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Breeding density and success, and diet composition of Little Owls *Athene noctua* in steppe-like habitats in Portugal

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We studied the breeding density and success, and diet composition of Little Owls *Athene noctua* during 1997–1999 in a treeless pseudo-steppe and open woodland in Portugal. Breeding density was higher in the woodland area (7.0 pairs/km^2) than in the pseudo-steppe (2.5 pairs/km^2), probably due to greater availability of potential nest-sites. In the woodland, the number of owl pairs was higher in areas with intermediate tree density. The overall breeding success (yearly mean: 0.61–2.26 fledglings) and the proportion of vertebrates in the diet (1.5% of prey number) were lower than those in most studies in Central and Southern Europe. The overall breeding success per pair was higher in the woodland, although no obvious inter-area differences were found in the number of fledglings per successful pair. We suggest that a higher predation rate in the pseudo-steppe accounts for the higher proportion of failed nesting attempts. The body mass and breeding performance of owls was lower after a rainy winter and spring, but was not reduced in a dry year. Little Owls seem to be well adapted to the predominantly dry climate in these areas.

1. Introduction

Owl and raptor populations are generally limited by the availability of food and nest-sites (Newton 1979, Korpimäki 1992). Little Owls *Athene noctua* are small predators that nest in cavities and feed mainly on small mammals and invertebrates, hunting mostly at night and dusk (e.g., Génot & van Nieuwenhuyse 2002). The number and distribution of nest-sites and the availability of prey have been considered the main factors limiting the density of Little Owl populations across a large part of the species range (e.g., Loske 1986, Exo 1992, Bultot *et al.* 2001). Also weather has been shown to influence breeding success (Génot & van Nieuwenhuyse 2002).

In Europe, Little Owl populations have suffered a marked reduction during the last decades, mainly due to large-scale habitat changes associated with the intensification and mechanization of agriculture, which have in turn caused a reduction in prey and nest-site availability (Tucker & Heath 1994). In Central Europe, the Little Owl is a relatively well-studied species (e.g., Glue & Scott 1980, Exo 1992, Schönn *et al.* 1991). In the Mediterranean area, however, the species is still quite abundant and occurs in different habitats, but relatively little research has been conducted on it (Génot 2001b).

Pseudo-steppes of the Iberian Peninsula are relatively unique habitats in Europe (Valverde 1958), characterized by the extensive cultivation of cereals on a rotational basis, where climate is dry and soil productivity is low (cereal steppes; Suárez *et al.* 1997, Moreira 1999). Cereal steppes originated mostly from the clearance of native oak *Quercus* forests (Moreira 1999), and open oak woodlands in the same regions share most of the same steppe-like characteristics.

Our main objective was to study how the breeding density and breeding success of Little Owls varied in two types of steppe-like habitats in Portugal, and to assess which factors – weather, body condition, diet composition, prey and nest-site availability – could contribute to possible inter-annual and inter-area differences. In addition, we analysed basic ecological parameters of the studied populations in a European context.

2. Material and methods

2.1. Study areas

The study was conducted in two areas located 22 km apart within the Castro Verde region, Southern Portugal: São Marcos da Atabueira (37°42’ N, 7°50’ W) and Cabeça da Serra (37°37’ N, 8°09’ W). São Marcos da Atabueira is a treeless pseudo-steppe covering 16.8 km^2. Most of the area is occupied by pasture, while 15%–25% consists of cereal fields (Delgado & Moreira 2000). Cabeça da Serra comprises 6.1 km^2 and is mostly covered by open woodland of holm oaks *Quercus ilex rotundifolia*. Pastures cover most of the area and cereal fields cover a smaller proportion (5%–30%). In both areas, agriculture and livestock farming are carried out in traditional ways, maintaining a rotation between cereal fields and fallows used as pastures (Suárez *et al.* 1997, Moreira 1999). Climate is dry in the region, with the average annual precipitation under 600 mm. Nevertheless, marked inter-annual variation in rainfall may occur (e.g., 730 mm in 1997/98 and 180 mm in 1998/99; [DRAA 2000]). Temperature is mild in winter (monthly average ca. +11° C) and summers may be hot (monthly average over +25° C, with maximum values exceeding +40° C) (DRAA 2000).

