Distribution of woodland raptors along a Mediterranean-temperate gradient in Latium (central Italy)

L. Salvati, A. Manganaro, L. Pucci and L. Ranazzi

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Forest raptors are valuable indicators of habitat quality and show high sensitivity to woodland fragmentation. In this paper we provide data on the distribution of eight raptors including Honey Buzzard Pernis apivorus, Black Kite Milvus migrans, Short-Toed Eagle Circaetus gallicus, Sparrowhawk Accipiter nisus, Common Buzzard Buteo buteo, Hobby Falco subbuteo, Tawny Owl Strix aluco, and Long-Eared Owl Asio otus in 27 forests along a Mediterraneantemperate gradient in Latium, central Italy. Species richness (mean = 2.6±1.2) was positively correlated with forest size and mean tree diameter and not correlated with altitude. The most common species was S. aluco, breeding in all forests considered, followed by B. buteo, breeding in 20 forests (74.1%). C. gallicus occurred as a breeding species in only one forest. Based on raptor distribution, cluster analysis separated three groups including raptors associated to coastal woods (M. migrans, C. gallicus, P. apivorus, and F. subbuteo), raptors associated to mesophilous vegetation (A. nisus and A. otus), as well as ubiquitous species (B. buteo and S. aluco), with broad habitat and prey preferences, able to successfully colonize both woodland types. To assure the maintenance of good habitat quality in most woodlands, regulation of water diversion, prevention of summer fires, and a general reduction of human activities inside forests seem to be useful conservation tools.

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1. Introduction

Intensive agricultural practices, as well as tourism development, summer fires, urbanization and air pollution represent a serious threat for many woodlands in Mediterranean Europe (e.g. Sánchez-Zapata & Calvo 1999, Scarascia-Mugnozza *et al.* 2000). Forest raptors show high sensitivity to wood fragmentation (e.g. Bosakowski & Smith 1997, Penteriani 1997, Penteriani & Faivre 1997), and are valuable indicators of habitat quality (e.g. Bosakowski & Smith 1997, Sánchez-Zapata & Calvo 1999). Assessing the association between raptors and their habitat may provide useful tools for conservation and management of forested habitats (Sánchez & Zapata 1999). As many aspects of habitat-relationships of Mediterranean birds of prey remain still unknown (e.g. Sánchez-Zapata & Calvo 1999), we provide first data on the distribution of eight woodland raptors along an elevation gradient in central Italy. Despite the explanatory limitations imposed by the descriptive nature of this study, our empirical data on raptor distribution in different forest types may provide information useful for conservation and management planning.

2. Methods

The study area was located in Latium (central Italy), with Rome (41°53 N, 12°28 E) situated approximately at the center of the region. The coastal sub-

region bordering the Tyrrhenian sea shows a typical Mediterranean climate with three to four months of summer drought and mean annual rainfall less than 700 mm. The hilly sub-region shows a more temperate climate, with one to two months of summer drought and mean annual rainfall ranging from 800 mm and 1100 mm. The mountain Apennine region shows a typical temperate climate, with mean annual rainfall higher than 1100 mm (Penteriani 1997, Blasi *et al.* 1999). Twenty-seven



Fig. 1. Map of Latium region showing the location of 27 forests studied. Symbols indicated the different wood types as follows: hilly and mountain beech forests (A), hilly mesophilous oak forests (B), lowland oak forests (C), wet flat coastal oak forests (D), dry coastal termophilous oak forests (E).

deciduous forests were chosen along a Mediterranean-temperate gradient from the coastal belt to the mountain massifs of Apennine (Fig. 1) as follows: five dry coastal thermophilous woods (dominant species: Quercus ilex and Q. suber), seven wet-flat coastal woods (dominant species: Q. cerris, Q. frainetto, and Q. robur), five lowland woods (dominant species: Q. cerris, Q. frainetto, and Q. pubescens), five hilly mesophilous woods (dominant species: Q. cerris), and five hilly and mountain woods (dominant species: Fagus sylvatica) (see Blasi et al. 1999 for details). Forest elevation ranged from 10 m to 1500 m above the sea level. The area of most forests was in the range 100-500 ha (mean \pm sd = 749 \pm 1184 ha), with only a few > 2000 ha. All forests have been previously cut within the last 200 years. However, older forest patches with > 50years of age are extremely common.

A previous study (Boano et al. 1995) revealed eight woodland raptors breeding in the study area, including Honey Buzzard Pernis apivorus, Black Kite Milvus migrans, Short-Toed Eagle Sparrowhawk Circaetus gallicus, Accipiter nisus, Common Buzzard Buteo buteo, Hobby Falco subbuteo, Tawny Owl Strix aluco, and Long-Eared Owl Asio otus. The distribution of Northern Goshawk Accipiter gentilis was restricted to marginal areas in Apennine massifs (Boano et al. 1995, Arcioni 1996), therefore this species was not considered here.

The breeding occurrence of forest raptors was assessed mainly from 1998 to 2000, with complementary information from the period between 1995 and 1997, and we also included data published recently (De Giacomo *et al.* 1993, Boano *et al.* 1995 and the papers listed below). The field work was carried out through the breeding season (March-August), and the selection of the exact period for each survey was based on regional nesting phenology when available (Boano *et al.* 1995).

We used different field techniques to detect raptors according to previous regional works (e.g. Petretti & Petretti 1981, Petretti 1988, Cerasoli & Penteriani 1992, Pinchera 1995, Castaldi et al. 1997, Cauli & Ceccarelli 1997, Penteriani 1997, Penteriani & Faivre 1997, Ranazzi et al. 2000, Salvati et al. 2000). For diurnal raptors, we recorded nuptial displays, territorial flights, and any type of calls in the interior of forests and from panoramic spots during early stages of breeding. We searched for fledged young near the nest, and pellets and prey remains, as well as feathers, droppings, and other traces near roosting sites. Systematic, on-foot searches of adults carrying nesting materials, or hunting in the forest interior, were also performed. During the same period, we used playback of taped recordings to elicit responses of the most secretive raptors like Sparrowhawk and Hobby according to Cerasoli & Penteriani (1992). For nocturnal raptors, we performed playbacks using recordings of conspecific calls. The number of playback stations ranged from 1 to 15 according to the forest size. We performed diurnal visits searching for other traces (e.g. feathers, pellets). During the post-fledging period, fledglings, especially those of Tawny Owl, uttering their typical begging calls, often allowed us to locate the nesting site (e.g. Ranazzi et al. 2000). For all raptors, diurnal and nocturnal visits outside the nesting period searching for indirect signs of their occurrence during breeding (e.g. stick nests on

Tab. 1. Distribution of eight forest raptors in five woodland types of Latium, central Italy, expressed as the number and percentage (in parenthesis) of forests occupied. Forest types are presented along a Mediterranean-temperate gradient; the first three types are thermophilous, the last two are mesophilous.

