Influence of Perch Height and Vegetation Structure on the Foraging Behaviour of Little Owls Athene noctua: How to Achieve the Same Success in Two Distinct Habitats

Authors: Tomé, Ricardo, Dias, Maria P., Chumbinho, Ana Cláudia, and Bloise, Carolina

Influence of perch height and vegetation structure on the foraging behaviour of Little Owls *Athene noctua*: how to achieve the same success in two distinct habitats

Ricardo Tomé[1,2,*], Maria P. Dias[3,4], Ana Cláudia Chumbinho[5] & Carolina Bloise[6]
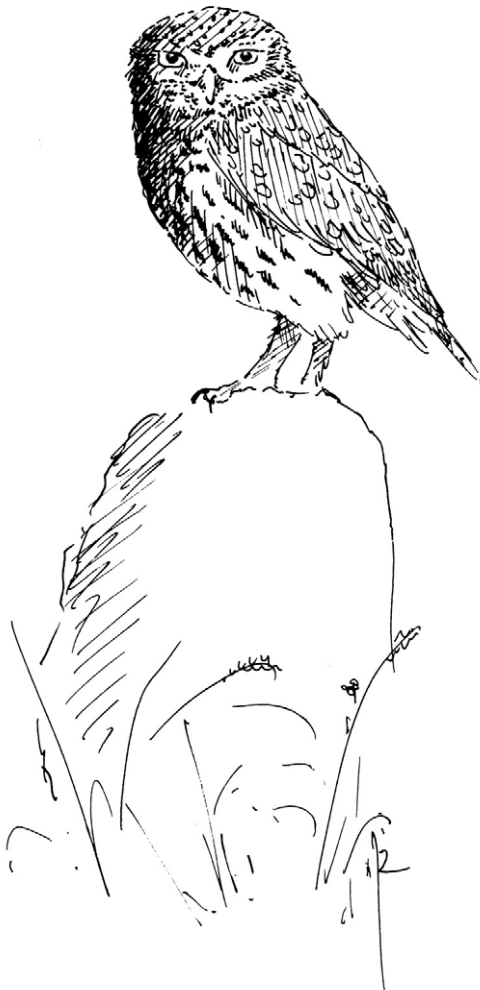
We compared the diurnal hunting behaviour of a mainly perch-hunting species, the Little Owl *Athene noctua*, in two structurally different habitats: a treeless pseudo-steppe and a Holm Oak *Quercus ilex rotundifolia* woodland in Portugal. While the overall prey availability was similar, perch and vegetation characteristics differed between habitats. Using focal sampling in 29 territories, we measured the type and height of utilized perches, time spent on perches and attack and giving-up distances involved in insect hunting. Moreover, we analysed the interrelationships between behaviour and habitat-specific vegetation characteristics. Little Owls adapted their hunting strategies to habitat features, achieving similar prey detection rates and the same hunting success in the two habitats. In the pseudo-steppe, where only low stone piles were available as perches, owls selected the highest spots (average 0.77 m). In this area, a positive correlation was found between perch height and distance to prey attacked, indicating that perching higher resulted in increased prey detectability. In the woodland, owls selected perches that were lower than maximally available (averages 2.67 m vs. 4.99 m, respectively). Attack distance did not differ between habitats, despite the use of higher perches in the woodland. These results indicate that the more developed ground vegetation in the woodland possibly hampered detection of prey, counterbalancing the possible advantages for prey detection due to the use of higher perches. In such situations, Little Owls seemed to select an intermediate foraging height to maximize prey detectability.

Key words: foraging behaviour, hunting success, optimal search height, visual detection, acoustic detection

[1]Section of Ecology, Department of Biology, University of Turku, FIN 20014 Turku, Finland; [2]STRIX, Tagus Space, Ed. Galileo, 1º B, 2740-278 Porto Salvo, Portugal; [3]Eco-Ethology Research Unit, ISPA, Rua Jardim do Tabaco 34, 1149-041 Lisboa, Portugal; [4]Museu Nacional História Natural, Universidade de Lisboa, Rua da Escola Politécnica 58, 1250-102 Lisboa, Portugal;
[5] Rua Nobrega e Sousa, 9D, 4E. 1750-407 Lisboa, Portugal; [6] Rua Barbosa do Bocage, 31 Lourel. 2710-353 Sintra, Portugal;
*corresponding author (ricardo.tome@strix.pt)

Foraging behaviour is expected to be adjusted to the type and distribution of prey, to habitat characteristics and, consequently, to the resulting accessibility and vulnerability of prey (Andersson 1981, Fitzpatrick 1981, Widén 1994, Quinn & Cresswell 2004). As prey detection is constrained by the ability of an animal to use different types of sensorial information (Ali 1978, Rice 1983), differences in hunting behaviour are expected depending on whether predators use visual or acoustic signals to detect their prey (Andersson 1981, Rice 1983, Bye *et al.* 1992, Andersson *et al.* 2009).

Choice of perch height is one the main aspects of foraging behaviour in predators that adopt a perch-hunting strategy (e.g. Andersson 1981, Fitzpatrick 1981, Rice 1983, Thiollay & Clobert 1988, Andersson *et al.* 2009). Perch height is particularly important in the

case of species that use mostly visual cues to detect their prey. In general, a higher perch renders a larger field of view allowing the detection of more distant prey (Greig-Smith 1983, Moreno 1984, Thiollay & Clobert 1988, Sonerud 1992; see also Andersson 1981). If more distant prey can be caught, then the resulting increase in detectability results in increasing prey availability (Gillings 2004) and in an increased likelihood of finding and attacking prey (Andersson 1981, Rice 1983, Sonerud 1992).