2.2. Field work

2.2.1. Territories and density

The study areas were nearly continuously monitored between February and mid-August during 1997–1999. We mapped Little Owl territories on the basis of responses to playbacks, between February and April (Zuberogoitia & Campos 1998, Centili 2001), and from successive observations of individuals and their movements. Territory size was estimated based on observations of colour-marked birds and telemetry (A. Chumbinho & R. Tomé, unpubl. data).

Owls were captured using mist-nets, bal-chatri traps, a torch and a dip-net, and a baited trap. We measured the body mass and wing length of all captured adult owls. We also weighed all captured juveniles that were over the age of fledging (35 days; Génot & van Nieuwehuyse 2002; see also Juillard 1979).

To examine the relationship between the number of territories and the density of trees in the woodland area, we applied a grid to aerial photographs (scaled 1:15,000) to subdivide the area into plots of 20.25 ha. In each plot, we counted the number of trees (mostly oaks) and the number of Little Owl territories, based on the presence of known nests (Tomé et al. 2004) or territory centres (a tree or a group of trees where an owl pair had previously been frequently observed).

2.2.2. Breeding parameters

The depth and complexity of cavities used as nest sites (Tomé *et al.* 2004) hampered a meticulous inspection of nest chambers in most cases. Therefore, only a small number of complete clutches and laying dates could be confirmed during our study. In most cases, laying dates were estimated backwards based on known incubation times and the development of handled nestlings (Génot & van Nieuwehuyse 2002).

Breeding success was determined from the number of fledged young observed near the entrance of each nest. The detectability of successful nests is higher than that of unsuccessful nests, which might bias the determination of breeding success. For this reason, we randomly selected a sub-sample of territories to monitor in each area.

2.2.3. Precipitation and vegetation variables

Data on local monthly precipitation was obtained from a meteorological station located in Castro Verde, approximately half-way between study areas (SNIRH 2005).

Data on vegetation variables was obtained at 10 Little Owl territories randomly selected in each area (Tomé *et al.* 2004). The same territories were sampled in each year of the study. In each territory, vegetation characteristics were recorded from within eight sample-plots, located at 20 m and 40 m from the nest or territory centre in a north, south, east and west direction.

A sample quadrat of 50 cm x 50 cm was used within each plot to estimate the percentage cover of ground vegetation. A profile board with 8 horizontal bands was used to calculate the horizontal density of vegetation (Hays *et al.* 1981). We also calculated an Index of Vegetation Volume (IVV) for each sample plot by multiplying the% ground vegetation cover by the average horizontal density of vegetation.

2.2.4. Diet and prey availability

We collected Little Owl pellets between February and May 1998 in 10–15 territories in both study areas. Prey items in the pellets were identified in the laboratory to the lowest possible taxon. Values of prey biomass were taken from the literature (e.g., Franco & Andrada 1976, Adanez & Hontanilla 1983) and from other studies in the same region (M. Boieiro, unpubl. data).

Prey availability was estimated in June each year, in the same 10 territories sampled for vegetation in each area. To sample the availability of ground invertebrates, four pitfall traps were buried 20 m from the nest or territory centre to north, south, west and east directions. Pitfall traps were kept open during three nights plus a continuous 48-h period.

Additionally, we used a sweep-net to sample invertebrates in standing vegetation in the same territories. A series of ten sweeping movements was performed while walking from the pitfall trap location toward the north, south, east and west. For insect sampling methods, see e.g. Sutherland (1996).

The abundance of small mammals was sampled using snap-traps during the spring of each year. Eight traps were set per territory during four nights. Likewise, bird abundance was sampled during the spring of 1998, from 150-m linear transects crossing each territory.

2.3. Data analysis

The comparison of adult body mass between years and areas was done using only data on birds captured between February and April, before the laying period. Analysis of covariance (ANCOVA) was applied for this comparison, correcting the body mass for size by including wing length as a covariate (e.g., García-Berthou 2001). Juvenile birds were captured between June and August, but wing length was not used to adjust their body mass value because wing feathers were usually not fully grown by this time.

Vegetation measures taken from sample-plots were used to calculate mean values for each habitat (fallow or cereal field) that occurred within a sampled territory. Only one mean value of% vegetation cover, vegetation horizontal density and IVV were used for each habitat in each territory.