	Dry coastal oak	Wet-flat coastal	Lowland	Hilly	Beech	Total
	forests	oak forests	oak forests	oak forests	forests	
Number of forests	5	7	5	5	5	27
Pernis apivorus	0	2 (28.6)	0	0	0	2 (7.4)
Milvus migrans	0	3 (42.9)	2 (40.0)	0	0	5 (18.5)
Circaetus gallicus	0	1 (14.3)	0	0	0	1 (3.7)
Accipiter nisus	0	0	0	1 (20.0)	2 (40.0)	3 (11.1)
Buteo buteo	0	6 (85.7)	5 (100)	4 (100)	5 (100.0)	20 (74.1)
Falco subbuteo	1 (20.0)	3 (42.9)	0	1 (16.7)	0	5 (18.5)
Strix aluco	5 (100)	7 (100)	5 (100)	5 (100)	5 (100)	27 (100)
Asio otus	0	2 (28.6)	1 (20.0)	2 (33.3)	1 (20.0)	6 (22.2)
Number of species (mean \pm sd)	1.2 ± 0.4	3.4±1.6	2.6±0.6	2.6±0.9	2.6±0.9	2.6 ± 1.2

trees, spontaneous hooting of Tawny Owls) were carried out each year.

The study areas in the five wood types were surveyed as equally as possible to avoid regional bias. Field effort was estimated as about 80 hours per habitat type per breeding period, plus 10-20 hours per habitat type per winter from 1998 to 2000.

We regarded as present all species for which we collected evidence of probable or confirmed breeding, irrespective of the number of pairs present and the number of years in which the species was observed. These criteria correspond to the categories 'Confirmed' and 'Probable breeding' commonly used in breeding bird atlases (e.g. Boano et al. 1995). We regarded as absent all species observed only once in a suitable nesting habitat without any evidence of breeding. This protocol cannot give precise information on population size or breeding density at a regional scale, but it provides data on raptor distribution and a preliminary assessment of their habitat preferences.

For each forest we determined woodland area (SIZE) and elevation (ALT). Also, for seven forests we obtained mean diameter at the breast height (DBH) from literature data (Bernoni *et al.* 1985, Bernoni & Ianniello 1989). Spearman rank correlation tests were used to evaluate the relationship between the number of breeding species and SIZE, ALT, and DBH. For all raptors but C. gallicus, we compared SIZE and ALT of occupied and unoccupied forests by means of Mann-Whitney U-tests. Since we made separate tests for two habitat variables, we used a Bonferroni adjustment of the p-value (Rice 1989), testing for significance at P<0.025 instead of P<0.05. Cluster analysis (Euclidean distances, Ward's clustering strategy) was applied on the matrix of binary data (see Appendix I) to provide an ordination of the eight raptors based on their distribution in 28 forests. All analyses were performed by STATISTICA 4.5 (Statsoft Inc., 1993).

3. Results

In 27 forests studied we observed eight species with probable or confirmed breeding, with a mean species richness of 2.6- ± 1.2 . Species richness was positively correlated with SIZE ($r_s=0.45$, P<0.018, N=27) and DBH ($r_s=0.93$, P<0.003, N=7), but was not correlated with ALT ($r_s=0.17$, P=0.39, N=27). The most common species



Fig. 2. Cluster analysis (Euclidean distance amalgamation, Ward's clustering strategy) showing similarities in raptor distribution within the forests studied.

was S. aluco, breeding in all forests, followed by B. buteo, breeding in 20 forests. C. gallicus occurred as a breeding species in only one forest (Tab. 1). The size of occupied forests was greater than unoccupied ones for P. apivorus (U=0, P=0.02) and B. buteo (U=25.5, P=0.013). The elevation of occupied forests was higher than unoccupied ones for A. nisus (U=6, P=0.020), B. buteo (U=29.5, P=0.025), and Falco subbuteo (U=22, P=0.039). Based on raptor distribution, cluster analysis separated three clusters, the first including M. migrans, C. gallicus, P. apivorus, and F. subbuteo, the second including A. nisus and A. otus, and the third including Buteo buteo and Strix aluco (Fig. 2).

4. Discussion

Fragmentation-sensitive species respond negatively to decreasing forest size clearly showing a threshold in habitat-occupation during breeding (e.g. Bosakowski & Smith 1997, Penteriani & Faivre 1997). In Latium, large-sized species, like *C. gallicus*, are very scarce and occupy only large forest fragments, but some small-sized raptors, like Accipiter nisus and Asio otus, also showed a restricted distribution, generally avoiding close and small woodlands. Conversely, the broad distribution of Tawny Owls (Salvati *et al.* 2000) clearly suggest that close woodlands are optimal habitats for this species.

Wood characteristics, influenced by altitude and local climate, are also important in affecting raptor distribution (e.g. Penteriani 1997, Penteriani & Faivre 1997, Sánchez-Zapata & Calvo 1999). The distribution of raptors clearly differs at the habitat level in our study-area. M. migrans, C. gallicus, P. apivorus, and F. subbuteo were strictly associated to thermophilous vegetation forming coastal oak woods. Conversely, A. nisus and A. otus were associated to mesophilous oak woods in hilly areas. Different vegetation diversity, forest structure, and prey productivity, in turn linked to land productivity and weather conditions, may be regarded as general causes accounting for different composition of raptor communities breeding in coastal and mountain forests in central Italy. Notably, ubiquitous species like Buteo buteo and Strix aluco, with broad habitat and prey preferences (e.g. Penteriani & Faivre 1997, Manganaro et al. 2000), are able to successfully colonize both habitats.

High species richness make Mediterranean forests unique habitats for conservation purposes (e.g. Scarascia-Mugnozza *et al.* 2000). Regulation of water diversity for agricultural purposes, prevention of summer fires during late spring and summer especially in hilly and coastal forests, as well as a general reduction of human activities inside forests, may assure the maintenance of good habitat quality in most woodlands.

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Összefoglalás

Ragadozó madarak előfordulása egy mediterrán - mérsékeltövi grádiens mentén közép-olaszországi erdőkben

Az erdőkhöz kötődő ragadozó madarak jól indikálják az élőhely minőségének változásait, illetve fragmentációját. Jelen tanulmányban egy laciumi (Közép-Olaszország) mediterrán - mérsékeltövi grádiens mentén elhelyezkedő 27 erdőt vizsgáltunk. Nyolc ragadozó költésének előfordulásával foglalkoztunk: darázsölyv, barna kánya, kígyászölyv, karvaly, egerészölyv, kaba, macskabagoly és az erdei fülesbagoly. Az erdők fajgazdagsága (átlag = $2,6\pm1,2$) pozitívan korrelált az erdők nagyságával és az átlagos fatörzs átmérõvel, de nem korrelált a magassággal. A leggyakoribb faj a macskabagoly volt, amely mindegyik erdőben előfordult, a második az egerészölyv, amely 20 erdőben (74,1%) költött. A kígyászölyv csak egyetlen erdőben költött. Kluszter-analízissel három csoportot lehetett elkülöníteni: a leginkább parti erdőkhöz kötõdõ fajok (barna kánya, kígyászölyv, darázsölyv, kaba), a mezofil erdőkhöz kötődő ragadozók (karvaly, erdei fülesbagoly), és a nem szelektáló fajok (egerészölyv, macskabagoly), melyek széles élőhely- és táplálék-spektrumuk révén mindkét erdőtípusban sikeresen megtelepedhetnek. Az erdőkben a megfelelő élőhelyi minőség fenntartása szükségessé teszi a vízrendezést, a nyári tüzek megakadályozását, és az emberi tevékenység csökkentését.