Predators foraging from higher perches are expected to take longer before launching an attack or giving up and moving to another perch. This is due to the time required to search a greater detection area and also to compensate for a reduction in detection intensity (i.e. the predator's probability of discovering prey in a given area) due to increased distance to prey (Andersson 1981, Fitzpatrick 1981, Moreno 1984). In addition, a predator abandoning a perch to move to another should travel far enough to leave the field of view already searched. Therefore, in this situation the distance between perches (giving-up distance) is expected to correlate positively with perch height (Andersson 1981, Fitzpatrick 1981, Moreno 1984).

In open habitats, prey visibility depends on predator perch height and distance, but also on vegetation height and on prey stature (Thiollay & Clobert 1988, Andersson et al. 2009). For instance, vegetation characteristics may be of critical importance when prey is much smaller than surrounding vegetation. In this case, vegetation may conceal prey completely, turning it visible only from almost directly above, irrespectively of perch height (Andersson et al. 2009).

The Little Owl *Athene noctua* is a perch-hunting small owl that occurs in open and semi-open habitats, where it feeds mainly on insects and small mammals (Van Nieuwenhuyse *et al.* 2008). The method of hunting it uses is related to the type of vegetation and prey (Schönn *et al.* 1991) and may consist of running or hopping on the ground (Exo 1991, Schönn *et al.* 1991) or, more frequently, in perch-hunting (Fajardo *et al.* 1998), using a 'perch and pounce' (Génot & Van Nieuwenhuyse 2002) or pause travel (*sensu* Andersson 1981, Bye *et al.* 1992) technique. Hunting occurs predominantly in twilight and at night (Exo 1989, Schönn *et al.* 1991, Van Nieuwenhuyse *et al.* 2008), but Little Owls may also hunt in daytime, especially during the breeding season (Negro *et al.* 1990). Little Owls often seem to hunt by sight rather than by hearing (Ille 1983, Norberg 1987, Van Nieuwenhuyse *et al.* 2008), although information on this subject is scarce. Likewise, there is a lack of information on how Little Owls adapt

their strategy to the foraging conditions of the habitat and how this affects hunting success (Van Nieuwenhuyse *et al.* 2008).

In this study we investigated how Little Owls adapt their foraging behaviour to habitat structure by comparing their strategies in two different areas – a pseudo-steppe and a woodland. In particular, we examined if (1) increased perch height resulted in higher prey accessibility rendering higher hunting success, and (2) the structure of vegetation affected the hunting behaviour of Little Owls.

METHODS

Study areas

The study was conducted in two areas located 22 km from each other, in the Baixo Alentejo province, Southern Portugal: São Marcos da Atabueira (37°42' N, 7°54' W) and Cabeça da Serra (37°37' N, 8°09' W). São Marcos da Atabueira comprises 16.8 km² of a treeless pseudo-steppe, used for pastures or cereal cultivation. Stone piles are frequent all over the area and they are used both as nesting sites (Tomé *et al.* 2004) and as hunting perches by Little Owls. Density of Little Owls is 2.5 pairs/km² (Tomé *et al.* 2008). Cabeça da Serra covers 6.1 km² and is mostly occupied by open (16.5 trees/ha) to very open (0.25 trees/ha) woodland/parkland of Holm Oaks *Quercus ilex rotundifolia* (Tomé *et al.* 2008). The area is also used for pastures or cereal cultivation and a small part is covered by a young forestation of Stone Pine *Pinus pinea*. The density of Little Owls in this area is high, reaching 7 pairs/km² (Tomé *et al.* 2008). Both study areas are included in the proposed network of Vital Sign monitoring areas for evaluating population trends and key habitat components for Little Owls (Van Nieuwenhuyse *et al.* 2008).

In both areas, agriculture and cattle farming are carried out in traditional ways, maintaining a rotation every 4–5 years between cereal fields and fallows used as pastures (Suárez *et al.* 1997, Moreira 1999). During the period of the study, 86% of the Little Owl territories in the pseudo-steppe were mostly occupied by fallows. In the woodland fallow was the dominant habitat in 67% of the territories, while the remainder was mostly young forestations or cereal crops.

In the region, the climate is dry, with an average annual precipitation of less than 600 mm (DRAA 2000). The temperature is mild in winter (monthly average c. 11°C) and summers are hot (monthly average over 25°C, with maximum values exceeding 40°C; DRAA 2000).

Behavioural observations

We searched for Little Owls during daytime (approximately 1 h after sunrise until sunset) by monitoring the study areas several days a week between January and early August 1999. We made car transects that fully covered both areas, stopping periodically at strategic points, from which we surveyed the area to locate Little Owls, using binoculars and telescope. When we detected an owl that was actively hunting, we started a 40-min period of continuous observation ('focal animal sampling'; Altmann 1974, Martin & Bateson 1993). Observations were made from a minimum distance of 30 m to a maximum of several hundred meters. Each focal period began after the owl perched following an attack (irrespectively of its success). When the owl abandoned a perch due to disturbance (caused by raptors or people) or changed its behaviour (roosting, preening, singing), the sampling period was not considered in the analyses.