When analysing the availability of invertebrate prey, the samples obtained in each pitfall trap and associated sweep-net samples were combined. Therefore, four samples of invertebrate prey were used to calculate an average for each sampled territory. We only analyzed data for the main taxa of Coleoptera and Orthoptera consumed by Little Owls in the study areas (Table 3).

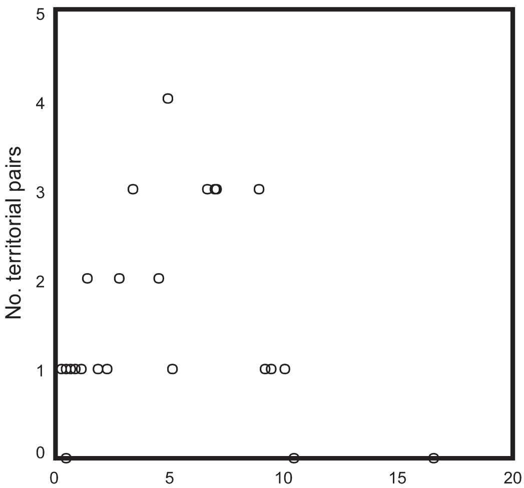

Fig. 1. Number of territorial pairs of Little Owls in relation to the density of oaks in sample plots (20.25 ha) in the woodland area.

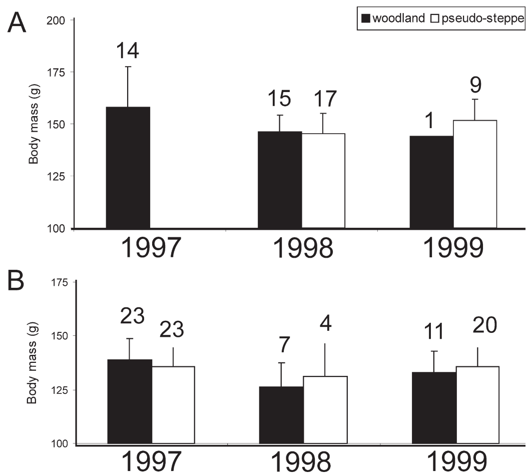

Fig. 2. Mean (± SD) body mass of (A) adult and (B) fledged juvenile Little Owls in the woodland and pseudo-steppe areas during 1997–1999. Numbers above bars show sample sizes.

Two-way ANOVA models were used to examine the similarity in body mass of juveniles, average IVV, insect prey availability and the number of fledglings in successful nests, between years and areas. The average IVV per habitat per territory was the only vegetation variable applied to models.

The effect of area and year on breeding success was analysed with a Generalized Linear Model (GLM) with a Poisson error term and log link function (R Development Core Team 2005). A logistic regression was used to evaluate the effect of area and year on the success of breeding attempts, i.e., comparing nests with at least one fledged juvenile to those with none (e.g., Hosmer & Lemeshow 1989).

Statistical tests were two-tailed and, if required, variables were log or square-root transformed to meet normality and variance homogeneity (Sokal & Rohlf 1981, Zar 1996). Means are presented with standard deviations.

3. Results

3.1. Density

The number of territorial pairs varied little between three years: 41 to 43 in the woodland and 39 to 42 in the pseudo-steppe. The density was higher in the woodland than in the pseudo-steppe (7.0 vs. 2.5 pairs/km^2). Interestingly, in the woodland a sub-area of 0.8 km^2 held 15 pairs (18.5 pairs/ km^2).

In the woodland area, the number of territorial pairs peaked in areas with an intermediate density of oaks (Fig. 1). A curvilinear model significantly explained this relationship ($r^2 = 0.37$, $F_{2,21} = 6.04$, $P = 0.008$) while a linear model did not ($r^2 = 0.00$, $F_{1,22} = 0003$, $P = 0.96$).

3.2. Body mass

The pre-breeding body mass of adult Little Owls differed among years but not between areas (Table 1), being highest in 1997, lowest in 1998 and intermediate in 1999 (Fig. 2). The same patterns were detected for the body mass of fledged juveniles (Table 1, Fig. 2).