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Appendix I. Distribution of eigh	t woodland raptors in 27	forests in Latium,	central Italy
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	1		· · · · · · · · · · · · · · · · · · ·		2			
	Pernis	Milvus	Circaetus	Accipiter	Buteo	Falco	Strix	Asio
	apivorus	migrans	gallicus	nisus	buteo	subbuteo	aluco	otus
Hilly and mountain beech forests								
Faggeta di Camposecco (Rome)					+		+	
Faggeta di Prato di Campoli (Frosinone)					+		+	
Faggeta di Valle Cavalera (Rome)				+	+		+	
Faggeta di Monte Venere (Viterbo)				+	+		+	+
Faggeta di Oriolo Romano (Viterbo)					+		+	
Hilly mesophilous oak forests								
Bosco di Trisulti (Frosinone)				+	+		+	+
Bosco del Cerquone (Rome)							+	+
Bosco di Castelliri (Frosinone)					+		+	
Macchia di Gattaceca (Rome)					+		+	
Macchia di Manziana (Rome)					+	+	+	
Lowland oak forests								
Bosco Trentani (Rome)					+		+	
Arrone-Galeria (Rome)					+		+	
Macchia di Acquatraversa (Rome)		+			+		+	
Marcigliana (Rome)					+		+	+
Macchia dell'Infernaccio (Rome)		+			+		+	
Wet-flat coastal oak forests								
Macchia della Capocotta (Rome)					+		+	
Lecceta di Castelfusano (Rome)						+	+	
Tenuta di Castelporziano (Rome)	+	+	+		+	+	+	
Bosco di Foglino (Rome)					+		+	
Foresta Demaniale del Circeo (Latina)	+				+	+	+	+
Macchia di Decima (Rome)		+			+		+	
Macchia Grande di Fregene (Rome)		+			+		+	+
Dry coastal termophilous oak forests								
Macchia Grande di Focene (Rome)						+	+	
Pineta di Procoio (Rome)							+	
Sughereta di Pomezia (Rome)							+	
Sughereta di Vallerano (Rome)							+	
Tumuleti di Bocca di Leone (Rome)							+	

BOOK REVIEW - KÖNYVISMERTETÉS

Helmut Engler (2000): Die Teichralle oder das Teichhuhn *Gallinula chloropus*. - Die Neue Brehm- Bücherei Bd. 536, Westarp Wissenschaften. Hohenwarsleben. 360 pp.

A megújult külsővel megjelenő Neue Brehm-Bücherei sorozat 536. kötete a nagy elterjedésû vízityúk (Gallinula chloropus) életét veszi vizsgálat alá. A monográfia bevezető fejezeteiben ismerteti a faj rendszertani helyzetét, rokonsági körét, kitér az alfajokra, azok földrajzi elterjedésére, majd a mû nagy részében elsősorban az európai, illetve közép-európai vízityúk alfaj életmódját, élettörténetét ismerteti. A szerző, Helmut Engler vízityúk monográfiája a Brehm-füzetek sorozatban már két kiadást megért (1980, 1983). E harmadik kibővített kiadást indokolták az újabb kutatási eredmények, s az időközben -1989-től kezdődően- az Eurázsia politikai térképén bekövetkezett nagyarányú pozitív változások, melyek következtében a szerzőnek kedvezőbb kitekintése nyílhatott a faj areájának távolabbi részeire.

A mû behatóan tárgyalja a faj fészkelés

ökológiáját, súlyt helyezve a fészkelőhely és a fészekhely különféle változatainak leírására, a fészkelőhelyen mutatott territoriális viselkedésre. Ezt követően rátér a költésbiológiai jellemzők taglalására, külön elemezve a kotlás és a fiókanevelés időszakát. Végül foglalkozik a táplálkozás biológiával, majd a különféle komfort viselkedési formák leírásával.

A könyv értékét számunkra csak növelik a magyar ornitológusokra történő hivatkozások. Keve András több tanulmányát is idézi a szerző, főként a vízityúk alfaji kérdéseivel foglalkozó munkákat. Molnár Gyula nádi fészkelő madarakon végzett alliancia vizsgálatainak eredményei, - melyről éppen az Ornis Hungarica hozott le cikket - a faj fészkelési szokásainak ismertetésénél nyernek említést.

Helmut Engler példásan összeállított vízityúk monográfiája alapos áttekintést nyújt a faj biológiájáról, egyben vezérfonalként is szolgálhat más fajok élettörténetének feldolgozásához, ezért minden elemző szemléletû hazai ornitológus figyelmét felhívom rá.

Dr. Bankovics Attila

Ornis Hungarica 11: 9-18. 2001

Habitat selection of Corncrakes (Crex crex L.) in Szatmár-Bereg (Hungary) and implications for further monitoring

W. Wettstein, T. Szép and M. Kéry

Wettstein, W., Szép, T. and Kéry, M. 2001. Habitat selection of Corncrakes *Crex crex* in Szatmár-Bereg (Hungary) and implications for further monitoring. – Ornis Hung. 11: 9-18.



In 1997 we carried out a survey of the corncrake in Szatmár-Bereg in eastern Hungary in an area covering 1170 km² and containing 137 km² of natural grassland. To study corncrake habitat preferences, we compared habitat factors of 17 clearly delimited grassland sites with at least two singing corncrakes with the respectively closest grassland sites of similar size where no corncrakes occurred. We assessed the area of the site, measured vegetation height and density, wet standing crop, an index of humidity and an index of habitat structure and recorded land-use at each site. Corncrake habitats were more productive, more humid and showed more additional structures than grasslands without corncrakes. Concerning land-use, corncrake habitats contained more currently abandoned parts (set-asides) and less intensively grazed parts than non-corncrake habitats. In a logistic regression model, vegetation height, vegetation density and the index of structure were selected as the variables with the largest explanatory power for the presence/absence of corncrakes. We suggest that these indices should be used as tools to monitor changes in corncrake habitat at a large scale.

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1. Introduction

The corncrake (*Crex crex*) is a globally threatened bird species living mainly in extensively used tall wet grasslands of Europe and Central Asia. It is classified as "Vulnerable" at both world and European scales due to a long-term and very steep decline across its entire range. Breeding occurs in 34 European countries but the species has been declining in Europe since the last century. The decline over the last

10 years has been estimated at about 20% to 50% in most European countries (Tucker & Heath 1994).