Little Owl territories were thoroughly mapped during a parallel study using playbacks (Zuberogoitia & Campos 1998, Centili 2001), individual continuous observations and colour-ringing (Tomé *et al.* 2008). Focal observation periods were obtained in fourteen and fifteen territories in the pseudo-steppe and in the woodland areas, respectively. Most (66%) of these periods were collected during the breeding season (April–June). The prey taken during observations were invertebrates, which are the main prey of Little Owls (by number and mass), in our study areas (Tomé *et al.* 2008).

During the observation periods, we measured detection and giving-up times (Bye *et al.* 1992) to the nearest second. Detection times corresponded to the period spent on a perch before an attack, and giving-up times corresponded to the period spent on a perch before abandoning it and moving to another. The success of each attack was also recorded. We assumed that the sampled periods were dedicated to hunting, as owls were exposed and they actively scrutinized the ground.

After each observation period, we measured the heights of used perches (Hays *et al.* 1981) and distances flown by the owls to the nearest cm. Perches were classified as detection perches (from which an attack was launched; *sensu* Carlson 1985, Bye *et al.* 1992) or giving-up perches (perches abandoned for other perches, without an attack; *sensu* Andersson 1981, Moreno 1984, Bye *et al.* 1992). We considered any structure used by the owls as an individual perch (i.e. different branches of the same tree were considered as different perches), except when mentioned differently.

Habitat variables

For each focal observation period we also determined: the average percentage of vegetation coverage, estimated from three $1 m^2$ squares randomly distributed throughout the area where attacks took place; and the average vegetation height, estimated from measurements of the plants nearest to the corners of the same squares (Thiollay & Clobert 1988). An Index of Vegetation Cover (hereafter IVC; Thiollay & Clobert 1988) was determined for each sample plot by multiplying the % vegetation cover by the average vegetation height.

To estimate perch availability and the average available perch height in each area, we randomly selected ten Little Owl territories and measured the height of all perches ≥50 cm (considering each structure, tree or stone pile, as one perch) present in a 100 m radius area around the nest or territory centre (Tomé *et al.* 2004). In order to compare differences in vegetation between areas, we sampled vegetation features in the same twenty territories. Measurements were made in late June/early July from within eight sample-plots, located at 20 m and 40 m from the nest or territory centre in the four cardinal directions (Tomé *et al.* 2008). Vegetation cover and height were estimated from a 50 cm × 50 cm sample quadrate within each sample plot, together with IVC (see above).

The same territories were sampled in June to estimate invertebrate availability, following procedures described by Sutherland (1996). Four pitfall traps were buried 20 m from the nest (or main roost) to north, south, west and east directions. The traps were kept open during three nights and an additional continuous 48 h period. Sweep-netting was used to sample invertebrates in standing vegetation: a series of ten sweeping movements was performed while walking from the pitfall trap location toward north, south, west and east.

Data analysis

Habitat variables (perch and vegetation characteristics and prey availability) in the territories in both study areas were compared by Mann–Whitney U-tests. When analysing the availability of invertebrates, the samples obtained in each pitfall trap and associated sweep-netting were combined. Hence, four samples of invertebrate prey were used to calculate an average for each territory. In the present study we only analyzed data for Coleoptera (beetles) and Orthoptera (grasshoppers and locusts), the main invertebrate taxa consumed by Little Owls in both study areas, representing more than 60% of consumed prey items (Tomé *et al.* 2008).

In comparisons involving focal sampling we used average values for each variable calculated from all measurements made during the same focal period per territory. The comparisons of the use of different perch types by the owls with those available in random territories were made with Chi-square and likelihood ratio tests. Differences in the number and height of perches and in variables associated with hunting success between areas or between samples from focal observations and random territories were tested by Mann–Whitney U-test or *t*-test.

For comparisons between detection vs. giving-up variables within the same habitat we used paired tests per territory (Wilcoxon test), whereas Mann–Whitney tests were used in inter-area comparisons. In these comparisons we only analyzed territories where both attack and giving-up behaviours were observed during focal periods ($n = 13$ in the pseudo-steppe and $n = 14$ in the woodland). Spearman correlations were used to test for relationships between behavioural variables (perch height and attack distance). Multiple linear regressions were used to investigate the relationships between vegetation characteristics (vegetation height, vegetation cover and IVC) and behavioural variables.

To analyze how the behaviour of owls varied in detection and giving-up perches, we calculated the 'survivorship' plots of perch times (Moreno 1984, Bye *et al.* 1992), which represent the variation in the proportion of birds that remain on a perch as search time increases. Means are presented with standard errors. Statistical tests were two-tailed and all analyses were performed using R statistical software (R Development Core Team 2009).

RESULTS

Habitat characteristics
In the pseudo-steppe, most of the available perches were stone piles (51%) and fence poles (49%), whereas in the Holm Oak woodland trees were dominant

Table 1. Perch abundance and height, vegetation characteristics and prey availability in randomly selected territories in pseudo-steppe ($n = 10$) and woodland ($n = 10$) areas (mean ± SE).

	Pseudo-steppe	Woodland	Mann–Whitney test	
			U	P
Number of perches (per ha)	6.21 ± 2.48	6.46 ± 1.46	33	ns
Maximum height of perches (m)	0.90 ± 0.20	4.99 ± 1.20	0	< 0.001
Vegetation height (cm)	7.16 ± 1.32	15.43 ± 2.33	13	< 0.01
Index of vegetation cover	3.78 ± 0.77	7.52 ± 0.92	14	< 0.01
Vegetation cover (%)	54 ± 1.9	73 ± 1.5	62	ns
Number of Coleoptera (caught individuals per territory)	3.90 ± 1.07	14.10 ± 1.28	15.5	< 0.01
Number of Orthoptera (caught individuals per territory)	11.20 ± 1.90	4.50 ± 1.28	15.5	< 0.01

Table 2. Comparison between detection and giving-up hunting behaviour in pseudo-steppe (number of territories = 13) and woodland ($n = 14$) (mean ± SE).