3.3. Breeding success

Only 15 complete clutches were found throughout our study. The average clutch size was 3.3 ± 1.2 eggs (range from 1 to 5). Laying dates varied between 7 April and 3 May ($n = 32$; mean 19 April ± 1.3 days). The average laying date did not vary be-

Table 1. ANCOVA (*) and two-way ANOVA (other analyses) for the effects of year and area on Little Owl adult body mass, body mass of fledged juveniles, and number of fledglings per pair in successful nests, and the same models for the Index of Vegetation Volume (IVV) in fallows, and the abundance of Coleoptera and that of Orthoptera. Wing length was used as a covariate in the ANCOVA.

Dependent variable	Source of variation	df	MS	*F*	*P*
*Adult body mass	Year	2	951.77	7.76	0.001
	Area	1	0.05	0.001	0.98
	Year X Area	1	2.55	0.02	0.89
	Wing length	1	2000.48	15.31	<0.001
	Error	54	122.54		
Juvenile body mass	Year	2	321.56	3.29	0.04
	Area	1	36.55	0.37	0.54
	Year X Area	2	116.85	1.20	0.31
	Error	82	97.61		
No. fledglings/successful nests	Year	2	3.14	3.30	0.045
	Area	1	0.03	0.03	0.87
	Year X Area	2	0.11	0.11	0.90
	Error	52	0.95		
IVV	Year	2	100.40×10^4	11.24	0.08
	Area	1	17.79×10^4	1.98	0.28
	Year X Area	2	8.93×10^4	0.89	0.42
	Error	41	10.03×10^4		
No. Coleoptera	Year	2	12.13	5.49	0.007
	Area	1	12.32	5.58	0.02
	Year X Area	2	12.63	5.72	0.006
	Error	53	2.21		
No. Orthoptera	Year	2	3.45	1.29	0.29
	Area	1	23.75	8.84	0.004
	Year X Area	2	5.90	2.20	0.12
	Error	54	2.69		

tween the two areas ($F_{1,26} = 0.16$, $P = 0.69$) but was 5–8 days later in 1998 than in 1997 or in 1999 ($F_{2,26} = 2.85$, $P = 0.076$).

Breeding success was significantly higher in the woodland than in the pseudo-steppe ($Z = -2.20$, $P = 0.028$), and the number of fledglings per pair was significantly lower in 1998 than in 1997 or 1999 ($Z = -2.45$, $P = 0.014$; Fig. 3). In the analysis, using only successful breeding attempts, the number of fledglings per pair differed significantly among years but not between areas (Table 1).

The logistic regression indicated that the success of breeding attempts (at least one fledged juvenile) was influenced by area (Wald $\chi^2_1 = 6.13$, $P = 0.013$). In the same model, year had a marginally non-significant effect (Wald $\chi^2_2 = 5.51$, $P = 0.064$). The proportion of successful nests was higher in the woodland than in the pseudo-steppe in 1997 (87% vs. 42%) and in 1998 (55% vs. 28%). In 1999 this proportion was similar in both areas (54% vs. 56%). Hence, the lower breeding success in the pseudo-steppe was largely correlated with a higher proportion of unsuccessful nests in that habitat.

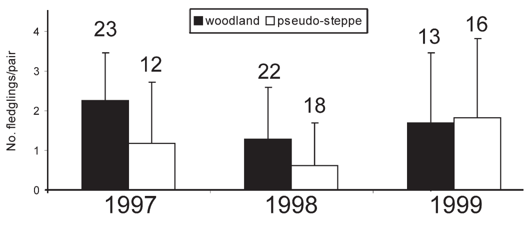

Fig. 3. Mean (± SD) breeding success (number of fledglings per pair) of Little Owls in the woodland and pseudo-steppe areas during 1997–1999. Numbers above bars represent sample sizes.

Table 2. Precipitation and Index of Vegetation Volume (IVV) in fallow and cereal fields in woodland and pseudo-steppe areas during 1997–1999 (mean ± SD, *n* = number of territories).

Precipitation (mm)				IVV				
Year	Oct–Mar	Apr	May	Year	Fallow	*n*	Crops	*n*
1996/97	410.9	80.9	32.0	1997	345.06 ± 251.82	18	565.42 ± 160.48	3
1997/98	571.8	25.4	66.9	1998	732.15 ± 450.92	16	1811.67 ± 1613.66	3
1998/99	130.8	5.5	0.5	1999	159.97 ± 155.91	13	573.86 ± 547.00	5

Table 3. Diet composition (% no. = percentage of prey items by number and% mass = percentage of prey items by mass) of Little Owls in the woodland and pseudo-steppe areas. For calculations of prey mass, see text. Invertebrate taxa identified to the level of O = order, SF = super-family and F = family.