Corncrakes are rare in south-western Europe but more widespread in Central and north-eastern Europe, where they may occur at high densities in suitable areas. Hungary is one of the westernmost countries with strong corncrake populations. Here, most corncrakes occur in the northeastern floodplains along the rivers Tisza, Bodrog and Szamos. Recent estimates of the total Hungarian population of the

species are ranging from 350-900 singing males (Szép 1991, Miklós Tóth pers. comm.). Previous counts showed large annual fluctuations. The corncrakes in the Szatmár-Bereg area near the river Tisza in Eastern Hungary occupy fragments of grasslands mainly dominated bv Alopecurus pratensis in a matrix of various seminatural habitat types in an area of about 1170 km². These sites can be surveyed from a single point or easily accessible monitoring tracks, and the probability of double-recordings is low because relatively few males call simultaneously at one site. The fragmentation of the population into many clearly separated groups makes it possible to record accurately the corncrake population and to detect small changes in population size and geographical distribution.

Several studies on habitat preferences of corncrakes in Europe (e.g. Flade 1991, Schäffer & Münch 1993, Stowe et al. 1993, Schäffer 1999) were mainly based on time-demanding analyses of plant sociology. Such methods are unsuitable for any large-scale monitoring of corncrake populations and their habitats in eastern Europe. Instead, simple quantitative habitat factors should be found to predict patterns of presence/absence of corncrakes or temporal changes in distribution and abundance. Mainly regarding the expected changes of the landuse after the reprivatisation of agricultural lands in Hungary it will become increasingly important to find objective measures of habitat quality.

Here we present results of an ecological corncrake survey conducted using simple field methods for a quick assessment of the structure, productivity, humidity,

and the management of corncrake habitat. They confirm results of the previously cited studies and strongly emphasize the importance of high but not dense vegetation in combination with a distinct largescale structure of the grassland. Our results suggest that these habitat factors are suitable for long-term monitoring. They perform well at predicting the presence or absence of corncrakes, are very quick to record, and they do not require any special biological knowledge. Hence they could also be used by ornithological laypeople. Our methods should prove suitable for efficient monitoring of corncrakes on a much larger scale than has hitherto been made.

2. Methods

2.1. Study species

The corncrake *Crex crex* is a small rail weighing approx. 125 g. It lives in open habitats, mainly wet, tall grasslands, and is a long-distance migrant wintering in the sub-Sahara. Corncrakes arrive on their breeding sites in Eastern Europe at the beginning of May and leave them again from August to October (Green *et al.* 1997).

Male corncrakes are calling more or less continuously between 22.00 hours in the evening and 3.00 hours in the morning from mid-May to early July. Their call can be heard over between 500 and 1000 m depending on weather conditions. If an occupied site is visited twice at a suitable time, the probability of detecting a male corncrake has been estimated at 0.95 (Stowe *et al.* 1993).

2.2. Study area and site selection

Our study area was the Szatmár-Bereg lowland (Important Bird Area HU35, category A1; see Nagy 1998) in the easternmost part of Hungary in a triangle between the rivers Tisza and Szamos and the border with the Ukraine and Romania (48°0'N, 22°40'E, see Fig. 1). A pilot survey of calling corncrakes covering 137 km² of grassland was carried out between 15 May and 12 June 1997. The pool of investigated grasslands was determined from Hungarian maps (1:25'000) dating from 1974 that show the extent of natural grasslands. We found 17 clearly delimited grassland sites with at least two singing males (+sites), which we selected for the habitat analyses. On the selected +sites, altogether 68 male corncrakes were recorded with up to seven corncrakes calling at one site.

Additionally, we selected 17 grassland fragments of similar size and habitat type but without calling males (-sites) to com-



Fig. 1. Location of the study sites for the habitat analysis in Szatmár-Bereg, Hungary.

pare occupied with unoccupied grasslands. To assure an even geographic representation of +sites and -sites, we selected for each +site the closest site with no calling corncrakes. Corncrakes are known to move strongly within their breeding habitat during the season (Stowe & Hudson 1991) and even within 24 hours (Schäffer & Münch 1993, Schäffer 1999). Therefore, we selected entirely different, unoccupied sites as a comparison with the occupied habitats rather than selecting just the unoccupied parts within an occupied meadow.

Our study therefore bears on 34 grassland fragments for a comparison of habitats with or without corncrakes present (Fig. 1). We used the MapInfo v4.0 GIS software for measuring the size of the potential breeding habitats, by identifying the border of the habitats on the digitised and geocoded 1:25'000 map and calculated the area of the identified polygons.

A second survey was made between 26 June and 6 July 1997 in order to check the status of the sites. It concentrated on the central and northern parts of Szatmár-Bereg only because bad weather conditions followed by infrequent calling in later summer did not allow a complete survey any more. The second survey comprised 22 among the 34 original sites from the first survey and confirmed the status of occupancy of all checked study sites that were used for the habitat analysis; at all +sites, calling corncrakes were confirmed while no birds could be found at any of the -sites.

2.3. Data collection

In June 1997, at every study site, we analysed the structure of the vegetation, established an index of humidity and an index of habitat structure for each site.

For the analysis of vegetation, we took five points along a transect across the sites by selecting the points of the left foot-tip after walking intervals of exactly two minutes at constant speed. The total linear transect length was between 600 - 650m. In the -sites, the transects were placed randomly, while in the +sites, they were placed across the area with the highest corncrake density. We did not place them randomly in the +sites, because some of them were so large that they also held large parts of habitat with a very different structure compared with the parts where corncrakes were calling. These could therefore be unsuitable habitats and it would not have been justified to call them typical for corncrakes.

At the selected points, height, density and biomass of the vegetation was measured. As a measure of vegetation height, we took the distance between the soil and the centre of a desk pad (33×24 cm, 420g) that we carefully placed by hands horizontally on top of the vegetation. As a measure of vegetation density, we recorded the average "drag weight" in grams of a corncrake dummy leashed to a spring scale and dragged through the vegetation. This simple model corncrake was made with an empty "Boule"-ball, cardboard and water resistant Scotch tape, building an eggshaped structure with a 30 cm long cord at the tip (120g, 15×7 cm). As a measure of the biomass of the vegetation, we harvested the standing crop in one randomly placed square of 33×33 cm and weighed it immediately to the nearest gram using a spring scale.

Other habitat variables recorded along the transects were an index of humidity and an index for habitat structure. The index for humidity was meant to quantify the degree to which a site was wet or dry and was calculated as a sum of the following factors:

- the abundance of five typical and conspicuous wetland plants (*Iris pseudacorus, Lythrum sp., Euphorbia palustris, Peucedanum officinale* and *Sanguisorba officinalis* estimated in three categories (0 points: <3 plants; 1 point: 3-10 plants; 2 points: >10 plants found on the transect counting for every species separately)
- the abundance of a common grass indicating wet soils (*Alopecurus pratensis*) and of a grass typical of dry soils (*Festuca pseudovina*) (0 point: absent or rare; 1 point: not dominant; 2 points: partly dominant; 3 points: dominant at the whole site). Scores for *Festuca pseudovina* were subtracted.