	Detection/attack				Giving-up			
	Pseudo-steppe	Woodland	Mann–Whitney test		Pseudo-steppe	Woodland	Mann–Whitney test	
			U	P			U	P
Perch height (m)	1.00 ± 0.10	2.79 ± 0.27	8	<0.001	0.68 ± 0.08	2.91 ± 0.16	0	<0.001
No. of movements (per 40 min)	5.77 ± 0.86	5.64 ± 1.12	100	ns	5.31 ± 1.08	6.71 ± 1.02	68.5	ns
Time on perch (min)	4.57 ± 0.62	3.11 ± 0.55	49	<0.05	1.65 ± 0.36	2.60 ± 0.47	54	ns
Distance (m)	10.90 ± 1.41	11.08 ± 1.47	90	ns	9.41 ± 3.14	10.99 ± 1.86	63	ns
					[a]20.51 ± 8.02	[a]20.48 ± 3.28	46	ns

[a]Perches within a structure are treated as one unit (all branches of a tree correspond to the same perch).
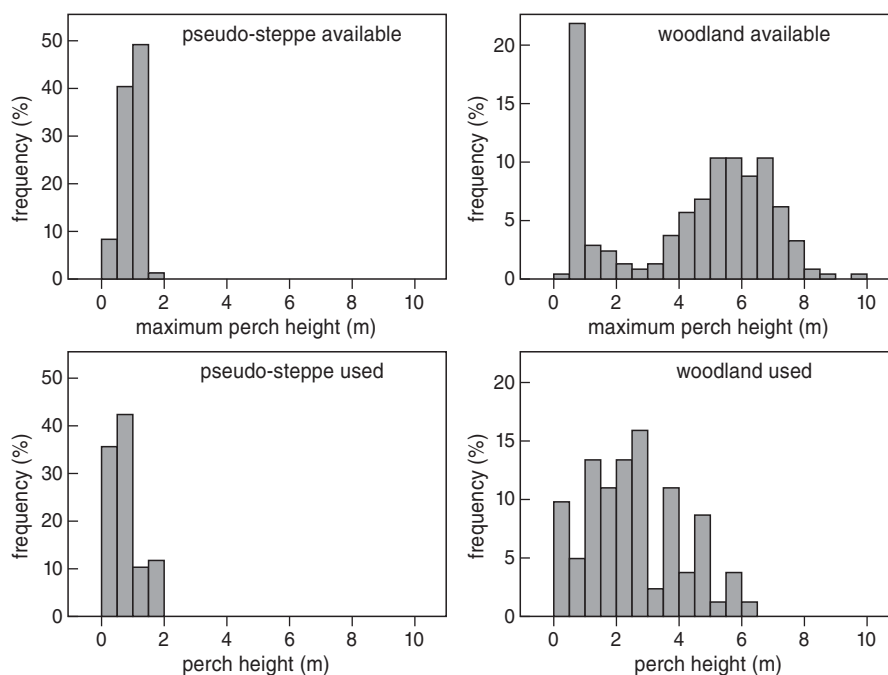
Figure 1. Distribution of perch heights utilized by Little Owls during focal sampling (pseudo-steppe: *n* = 14; woodland: *n* = 15 territories) and available in randomly selected territories in the pseudo-steppe (*n* = 10) and woodland (*n* = 10).

(80%), followed by fence poles (15%) and stones (3%). As a consequence, the maximum height of available perches was five times higher in the woodland than in the pseudo-steppe (Table 1). Despite this difference in the type of perches, the density of perches was similar in both habitats (Table 1).

Pseudo-steppe and woodland differed in both the vegetation (which was higher and denser in the woodland) and the availability of invertebrates. Coleoptera (beetles) were more abundant in woodland, and Orthoptera (grasshoppers and locusts) in pseudo-steppe (Table 1).

Hunting behaviour by habitat

PERCH CHARACTERISTICS AND MOVEMENTS

In the pseudo-steppe, Little Owls perched exclusively on stone piles, which were preferred above the equally available fence poles (χ^2 = 46.51, *df* = 1, *P* < 0.001). In the woodland, owls used trees as hunting perches in proportion to their availability (72%), whereas stones were used more often (12.5%) than expected (likelihood ratio = 10.77, *df* = 3, *P* < 0.05).

The number of movements during each 40 min focal sample did not differ between habitats (Table 2), and within each habitat the number of attack and giving-up movements were similar (Table 2).

Perches used in pseudo-steppe were significantly lower than those used in the woodland (pseudo-steppe: 0.77 ± 0.06 m; woodland: 2.67 ± 0.19 m; Mann–Whitney *U* = 0, *P* < 0.001; Fig. 1), which was also the case for attack and giving-up perches separately (Table 2). In the woodland, Little Owls used perches lower than the average of those available (2.67 ± 0.19 m vs. 4.99 ± 1.20 m; *t* = 4.73, *P* < 0.0001; Fig. 1). In pseudo-steppe, detection perches were higher than giving-up perches (Wilcoxon-test *V* = 79, *P* < 0.05), a difference that was not found in woodland (Wilcoxon-test *V* = 46, *P* > 0.05; Table 2).