	Woodland (*n* = 1,451)		Pseudo-steppe (*n* = 1,840)	
Taxon	% no.	% mass	% no.	% mass
Invertebrates				
O Coleoptera				
SF Scaraboidea	13.85	12.49	32.77	27.39
F Tenebrionidae	18.13	8.85	12.28	5.47
F Carabidae	8.06	4.92	4.02	2.24
Other/unidentified	3.93	2.12	5.76	2.25
Total Coleoptera	43.97	28.38	54.83	37.35
O Orthoptera				
F Gryllotalpidae	2.00	6.10	0.49	1.36
F Acrididae	7.24	11.30	9.51	13.57
F Tettigonidae	3.24	7.11	0.49	0.98
Other/unidentified	1.17	2.10	6.20	10.32
Total Orthoptera	13.65	26.61	16.69	26.23
Other invertebrates	40.93	11.04	27.23	13.50
Total invertebrates	98.55	66.03	98.75	77.08
Vertebrates				
Mammals	1.24	28.93	0.98	16.87
Birds	0.21	5.05	0.27	6.06
Total vertebrates	1.45	33.97	1.25	22.92
Total	100	100	100	100

3.4. Precipitation and vegetation growth

Precipitation values were high in the winter of 1997/98 and during May 1998, and lower during 1999 (Table 2). Vegetation growth in fallows of both areas reflected the inter-annual differences in precipitation (Table 2), and a significant year effect in the IVV was detected ($F_{2,44}$ = 12.63, P < 0.001). After accounting for the effect of year in a two-way ANOVA, the IVV values between the areas were similar (Table 1).

3.5. Diet composition and prey availability

Owls preyed mostly on invertebrates, mainly insects, in both study areas (Table 3). Beetles (Coleoptera) and grasshoppers and locusts (Orthoptera)

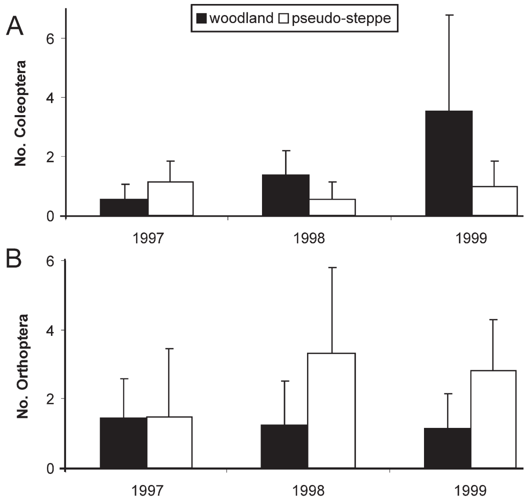

Fig. 4. Catches of (A) beetles (Coleoptera) and (B) grasshoppers (Orthoptera) captured using pitfall traps and sweep-net series in the woodland and pseudo-steppe areas during 1997–1999. Values are means (± SD) calculated from 10 sampled owl territories per each area (see text).

were the most abundant prey, whereas earwigs (Dermaptera) and ants (Hymenoptera, Formicidae) were also numerous. Vertebrates (mostly mice *Mus* spp. and *Apodemus sylvaticus*, and passerines) were less abundant. In terms of biomass, Coleoptera, Orthoptera and vertebrates produced similar contributions (Table 3). The abundance of Coleoptera and Orthoptera differed among years and between the two areas (Table 1, Fig. 4).

Only 17 small mammals were captured in the three-year study period, mostly in the pseudo-steppe. The number of birds counted along transects also did not differ significantly between the pseudo-steppe and the woodland areas (9.8 ± 6.1 and 20.9 ± 20.1 birds per transect, respectively; $t = 1.66$, $P = 0.11$, $n = 20$).