The index for habitat structure was conceived as a measure of the amount of additional large-scale structures that influence the characteristics of the grassland and could therefore influence the habitat choice of the corncrakes. It was calculated as the sum of four factors:

- number of isolated old bushes and number of isolated trees (0 points: <3; 1 point: 3-10; 2 points: >10 visible from the transect (always within the selected grassland site)).
- number of hedges (0 point: none; 1 point: 1-2; 2 points: >2 visible from the transect).
- presence of old riverbeds and other marshy areas caused by natural relief of the surface that were characterised by continuously wet soil (0 points: none; 1 point: 1 or 2 spots; 2 points: more spots or one very large expanse).
- presence of old flowers of *Dipsacus sp.* (0 points: rare or absent; 1 point: dis-

persed; 2 points: fields of old *Dipsacus* present).

We recorded the landuse of the sites until 5 August 97. To quantify the land-use we assessed the relative proportions of each of the following types of grassland: mowed, slightly or heavily grazed (<50% of the vegetation disturbed by the animals, respectively >50% of the vegetation disturbed by the animals), currently set-aside areas and other grasslands.

2.4. Statistical analysis

To determine which habitat variables were most important for the presence and abundance of corncrakes we analysed our data in two ways. First, we included presence/absence of the corncrake at all 34 sites in an analysis using a logistic regression model. Tests in the logistic model were carried out by computing appropriate ratios of mean deviances. Such mean deviance ratios are approximately F-distributed (Francis *et al.* 1993).

Applying a regression model to the presence/absence data of all 34 sites in some way violates statistical logic. Corncrake presence was not truly a random variable, but instead we selected the sites to have corncrakes present or not. One could therefore argue that it would have been more appropriate to analyse the two groups of sites with discriminant function analysis (Mardia et al. 1979). However, for three reasons we chose to use logistic regression in an exploratory way. The logistic regression framework has several advantages over discriminant function analysis. First, the fitted values of a logistic regression model of the presence/absence data have a very intuitive interpretation. They are the predicted

probability of occurrence of the corncrake at a site, given the statistical model. They can thus be used to predict which unoccupied sites could be the most probable to be occupied in a good corncrake year, or on the other hand, which of the occupied sites appears to be the least favourable. Second, the regression residuals can give valuable insights about which sites are unusual. Third, the effect of different factors can be formally tested, and thus the usual model selection techniques applied. We furthermore qualitatively checked the results from the logistic regression analysis with a discriminant function analysis, and the latter indicated the same important habitat variables as the regression analysis.

Second, we modelled the abundance of corncrakes in all sites (including the - sites) and at the +sites in an ordinary multiple regression analysis. In both the logistic and the ordinary regression, we selected the model that was best able to explain patterns in corncrake occurrence by forward selection of the explaining variables (Neter *et al.* 1990). All statistical analyses were performed with the statistical package Genstat 5.3.2. (Payne 1993).

Many of the measured variables were correlated among each other (Tab. 1) and without carrying out experiments it may therefore be difficult to identify the variables which are causally responsible for the distribution of the corncrakes. But to *predict* corncrake presence, we do not really need to know which variable was causally responsible for a corncrake occupying a certain habitat. Instead, if we are able to find a small set of variables that predicts corncrake presence well, we can make predictions about the occupancy status of hitherto unknown sites if we know the values for these predictor variables at that site.

Variable	Area	Standing	Vegetation	Vegetation	Index of	Index of
		crop	height	density	humidity	structure
Area	1.00	-0.03	-0.17	-0.10	-0.32	-0.04
Standing crop		1.00	0.77	0.81	0.38	0.44
Vegetation height			1.00	0.73	0.49	0.34
Vegetation density				1.00	0.29	0.37
Index of humidity					1.00	0.34
Index of structure						1.00

Tab. 1. Pearson correlation coefficients between the measured habitat variables. Bold-face numbers indicate a significant correlation with P < 0.05 (N = 34 habitats).

3. Results

The sites with corncrakes could be characterised as moist or temporary moist meadows or pastures with tall grasses. They were often structured by single-standing trees and bushes, hedgerows, old riverbeds and other marshy areas. On average, the occupied sites were 1.36 km² large, their fresh standing crop on an area of 33×33 cm weighed 173 g, their vegetation height under the desk pad was 30.6 cm and the drag weight needed to carry the model corncrake through the vegetation was 212 g. Except of the area and the proportions of mown and extensively grazed area, all measured habitat variables significantly differed between grasslands with and without corncrakes (Tab. 2). The aver-

age weight of the fresh standing crop was 31% higher and the average height of the vegetation was 46% higher in +sites than in -sites. The grasslands with corncrakes were also more humid because the typical wetland plants considered in the index of humidity were more abundant in +sites. Corncrake grasslands had more additional structure like isolated bushes or trees, hedgerows and soil relief than grasslands where corncrakes occurred. no Concerning land use, the two categories of grassland differed primarily in away that +sites held more currently unused or not yet used parts while in -sites more intensively grazed parts were found (Tab. 2, Fig. 2). Early mowing (before the end of June) was only occasionally observed and without exception, there were some refuge areas left. This could however be related

Tab. 2. Differences in habitat variables among grasslands holding corncrakes (+sites, N=17) and grasslands without them (-sites, N=17). One-way ANOVAs, **: P<0.01, ***: P<0.001.

Habitat variable	+site (means)	-site (means)	R^2 of model	F _{1, 32}	Р
Area of the grassland	$1.36 {\rm km}^2$	1.54 km^2	0.01	0.50	
Standing crop	173 g	132 g	0.29	13.40	***
Vegetation height	30.6 cm	20.9 cm	0.55	39.40	***
Vegetation density	212 g	178 g	0.21	8.70	**
Index of humidity	4.2	1.6	0.26	11.30	**
Index of structure	3.3	1.8	0.30	14.30	***
Proportion mown	24.1 %	20.6 %	0.01	0.20	
Proportion extensively grazed	10.0 %	12.3 %	0.004	0.10	
Proportion intensively grazed	7.6 %	40.0 %	0.26	11.50	**
Proportion set-asides	51.1 %	21.1 %	0.19	7.9	**



Fig. 2. Cumulated frequency of different landuse forms in 17 grasslands with corncrakes (+) and 17 grasslands without corncrakes (-). ** : significant difference with P<0.01 (t-test), N=34.

to the exceptionally wet conditions in the first half of 1997.

The variables explaining most of the variation between occupied and unoccupied sites were vegetation height, the index of structure and vegetation density (Tab. 3, Fig. 3). While vegetation density was higher in +sites than in -sites in a simple ANOVA (Tab. 1), the regression models show a negative relation between the vegetation density and corncrake abundance (Fig. 3). That is because in the regression models, vegetation density is adjusted for variation in vegetation height

Tab. 3. Analysis of deviance of cornerakes presence at the studied meadows in Eastern Hungary. Presence of cornerakes was modelled with a logistic regression model. Terms were selected by forward selection. Tests were carried out by dividing the mean deviances due to each term by the residual mean deviance. These mean deviance ratios are approximately F-distributed with 1 and 30 df. *** - P < 0.001.