DETECTION AND GIVING-UP TIMES

Survivorship curves of residence time on perches showed shorter giving-up times than detection times in the pseudo-steppe (significant difference between slopes; *P* < 0.001), whereas no difference was found in woodland (Fig. 2; see also Table 2). Giving-up times were shorter in the pseudo-steppe than in the woodland, while the opposite occurred with detection times (*P* < 0.001; Fig. 2).

ATTACK AND GIVING-UP DISTANCES

We did not find any differences in attack or giving-up distances between habitats (Table 2). In both habitats,
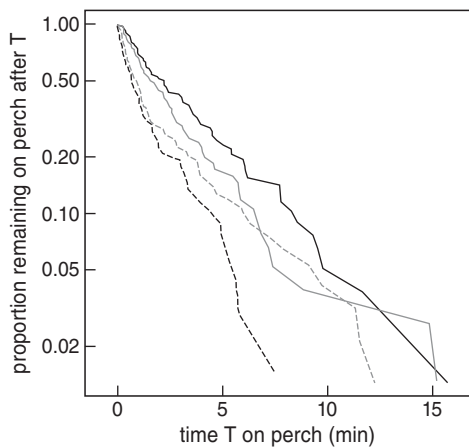
Figure 2. 'Survivorship' plots of perch times in the pseudo-steppe and woodland. Dark lines: pseudo-steppe; grey lines: woodland. Solid lines: detection times; dashed lines: giving-up times. Detection and giving-up times were pooled from all focal sampling periods (pseudo-steppe: $n = 78$ and 68, respectively; woodland: $n = 76$ and 94, respectively). The y-axis is represented on a logarithmic scale.

the average giving-up distance between structures (considering trees or stone piles as a unit) was almost twice as long as the average attack distance.

There was a positive correlation between perch height and attack distance in the pseudo-steppe, but not in the woodland (Fig. 3). No correlation was found between perch height and giving-up distance in pseudo-steppe ($r_S = 0.14$, $P > 0.05$) and in woodland ($r_S = -0.14$, $P > 0.05$).

Hunting success

We found no between-habitat differences in the number of prey capture attempts, the prey capture rate and, consequently, in hunting success (expressed as the percentage of successful capture attempts; Table 3).

Hunting behaviour and vegetation

In the pseudo-steppe, we found that perch height decreased with increasing vegetation height. In the woodland, vegetation cover had a negative effect on attack distance (Table 4).
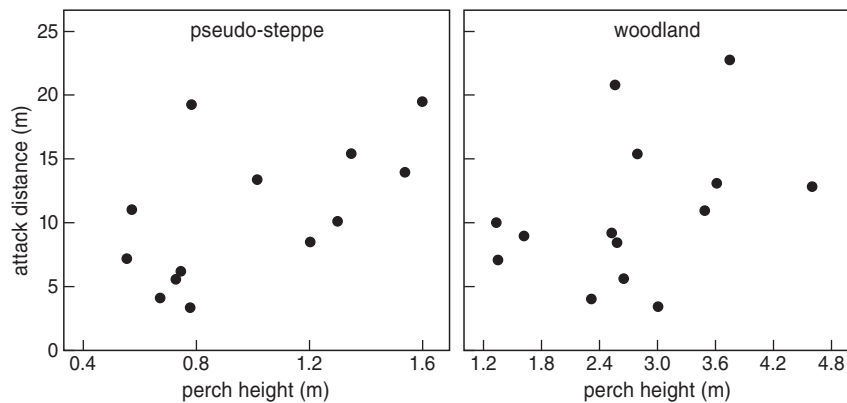

Figure 3. Relationship between perch height and attack distance in the pseudo-steppe ($n = 13$) and woodland ($n = 14$) areas; pseudo-steppe: $r_s = 0.65$, $P < 0.05$; woodland: $r_s = 0.43$, ns.

Table 3. Hunting success of Little Owls in pseudo-steppe ($n = 13$) and woodland ($n = 14$) areas (mean ± SE).

	Pseudo-steppe	Woodland	Mann–Whitney test	
			U	P
Prey capture attempts (per hour)	8.65 ± 1.34	8.46 ± 1.68	100	ns
Prey capture rate (per hour)	4.50 ± 0.83	3.86 ± 0.91	81.5	ns
Success (prey/attempt; %)	60.8 ± 8.6	66.5 ± 7.9	81.5	ns

DISCUSSION

Our results show that Little Owls attained a similar hunting success in two structurally distinct habitats, a treeless pseudo-steppe and a Holm Oak woodland. Little Owl territories in the woodland provided generally higher perches, along with higher and denser ground vegetation, than in the pseudo-steppe. The abundance of the main invertebrate groups of prey was also different, as Orthoptera were more numerous in the pseudo-steppe and Coleoptera in the woodland.

Theory predicts that for predators that use perch hunting, perch height is of great importance, as the use of higher perches should generally result in increased prey detectability and availability (Andersson 1981, Rice 1983, Thiollay & Clobert 1988, Andersson *et al.* 2009). In our study, however, the large differences in perch height between habitats did not affect the number of prey items detected by Little Owls, since we observed a similar number of prey capture attempts per hour (Table 3). Potentially, this result could be explained in two ways. First, the similar capture rates in the two habitats might result from a higher abundance of invertebrates in the pseudo-steppe, which then compensated for lowered prey detectability as a result of the low hunting perches. However, the overall abundance of the two main groups of invertebrate prey (i.e. the sum of Coleoptera and Orthoptera) was similar in both habitats (Table 1). Moreover, we would expect that in the pseudo-steppe Little Owls attack invertebrates at closer ranges from the perches as a consequence of the smaller field of view provided by the lower perches in this area. However, this was not observed: attack distances were similar in both areas (Table 2).