4. Discussion

4.1. Breeding success and diet in steppe-like habitats

In Central Europe, Little Owls are mainly associated with edge habitats of woodland and open areas, and mosaic-like landscapes (e.g., Dalbeck *et al.* 1999, van Nieuwehuyse *et al.* 2001), whereas in Iberia they occupy vast areas of fairly homogeneous biotopes (e.g., Martínez & Zuberogoitia 2004), including steppe-like areas. In the open woodland, we found one of the highest densities of territorial pairs reported in Europe (7.0 pairs/ km^2). Higher densities have only been recorded in small study areas (up to 1 km^2) in Central Europe (Exo 1988, Coppée *et al.* 1995) or by using a different estimation method in southern Iberia (Fajardo *et al.* 1998). In the pseudo-steppe, the density of Little Owls (2.5 pairs/km^2) was also among the highest values found in Europe (Fuchs 1986, Génot & van Nieuwehuyse 2002).

In our study, clutch size (average 3.3) was smaller than in many other Central and Eastern European countries (e.g., Glue & Scott 1980, Schönn 1986, Exo 1992). Our sample for the estimation of this parameter, however, was rather small. Although there might be a geographical gradient in clutch size among Little Owls, for example an increase from oceanic to continental climate (Génot 1992) or from western to eastern Europe (Génot & van Nieuwehuyse 2002), the complexity in establishing a pattern due to density-dependent effects (Bultot *et al.* 2001) hampers the conclusion that low clutch sizes and numbers of fledged young in our study areas are a consequence of geographical variation.

The number of fledged young per breeding pair in our study areas varied between 0.6 and 2.3 and was lower than those reported in the majority of studies from Central Europe; for example, 2.4 (Furrington 1998), 2.7 (Gassman & Bäumer 1993), 2.4 (Bultot *et al.* 2001) and 2.8 (Génot 1992). This poorer breeding success could be a consequence of smaller clutches, because the failure rate seems to be similar in our study areas and in Central Europe (e.g., Juillard 1984, Génot & van Nieuwehuyse 2002).

As with other sites in Iberia (e.g., Delibes *et al.* 1983, Mañez 1983), invertebrates – mostly insects – dominated the diet of Little Owls in our study areas whereas remains of small mammals were scarce in our pellet samples, probably reflecting low availability. The relative importance of vertebrates in the diet of Little Owls was lower in our study areas than in most other study areas in Southern and Central Europe (e.g., Delibes et al. 1983, Mañez 1983, Génot & Bersuder 1995, Génot & van Nieuwehuyse 2002).

4.2. Breeding density and performance in woodland and pseudo-steppe areas

Apart from differences in the presence of trees, both pseudo-steppes and open holm oak woodlands shared important environmental features. These included climate, landscape structure and the main form of land-use. Vegetation growth was similar, as was prey availability. Beetles, grasshoppers and locusts were abundant, while vertebrate prey, particularly small mammals, were scarce.

Despite these similarities, the breeding density and breeding success of Little Owls was higher in the woodland area than the pseudo-steppe. The difference in breeding density was probably associated with higher nest-site availability in the wooded area, where Little Owls nested mostly in oak cavities (Tomé *et al.* 2004). In the pseudo-steppe, trees were practically absent and the owls used stone piles as nest sites. Suitable cavities for nesting may be 1.9 times more numerous in the woodland than in the pseudo-steppe (Tomé *et al.* 2004).

Also intra-area differences may have contributed to a higher breeding density within the woodland area, as the peak owl density was recorded in plots with an intermediate density of oaks. The density of trees was not related to tree height or girth (R. Tomé, unpubl. data). However, plots with higher tree density produced a higher number of cavities per tree, although these plots still represented open woodland (Fig. 1). We suggest that the lower density of Little Owls in plots with higher tree density may be due to predation risk. An avoidance of forests and forest edges by the owls has been interpreted as being a response to the presence of a woodland predator, the Tawny Owl *Strix aluco* (Schönn 1986, Zuberogoitia 2002). In our study area, Tawny Owls are absent and the main predators of Little Owl nests are mammals, such as the Stone Marten *Martes foina* (see also Génot 2001, Schönn *et al.* 1991) and the Common Genet *Genetta genetta* (Tomé *et al.* 2004). These predators seek shelter in tree cavities and seem to be more frequent in areas with higher tree density, as indicated by the fact that we found several stone martens and genets roost in nest-boxes only in the densest wooded areas.

Food abundance can also explain the differential distribution of breeding density of owls. Nonetheless, we found no obvious indication that prey abundance was higher in plots with an intermediate density of trees, as compared with more open or densely wooded plots.