Source of variation	df	md	F	
Vegetation height	1	24.85	79.35	***
Index of structure	1	7.33	23.42	***
Vegetation density	1	5.56	17.76	***
Residual	30	0.31		
Total	33	1.43		

and index of structure. This suggests that corncrakes prefer the sparser vegetation at any given vegetation height. The discriminant function analysis confirmed the importance of the height and density of the vegetation and the index of structure. Using these three variables, the status of 32 of the 34 sites was correctly predicted.

Variation in the measured habitat variables could not explain the abundance of the corncrakes within the investigated



Fig. 3. The relationship between the probability of corncrake presence and vegetation height, the index of structure and vegetation density. Probability of corncrake presence was calculated based on an equation derived from a logistic regression model containing the three explanatory variables for which a graph is shown. The graphs therefore present smoothed relationships. For a definition of the habitat factors index of structure and vegetation density see the methods section.

Tab. 4. Regression model of the abundance of the Corncrake in the studied grasslands (including the sites not occupied). Terms in the minimal adequate model (which explained 45% of the variation in corncrake abundance) were selected by stepwise multiple regression. ***: P < 0.001, *: P < 0.05, (*): P < 0.1.

Source of variation	slope	df	SS	F	
Vegetation height	0.27	1	61.30	18.10	***
Index of structure	0.54	1	17.20	5.10	*
Vegetation density	-0.02	1	13.70	4.00	(*)
Residual		30	101.90		
Total		33	194.10		

+sites. None of the variables was significantly correlated with the abundance of the corncrakes when only the +sites were analysed. When the -sites were included, the same model as for the presence / absence data was selected (Tab. 4) which supports the validity of the model in Tab. 3. To summarise, our results show that the recorded habitat variables were distinctly different between occupied and unoccupied sites, but that they can not explain the abundance of the corncrakes within an occupied site. Therefore, we did find good correlates of corncrake presence, but no good correlates of corncrake abundance.

4. Discussion

The surveyed area in Szatmár-Bereg holds a significant part of the Hungarian corncrake population. It is a typical area of low intensity agriculture, providing good conditions for successful breeding of the corncrake (Green & Rayment 1996). In the survey year (1997), the distribution of the bird was not primarily determined by the actual mowing regime but by differences in the large and small scale structure of the grassland. The clear differences between occupied and unoccupied sites indicate, that the used measures of the habitat quality are indeed suitable for the use in a long-term monitoring of the occupied area, most efficiently by vegetation height and density and the index of structure selected by the logistic model.

Suitable corncrake habitats could be separated from unsuitable habitats by very simple physical measures of the grassland. So we may hope that aided by remote sensing a first assessment of the corncrake distribution in so far unsurveyed areas could be realised. This would be especially important for all the remote areas further east and north of the Carpathians, where detailed surveys are mostly lacking, but which are supposed to host significant parts of the whole European population (Mischenko et al. 1995, Keiss 1997). Further research would also be needed to find models to predict the abundance of the corncrakes, i.e. to identify a small set of variables that are strongly correlated with corncrake abundance.

Vegetation height seems to play a key function in the habitat selection of the corncrakes (Schäffer & Münch 1993, Schäffer 1999). Our measure of vegetation height not only gives the simple height of the vegetation, but also contains information about the small scale vegetation structure. It therefore better reflects the conditions relevant for the corncrakes than relatively abstract measures like standing crop. Vegetation height was incidentally also the easiest habitat variable to measure. It can be recorded at any visit to a grassland with a minimal effort. We therefore suggest that it should be measured in any corncrake survey. An international coordination would be helpful to define a small but standardised set of habitat variables and the detailed procedure of their measurement.

The negative relationship between vegetation density and corncrake presence at a given vegetation height indicates that too highly structured and dense vegetation, as for example artificially fertilised meadows with a high proportion of Fabaceae species, does not provide suitable habitat any more. It can be supposed that this makes the movements of the bird on the ground too difficult, similar to the effects observed with grasslands damaged by heavy rainfall (Schäffer & Weisser, 1996). Our method to measure vegetation density using a simple corncrake dummy, however, proved to be quite problematic in the heterogeneous vegetation of most grasslands. For the use in long-term monitoring, a better and even simpler measure should be found to measure the vegetation density from the corncrakes' point of view.

The importance of the large scale structure of the corncrake habitats has already been emphasised qualitatively (Flade 1991, Schäffer & Münch 1993). The quantitative results of Schäffer (1999) and of our study confirm this. Our results do not indicate an upper limit of additional structure, maybe resulting from strong bush growth on set-aside grasslands. But because of the fact that many +site were currently set-aside land, it will be interesting to follow the development of such sites with respect to large and small scale vegetation structure. Unfortunately, it has to be supposed that unless special conservation measures are taken, the grasslands will more and more develop into either poorly structured sites with intensive use on the one hand or into abandoned sites where a succession toward forests will start on the other hand. It will be a task of the conservationists to find alternatives (Schäffer & Weisser 1996, Crockford et

al. 1996, Green *et al.* 1997, Schäffer 1999) and to make them practicable for the farmers. The presented methods and models may be helpful tools for an efficient evaluation of conservation measures for corncrake habitats.

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Összefoglalás

A haris élőhelyválasztása a Szatmár-Beregi síkon, és javaslatok a további monitorozásra

A Szatmár-Beregi sík 1170 km2-ét mértük fel 1997-ben, benne 137 km² természetszerű gyeppel. A harisok élőhelyválasztásának vizsgálatához jól lehatárolható, és legalább 2 éneklő harist tartalmazó gyepeket hasonlítottunk össze a legközelebbi hasonló nagyságú gyepterülettel, ahol nem volt haris. A gyepek területét, a vegetáció magasságát és sûrûségét, friss biomassza per 33×33 cm, egy nedvességi indexet, egy élőhely-szerkezeti indexet, és a földhasználatot mértük, illetve becsültük minden mintavételi területen. A harisok által lakott gyepek produktívabbak, nedvesebbek, és összetettebb szerkezetûek voltak, mint a haris nélküli gyepek. A harisos élőhelyek több kezeléssel felhagyott illetve kevésbé intenzíven legeltetett részt tartalmaztak, mint a nem lakott gyepek. A haris jelenlétét prediktáló logisztikus regressziós elemzés a vegetáció magasságát, sûrûségét és az élőhely-szerkezetét építette a modellbe. Ezek azok a változók, amiknek a változását nagyobb területen is monitorozni szükséges, hogy a haris élőhelyek alakulását követni lehessen.