As a most likely explanation for the similar capture rates we suggest that prey detectability in both habitats was similar, despite the availability of higher perches in the woodland (Fig. 4). This was also indicated by the fact that attack distances did not differ between pseudo-steppe and woodland. Both results suggest the existence of constraints in the woodland that hamper the detection of prey, counterbalancing the possible advantages for prey detection due to a potentially larger field of view (Fig. 4).

Similar hunting success in two distinct habitats
Although the number of available and utilized perches was similar in territories of Little Owls in both habitats, in the woodland owls benefited from a wider range of perch heights. In this habitat, owls utilized generally higher perches than in the pseudo-steppe, but also foraged from perches at different heights, including big stones on the ground (Fig. 1). In spite of the maximum available perch height (consisting of the highest branches of Holm Oaks at approximately 5 m), Little Owls selected lower perches (average 2.76 m). This suggests the existence of an optimal foraging height above which hunting is less rewarding. As experimentally shown by Andersson *et al.* (2009), in open habitats where grass is much taller than prey, prey are only visible from almost directly above. This should have been the case especially in the woodland, where ground vegetation was higher and denser. The fact that we found no correlation between perch height and attack distance in woodland (Fig. 3) and that in territories with more developed ground vegetation, Little Owls produced attacks closer to their perches (Table 4), corroborate the hypothesis that in this habitat vegetation was reducing the available visual field and prey accessibility (Thiollay & Clobert 1988, Andersson *et al.* 2009).

In the pseudo-steppe the use of the highest available hunting perches (tops of stone piles) could pay,

Table 4. Relationship between vegetation characteristics and behavioural variables (perch height choice and attack distance) in the pseudo-steppe (*n* = 13) and woodland (*n* = 14) areas. The coefficients of multiple linear regressions are shown.

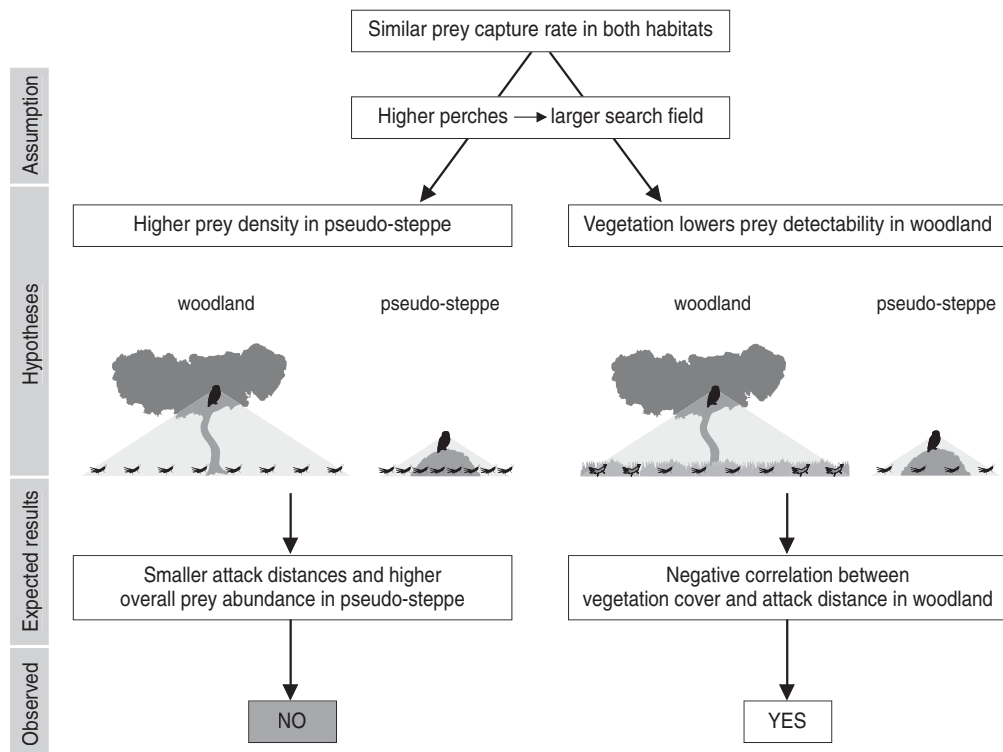|	Perch height				Attack distance			
	Pseudo-steppe	*P*	Woodland	*P*	Pseudo-steppe	*P*	Woodland	*P*
(Intercept)	1.74	<0.001	2.11	ns	20.07	<0.05	31.27	<0.001
Vegetation height	−0.16	<0.05	0.10	ns	−1.83	ns	0.58	ns
Vegetation cover	−0.06	ns	1.36	ns	−10.92	ns	−22.61	<0.05
IVC	0.11	ns	−0.18	ns	2.40	ns	0.50	ns
Adjusted R^2	0.43		0.05		0.12		0.50	
F-value	$F_{3,9}$= 3.99	<0.05	$F_{3,10}$= 1.25	ns	$F_{3,9}$= 0.56	ns	$F_{3,10}$= 5.27	<0.05

