standard rate of metabolism in the common barn owl (*Tyto alba*). Wilson Bull., 99: 704-706.

Exo K. M., 1992 - Population ecology of little owls *Athene noctua* in Central Europe: a review. *In*: C. A. Galbraith, I. R. Talylor, S. Percival & S. M. Davies (eds), The ecology and conservation of European owls. Edinburgh University, Edinburgh, pp. 64-75.

Frylestam B., 1972 - Movements and mortality of banded barn owls *Tyto alba* in Scandinavia. Ornis Scand., 3: 45-54.

Glue D. E., 1973 - Seasonal mortality in four small birds of prey. Ornis Scand., 4: 97-102.

Handrich Y., Nicolas L., Le Naho Y., 1993 - Winter starvation in captive Common barn-owls: Phisyological states and reversible limits. Auk, 110: 458-469.

Hone J., Sibly R. M., 2002 - Demographic, mechanistic and density-dependent determinants of population growth rate: a case study in an avian predator. Phil. Trans. R. Soc. Lond. Ser. B, 357: 1171-1177.

Ito Y., 1972 - On the methods for determining density-dependence by means of regression. Oecologia, 10: 347-372.

Juillard M., Beuret J., 1983 - L'aménagment des sites de nidification et son influence sur une population de chouettes effraies *Tyto alba*, dans le nord-ouest de la Suisse. Nos Oiseaux, 37: 1-70.

Kirsch E. M., 1996 - Habitat selection and productivity of least terns on the lower Platte River, Nebraska. Wildl. Monogr., 132: 5-48.

Krebs J. R., 1970 - Regulation of numbers in the great tit (Aves: Passeriformes). J. Zool. (Lond.), 162: 317-333.

Kuno E., 1973 - Statistical characteristics of the density-independent population fluctuation and the evaluation of density-dependence and regulation in animal populations. Res. Popul. Ecol., 15: 99-120.

Lens L., Wauters L. A., 1995 - Effects of population growth on crested tit (*Parus cristatus*) post-fledging settlement. Ibis, 138: 545-551.

Manly B. F. J., 1990 - Stage-structured populations: sampling, analysis and simulation. Chapman and Hall, London.

Marti C. D., 1994 - Barn owl reproduction - patterns and variation near the limit of the species distribution. Condor, 96: 468-484.

Marti C. D., 1997 - Lifetime reproductive success in barn owls near the limit of the species' range. Auk, 114: 581-592.

Marti C. D., Wagner P. W., 1985 - Winter mortality in Common barn-owls and its effect on population density and reproduction. Condor, 87: 111-115.

Mátics R., 2000 - A gyöbgybagoly (*Tyto alba*, Scop., 1769) mortalitása Magyarországon a gyűrűzési adatok tükrében. Aquila, 105--106: 125-133.

Percival S., 1992: Methods of studying the long-term dynamics of owl populations in Britain. *In*: C. A. Galbraith, I. R. Talylor, S. Percival & S. M. Davies (eds), The ecology and conservation of European owls. Edinburgh University, Edinburgh, pp. 39-48.

Ritter F., Görner M., 1977 - Untersuchungen über die Beziehung zwischen Futterungsaktivität und Beutetierzahl bei der Schleiereule. Der Falke, 24: 344-348.

Royama T., 1992 - Analitical population dynamics. Chapman and Hall, London.

Shawyer C. R., 1987 - The barn owl in the British Isles. Its past, present and future. The Hawk Trust, London.

Sibly R., Smith R. H., 1998 - Identifying key factors using λ contribution analysis. J. Anim. Ecol., 67: 17-24.

Taylor I., 1994 - Barn owls: predator-prey relationships and conservation. Cambridge University Press, Cambridge.

Thouzeau C., Duchamp C., Handrich Y., 1999 - Energy metabolism and body temperature of barn owls fasting in the cold. Physiol. Biochem. Zool., 72: 170-178.

Varley G. C., Gradwell G. R., 1960 - Key factors in population studies. J. Anim. Ecol. 29: 399-401.

Witt R., 1992 - Steinbachs grosser Naturführer, Vögel. Mosaik Verlag GmbH, München.

Zar J. H., 1996 - Biostatistical analysis. Prentice-Hall International Inc., New Jersey.

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