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Capture efficiency of small birds by mist nets

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The capture efficiency of 25-mm mesh-size mist nets was evaluated by direct observation in two habitats in a marshland in central Hungary. Bird activity was 0.85 birds/ mist net-h in reedbed and significantly less, 0.28 birds/mist net-h on a wet meadow. Vertical activity as well as capture efficiency was significantly different between the two habitats. Overall, 37% of the birds that hit the net escaped. The middle shelves of 4-shelved net were the most effective in both habitats, with a retaining efficiency of 67-75%. The bottom shelf retained 75% of birds in a pure reedbed but only 33% in a wet meadow area. The top shelves retained fewer birds than the middle ones and there was less between habitat difference (53 vs. 42% efficient in reedbed and wet meadow, respectively).

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1. Introduction

Mist nets, due to their ease of operation and effectiveness to catch birds when unattended, are widely used in ornithological studies. A mist net, when appropriately set up, is barely visible. Birds fly against the loosely hanging net, lose their momentum, become entangled, and are subsequently recovered from the net.

Standardised mist netting is a common bird censusing and monitoring technique, and several long-term projects have adopted it (Baillie 1990, Hagan *et al.* 1992, DeSante *et al.* 1993). As any sampling method with a passive catching device, where capture (sampling) results from the activity of the target organism, conditions influencing activity necessarily influence the numbers captured. Such effects for mist netting birds include mesh size (Heimerdinger and Leberman 1966, Pardieck and Waide 1992), material (Dorsch 1983), visibility and weather conditions (Karr, 1979, 1981, 1990, Jenni *et al.* 1996), habitat type (Bairlein 1981), bird size (Jenni *et al.* 1996), flight and territorial behaviour (Remsen & Good 1996). Nonetheless, a literature review (Remsen & Good 1996) found that many studies fail to mention, consider or attempt any correction of biases due to the above factors.

During a bird migration project in central Hungary, we observed mist nets in two plant associations, in order to determine their capture efficiency. In this paper we report that the retaining efficiency of the most frequently used mesh size, 25 mm, was about 63% for sparrow-sized small passerines. This escape frequency was different from that found in Switzerland and Italy (Jenni *et al.*, 1996).

2. Study area and methods

Our study site was located in the Ócsa Landscape Reserve (OLR), about 20 km SE of Budapest, Hungary. This reserve contains a number of different habitats, including reedbeds, wet meadows, bushes, poplar and alder forests. The OLR is the largest remaining wetland between the Danube and Tisza rivers on the Hungarian lowland. Such wetlands dominated the area until large-scale river regulation occurred in the last century. OLR has been the site of a long-term bird migration monitoring program since 1983 (Csörgõ, unpublished).

Mist nets set up at two sites representing the two dominant plant associations of the area were included in the observations. The first one was in a pure, dense reedbed (maximum vegetation height 2.7 m), the second one in a wet meadow with tall vegetation composed of (sparse) reed *Phragmites* communis. elderberry Sambucus nigra, and various tall herbs, grasses and vines. The maximum vegetation height in this habitat was 4.5m (due to a few tall elderberry bushes), but the main vegetation height was not different from that of the reedbed. The top line of the nets was about 20 cm above the top of the vegetation. Taller trees (up to 10 m) were min. 50 m away from the mist net sites. The mist nets (obtained from the British Trust for Ornithology, Thetford, U.K.) were made of black, tethered material, were 12 m long, and 2.7 m tall. The mesh size was 25 mm across, which is the most frequently used type in Europe to catch small passerines. Both mist net lines were 144 m long (12 nets \times 12 m long each), and were about 400 m from each other.

Observations took place between 17-24 August 1993, during the early phase of the autumn migration, in fine, still weather during the early morning hours (06:30-09:00) when bird activity was at its peak. Two observation sessions were taken during the evening activity period, between 18:00-20:00, on 17-18 August, 1993. Results were not different from the morning ones and the data were pooled. Observers took position about 10 m from the nearest net to be observed, hidden among the vegetation and behaving unobtrusively, watching four mist nets along the mist net line.

All birds that were, even if briefly, retained by the net were recorded. The species (if identifiable), position, and its eventual fate (escaped or captured) were also noted. All birds observed were of warbler size (Hungarian band size class 'A', inner diameter 5 mm). The body masses in this group range between 12-25 g. We classified them as similar in size, and did not evaluate the observations by size class. Mist nets were patrolled every hour.

Statistical tests were performed following Sokal & Rohlf (1995).

3. Results

3.1. Bird activity and general capture efficiency

A total of 133 mist net-hours were spent observing mist nets. During this time, 83 birds came into contact with the nets: 52 of them were caught, 31 escaped, giving an overall retaining efficiency of 62.6% (Tab. 1). On the meadow, the active density was, on average, 0.28 birds mist-net⁻¹ hour⁻¹ (*s.d.*= 0.27). Eighteen birds hit the net, and nine of these were caught, giving

Tab. 1. Mist net effectiveness at the Ócsa Landscape Reserve, central Hungary, August 1993.

Species	Caught	Escaped	% caught
Sylviid warbler, Sylvia	17	5	77.3
borin/S. atricapilla*			
Acrocephalus warbler,	8	0	100
Acrocephalus spp.**			
Greenfinch, Carduelis	1	0	100
chloris			
European Robin,	0	1	0
Erithacus rubecula			
Swallow, Hirundo rustica	2	1	66.7
Savi's Warbler, Locustella	1	0	100
fluviatilis			
Grey Flycatcher,	0	1	0
Muscicapa striata			
Black Redstart,	1	0	100
Phoenicurus ochruros			
Unidentified small passerine	22	23	48.9
Overall	52	31	62.6
+10 1 W 11 01 :	11 .1	D1 1	

* 1 Garden Warbler, S. borin; all others Blackcaps,

S. atricapilla

** 3 identified as A. schoenobaenus; 5 were A. scirpaceus/palustris

an overall success rate of 50%. In the reedbed habitat, mean active density was 0.85 birds mist-net⁻¹ hour⁻¹ (*s.d.*= 0.49), with an average retaining success of 70.3%. Overall, 43 of the 65 birds that hit the net were captured. The difference in activity between the two habitats was significant (Spjøtvoll-Stolin T'-test, T'=3.684, d.f.= 15, P < 0.05).

3.2. Species composition

The most common birds seen were Sylvia and Acrocephalus warblers. The species identified were: Blackcap (Sylvia atricapilla), Sedge Warbler (Acrocephalus schoenobaenus), Reed/Marsh Warbler (A. scirpaceus/palustris; this species is very difficult to confidently identify in the field when silent), Black Redstart (Phoenicurus ochruros), European Robin (Erithacus rubecula), Spotted Flycatcher (Muscicapa striata), Savi's Warbler (Locustella fluviatilis), Swallow (Hirundo rustica), and Greenfinch (Carduelis chloris).

The exact position of birds taken from the mist nets for ringing during the hourly mist net patrols was not noted. At ringing, only the capture area (mist net line) was recorded. An exact evaluation of the species or individual mist nets was thus not possible. The species composition of the birds ringed, originating from the reedbed + wet meadow mist net lines during the periods of observation was dominated by warblers: from the total of 87 birds, 41 were sylviids, and 30 were Acrocephalus spp. (Csörgõ, unpublished). The most common species were Blackcap, Reed Warbler, Greenfinch and Swallow (the last during the evening only).