Figure 4. Diagram illustrating the two hypotheses explaining the similar prey capture rate observed in the pseudo-steppe and in the woodland (see text).

since ground vegetation is lower and less dense (Table 1). In fact, and similarly to that found in other studies (Greig-Smith 1983, Moreno 1984, Thiollay & Clobert 1988, Sonerud 1992), in the pseudo-steppe there was a positive correlation between perch height and distance to prey attacked (Fig. 3). In this respect, differences between the habitats may also be tied to the range in variation of perch height available: according to Andersson *et al.* (2009), a variation between 0.5 m and c. 1.5 m in perch height (as in the pseudo-steppe) may account for a 100% increase in prey visibility, while a variation of between c. 1 m and 4.5 m (as in the wood-land) should involve a smaller effect. In the pseudo-steppe, detection perches were also higher than giving-up perches, suggesting that Little Owls may benefit from choosing the highest available perches to forage. The existence of a wider availability of perch heights in the woodland, which allowed the owls to select an optimal perch height, may explain why no difference was found between the height of detection and giving-up perches in this habitat (Bye *et al.* 1992, Sonerud 1992).

In both habitats, giving-up distances were practical-ly twice as long as attack distances (Table 2). This corresponds well to some of the assumptions underly-ing optimal foraging models (Fitzpatrick 1981): Little Owls do not search for prey in an area that they covered before, and they do not waste energy by flying further than is needed to find an unsearched area.

Interestingly, in the pseudo-steppe Little Owls attacked from lower perches when the vegetation was higher (Table 4). This result suggests that in this habitat vegetation may also influence the visual detection of prey (Andersson *et al.* 2009), though to a smaller extent than in the woodland (probably due to the reduced range of variation in height of vegetation in the pseudo-steppe). In these cases (small prey imbed-ded in dense vegetation and lack of high perches), Little Owls perhaps compensate for losses in visual detectability by increasing the efficiency of acoustic detection through foraging from lower heights (Rice 1983, Bye *et al.* 1992, Andersson *et al.* 2009).

While our work was not designed to investigate this question, the use of acoustic cues in prey detection by Little Owls is also suggested by the lack of correlation between perch height and giving-up distance in both areas (see Andersson 1981, Fitzpatrick 1981, Moreno 1984), and by the longer search times we observed in

the pseudo-steppe (see Bye *et al.* 1992), in spite of the use of lower perches in this area. Nevertheless, longer times could also reflect differences in the behaviour (and, therefore, the conspicuity) of the most abundant prey in the pseudo-steppe (Orthoptera) and in the woodland (Coleoptera) (Table 1). Clearly, additional, more focused, investigation is needed to examine the role of acoustic cues and of prey behavioural specificities on the hunting behaviour of Little Owls.

ACKNOWLEDGEMENTS

REFERENCES

Ali M.A. 1978. Sensory ecology. Plenum Press, New York.

Altmann J. 1974. Observational study of behaviour: sampling methods. Behaviour 49: 227–267.

Andersson M. 1981. On optimal predator search. Theor. Popul. Biol. 19: 58–86.

Andersson M., Wallander J. & Isaksson D. 2009. Predator perches: a visual search perspective. Funct. Ecol. 23: 373–379.

Bye F.N., Jacobson B.V. & Sonerud G.A. 1992. Auditory prey location in a pause-travel predator: search height, search time and attack range of Tengmalm's owls (*Aegolius funereus*). Behav. Ecol. 3: 266–276.

Carlson A. 1985. Prey detection in the Red-backed Shrike (*Lanius collurio*): an experimental study. Anim. Behav. 33: 1243–1249.

Centili D. 2001. Playback and Little Owls *Athene noctua*: preliminary results and considerations. In: Van Nieuwenhuyse D., Leysen M. & Leysen K. (eds) The Little Owl in Flanders in its international context. Proceedings of the Second International Little Owl Symposium. Oriolus 67, pp. 72–83.

DRAA 2000. Anuário de recursos hídricos do Alentejo. Ano hidrológico de 1998/99. DRRA, Ministério do Ambiente e do Ordenamento do Território, Évora.

Exo K-M. 1989. Tagesperiodische Aktivitätsmuster des Steinkauzes (*Athene noctua*). Vogelwarte 35: 94–114.

Exo K-M. 1991. Der Untere Niederrhein – ein Verbreitungsschwerpunkt des Steinkauzes (*Athene noctua*) in Mitteleuropa. Natur und Landschaft 66: 156–159.

Fajardo I., Pividal V., Trigo M. & Jimenez, M. 1998. Habitat selection, activity peaks and strategies to avoid road mortality by the Little Owl *Athene noctua*. A new methodology on owls research. Alauda 66: 49–60.

Fitzpatrick J.W. 1981. Search strategies of tyrant flycatchers. Anim. Behav. 29: 810–821.

Génot J.-C. & Van Nieuwenhuyse D. 2002. *Athene noctua* Little Owl. BWP Update 4: 35–63.

Gillings S. 2004. Prey detectability: significance and measurement using a novel laser pen technique. Wader Study Group Bull. 103: 50–55.

Greig-Smith P.W. 1983. Use of perches as vantage points during foraging by male and female stonechats *Saxicola torquata*. Behaviour 86: 215–236.

Hays R.L., Summers C. & Seitz W. 1981. Estimating wildlife habitat variables. Fish and Wildlife Service. U.S. Department of the Interior, Washington.