Differences in breeding success between habitats were probably not due to prey abundance or body condition for adult and fledged juvenile owls, which were similar in both areas. Moreover, breeding success of successful pairs did not vary between areas. A difference in predation rate might have been the main cause explaining why a larger proportion of nests in the pseudo-steppe failed to raise any young (see also Tomé et al. 2004).

4.3. Precipitation and breeding success

During our three-year study, annual precipitation varied considerably. Precipitation during the wet winter and spring of 1997/98 seemed to influence the body mass and breeding performance of Little Owls: adults were lighter during the pre-laying period, laying dates tended to be later, and also breeding success and fledgling condition were relatively poor.

Other studies on Little Owl have reported increased nestling mortality to be associated with rainy periods (Glutz & Bauer 1980, Finck 1988; see also Bultot *et al.* 2001). Long rainy periods decrease the activity of some types of prey, particularly insects, and make prey detection difficult, thus probably reducing hunting success. May 1998 was rather wet in comparison to other years (Table 2), and this difference could be responsible for the low breeding output and the low body mass of fledged juveniles recorded by us. Likewise, the rainy winter of 1997/98 could have reduced the probability of prey capture for adult birds before the breeding season, leading to the low body reserves reported here, with potential repercussions in breeding performance.

Contrary to what happened in the rainy year of 1998, the body mass of both adult and fledged juvenile owls, and their reproductive output, was not negatively affected by dry conditions in 1999. A study on the Lesser Kestrel *Falco naumanni*, a species that shares a similar invertebrate diet as the Little Owl (e.g., Rocha 1998), also reported a lower fledging success after the rainy spring of 1998 and a higher performance following the drier spring of 1999 in Southern Spain (Ferrero *et al.* 2001).

4.4. Conclusions

Open holm oak woodlands and cereal pseudo-steppes apparently hold high breeding densities of Little Owls and are thus important for the species' conservation in Europe. The traditional land-use management practiced in this area, creates a large number of suitable nest sites that are the basis for these high breeding densities. Breeding density was higher in the open woodland, where the availability of nest sites was greater than in the pseudo-steppe. In the more densely wooded areas, however, the owl density was lower, possibly due to a higher risk of predation by mammals.

Precipitation is highly variable in Southern Iberia. Despite the fact that water is often considered a critical limiting ecological factor in this region (Blondel & Aronson 1999), the body condition and breeding success of Little Owls was higher in the dry year of 1999. This result suggests they are well adapted to the predominantly dry Mediterranean climate, which is in some aspects similar the steppes and semi-deserts of the primary habitats in which the species may have evolved (Exo 1992).

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Minervanpöllön pesimäkannan tiheys, pesimämenestys ja ravinto aromaisissa ympäristöissä Portugalissa

Selvitimme minervanpöllön *Athene noctua* pesimäpopulaation tiheyttä ja pesimämenestystä Portugalissa 1997–1999 tutkimusalueella, joka koostui puuttomasta, aromaisesta alueesta sekä avoimesta metsämaasta. Tiheys oli korkeampi metsämaalla (7,0 pr/km^2) kuin aromaisella alueella (2,5 pr/km^2) luultavasti pesimäpaikkojen suuremman tarjonnan vuoksi. Paritiheys oli korkeampi tiheäpuustoisissa kuin keskitiheää puustoa kasvavissa metsäalueen osissa. Koko tutkimusalueen pesimämenestys (vuotuinen keskiarvo 0,61–2,26 lentopoikasta) ja selkärankaisten osuus pöllöjen ruokavaliossa (1,5 % saalisyksilöistä) olivat alempia kuin useimmissa muissa keski- ja eteläeurooppalaisissa tutkimuksissa.

Parikohtainen pesimämenestys oli korkeampi metsä- kuin aromaisella alueella, joskaan alueiden parikohtaiset lentopoikasmäärät eivät eronneet merkittävästi. Luultavasti korkeampi pöllöihin kohdistuva saalistuspaine aromaisella kuin metsäalueella selittää epäonnistuneita pesintöjä. Pöllöjen massa ja pesimämenestys olivat alhaisempia sateisen talven ja kevään jäljiltä, mutta kuivalla vuodella ei todettu samanlaista vaikutusta. Minervanpöllöt ovat erinomaisesti sopeutuneet näiden alueiden etupäässä kuivaan ilmastoon.

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