Ille R. 1983. Ontogenese des Beutefangverhaltens beim Steinkauz (*Athene noctua*). J. Ornitol. 124: 133–146.

Martin P. & Bateson P. 1993. Measuring behaviour, second edition. Cambridge University Press, Cambridge.

Moreira F. 1999. Relationships between vegetation structure and breeding bird densities in fallow cereal steppes of Castro Verde, Portugal. Bird Study 46: 309–318.

Moreno J. 1984. Search strategies of Wheatears (*Oenanthe oenanthe*) and Stonechats (*Saxicola torquata*): adaptive variation in perch height, search time, sally distance and inter-perch move length. J. Anim. Ecol. 53: 147–159.

Negro J.J., de la Riva M.J. & Hiraldo F. 1990. Daytime activity of Little Owls (*Athene noctua*) in southwestern Spain. J. Raptor Res. 24: 72–74.

Norberg R.A. 1987. Evolution, structure, and ecology of northern forest owls. In: Nero R.W., Clark R.J., Knapton R.J. & Hamre R.H. (eds) Biology and conservation of Northern Forest Owls. Gen. Tech. Rep. RM-142. Department of Agriculture, Fort Collins.

Quinn J.L. & Cresswell W. 2004. Predator hunting behaviour and prey vulnerability. J. Anim. Ecol. 73: 143–154.

R Development Core Team. 2009. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. URL: http://www.R-project.org.

Rice W.R. 1983. Sensory modality: an example of its effect on optimal foraging behaviour. Ecology 64: 403–406.

Schönn S., Scherzinger W., Exo K.-M. & Ille R. 1991. Der Steinkauz. Neue Brehm-Bücherei 606, Ziemsen, Wittenberg.

Sonerud G.A. 1992. Search tactics of a pause-travel predator: adaptive adjustments of perching times and move distances by Hawk Owls, *Surnia ulula*. Behav. Ecol. Sociobiol. 30: 207–217.

Suárez F., Naveso M.A. & De Juana E. 1997. Farming in the drylands of Spain: birds of the pseudosteppes. In: Pain D.J. & Pienkowski M.W. (eds) Farming and birds in Europe. The Common Agricultural Policy and its implications for bird conservation. Academic Press, San Diego, pp. 297–330.

Sutherland W.J. (ed.) 1996. Ecological census techniques. A Handbook. Cambridge University Press, Cambridge.

Thiollay J.M. & Clobert J. 1988. Comparative foraging adaptations of small raptors in a dense African savanna. Ibis 132: 42–57.

Tomé R., Bloise C. & Korpimäki E. 2004. Nest-site selection and nesting success of little owls (*Athene noctua*) in Mediterranean woodland and open habitats. J. Raptor Res. 38: 35–46.

Tomé R., Catry P., Bloise C. & Korpimäki E. 2008. Breeding density and success, and diet composition of Little Owls *Athene noctua* in steppe-like habitats in Portugal. Ornis Fenn. 85: 22–32.

Van Nieuwenhuyse D., Génot J.-C. & Johnson D.H. 2008. The Little Owl – Conservation, ecology and behaviour of *Athene noctua*. Cambridge University Press, New York.

Widén P. 1994. Habitat quality for raptors: a field experiment. J. Avian Biol. 25: 219–223.

Zuberogoitia I. & Campos L.F. 1998. Censusing owls in large areas: a comparison between methods. Ardeola 45: 47–53.

SAMENVATTING

De Steenuil *Athene noctua* jaagt vaak vanaf een uitkijkpost. In dit onderzoek in Portugal werd het foerageergedrag van de uilen vergeleken in twee habitats met een sterk verschillend aanbod aan zitplekken: een steppeachtig gebied zonder bomen en een parklandschap met Kurkeiken *Quercus ilex rotundifolia*. Het voedselaanbod, voornamelijk insecten, was in beide gebieden vergelijkbaar. Het gedrag van bij daglicht jagende Steenuilen werd in 29 verschillende territoria onderzocht: de aard en de hoogte van de uitkijkposten, de tijd die er doorgebracht werd, de afstand tussen de uitkijkpost en de plek waar de uil een prooi probeerde te pakken, of de afstand die de uil overbrugde naar de volgende uitkijkpost. Ondanks de grote verschillen in structuur tussen de habitats, was de zoektijd naar prooien vergelijkbaar, evenals het percentage aanvallen dat een prooi opleverde. In de steppe waren alleen stenen als uitkijkpost beschikbaar en de uilen kozen daar de hoogste plekken (met een gemiddelde van 0,77 m). Hoe groter de steenhoop was des te groter de afstand waarop een prooi werd gepakt. Dit wijst erop dat de uilen baat hadden bij een hogere uitkijkpost doordat ze prooien op een grotere afstand ontdekten. In het parklandschap gingen de uilen niet op de hoogste plekken zitten (de uitkijkposten waren op 2,67 m, terwijl de bomen gemiddeld 4,99 m hoog waren). De afstand waarop een prooi werd ontdekt verschilde niet tussen de habitats. Dat was tegen de verwachting omdat de uilen in het parklandschap hoger zaten en daardoor meer prooien zouden kunnen ontdekken. Vermoed werd dat het voordeel van de hogere uitkijkposten in het parklandschap teniet gedaan werd door de dichtere begroeiing tussen de bomen wat het zicht op prooien belemmerde. De Steenuilen hadden daardoor in het parklandschap de hoogste kans op succes door een middelhoge uitkijkpost te kiezen.   (JP)