3.3. Vertical distribution of activity & capture efficiency

The vertical distribution of activity was significantly different from uniform in both habitats (G-test, reedbed: G=27.62, d.f.=3, P<0.001; wet meadow G=21.26, d.f.=3, P<0.001). There was also a significant difference between the two habitats in the vertical distribution of both activity (Fig. 1, G-test, G=18.19, d.f.=3, P<0.001) and retaining efficiency (Fig. 2, G-test, G=27.50, d.f.=3, P<0.001).

In the reedbed, birds preferred to move at the level of the second shelf rather than higher (Fig. 1a). Very few moved near the bottom. The retaining efficiencies of the lower three shelves were almost identical: 67%, 75% and 75% (second, third, and bottom). The top shelf was less efficient (53%). Birds moving at higher levels in this habitat were underrepresented in the catch (Fig. 2a).

Birds on the wet meadow habitat tended to move high: >40% of birds contacted the net at top shelf level (Fig. 1b). The



Fig. 1. Vertical distribution of bird activity in mist nets in two marshland habitats, a reedbed and a wet meadow at Ócsa, Hungary. Number of birds observed: reedbed N=65, wet meadow N=18.

retaining efficiency of the top shelf was 42%. Few birds seemed to move at the lowest level of vegetation (3 of 28 individuals) and one of these only was retained in the bottom shelf. The two middle shelves retained 67% (second) and 72% (third) of the birds (Fig. 2). Consequently, birds moving at this height within the habitat were over-represented in the catch. For example, only 25% of all birds observed came into contact with the net at the level of the third shelf but 33% of the total catch came from this height.

3.4. Species-specific capture efficiencies

Although not all birds were identified to species, differences between species were evident. The *Sylvia* species were caught with a high efficiency (Tab. 1) and this varied little between shelves and habitats. This agrees with the findings of Jenni *et*



Fig. 2. Retaining efficiency of the different mist net shelves at the two marshland habitats at Ócsa, Hungary. Number of birds observed: reedbed, N=65, wet meadow, N=18.

al. (1996) who reported 0% escape for Blackcap and Garden Warbler (*S. borin*).

The observed retaining efficiency for the Acrocephalus warblers was also high. However, this is suspect as Acrocephalus spp. are plain-coloured birds and difficult to identify. It is probable that due to individual observer differences, those Acrocephalus spp. individuals that were not retained were not identified confidently and were recorded under the 'unidentified' category. If we classify all the unidentified birds as Acrocephalus spp., the calculated retaining efficiency would become 30/53 = 56.6%. The true retaining efficiency for Acrocephalus spp. probably fell between these two values. Jenni et al. (1996) found 68% capture success rate for Sedge Warbler (A. schoenobaenus), and 53% for Reed Warbler (A. scirpaceus). This seems to support our argument.

4. Discussion

As most of the observers were not trained ornithologists, birds that flew against the mist net and bounced back were not identified and thus not counted. Our estimate of the 'escape' probability is therefore conservative.

Size is an important factor in capture probability, and a difference of 15g in mass (in this case reflecting size differences between species, not the same species with different fat level) results in significant differences in catchability (Jenni *et al.* 1996). In addition, our observations showed that different species as well as birds moving at different levels reacted differently to the mist net. As a consequence, the capture probability varied by species and movement height.

It is plausible to assume that capture position would influence the intensity of attempted escape behaviour of a bird initially captured. Birds captured low on the wet meadow may well perceive an increased risk from ground-active predators, and struggle longer to escape than birds that are caught higher. Similarly, birds trapped in the top shelf and visible to aerial predators could be aware of their risky situation and struggle more vigorously to escape.

4.1. Comparison with other locations

Jenni *et al.* (1996) reported escape frequencies from three European locations, all of them more southerly than ours. Their evaluation and observation regime was somewhat different, so a direct comparison cannot be made. However, the overall escape rate at Lake Neuchatel, Switzerland, and Col de Bretolet on the Swiss-French border was much lower (7.7-10.5% under moderate or slower wind conditions) than in Hungary. Interestingly, escape rates of two common *Acrocephalus* species were high (29-46%). At our study site, few *Acrocephalus*-sized bird seemed to escape (0-23%).

The vertical distribution of capture effectiveness between reedbed habitats at Ócsa, Hungary and Lake Neuchatel, Switzerland (Jenni *et al.* 1996, Fig. 4), was not different (G-test, G=1.05, P<0.6). However, in the other comparable habitat ('bush' in Switzerland and 'wet meadow' in Hungary) there was a significant difference in vertical distribution of the retaining efficiency (G-test, G=17.6, d.f.=3, P<0.001). This indicated that there could be behavioural differences (for example in flight speed, vertical within-habitat activity, or awareness) by migrants along the migratory route.

4.2. Consequences of bird escape from nets

What is the significance of these observations? Birds build a mental picture of their habitats and, using this local information, behave so as to acquire resources they need and minimise risks (Weber et al. 1998). By using mist nets, where capture depends on the activity of the target, we introduce a 'risk' factor into the environment and induce birds to change their behaviour. This would be of little consequence if all birds would react the same way. Our sample would not be biased, because the capture effectiveness would change uniformly within the study population. We believe this is not the case. Not only birds captured and released but escapes such as observed in this study could contribute to the net avoidance behaviour of birds that is often observed during prolonged mist-netting. It is common experience that activity levels seemingly decrease during prolonged mist-netting sessions, even if all captures plus recaptures are counted. During migration studies, it is also frequently observed that an increase in activity level signal the arrival of a new, "naive" group of migrants (Lövei, unpublished).

Another consequence of the speciesspecific reactions to mist nets is that the quantitative species composition of the mist net catch is not a true representation of the density relationships of the bird assemblages sampled. This has been realised earlier (e.g. Karr 1968). There seems to be no similar evaluation of the possible consequences of this capture method for population studies. Population estimates using a capture-recapture method are not necessarily adversely affected: several of them allow for unequal probability of capture, distinguishing, for example, between local and transient birds (Manly 1977). For migration studies on individual species, we see the following problems:

- the possibility of overestimating fattening rates due to a higher probability of capturing and/or recapturing fat birds due to their reduced manoeuvring ability in flight;
- underestimating the ratio of small, lean birds in the population because they have a superior manoeuvring capability and thus avoid capture with a higher probability

Further, if mist nets are continuously in operation at standard sites for long, this could cause an underestimation of the length of stopover. This would result because the longer the bird stays, the more familiar it will become with the area, and this familiarity could decrease the probability of recapture.

A possible way to decrease these errors could be to establish a standard set of mist net locations, but not having actively catching mist nets at all of them, and frequently alternating the actual sites where mist nets are set up. It remains to be tested if this way of operation would be effective in reducing experimental errors of the type mentioned above.

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Összefoglalás

Függönyháló fogási eredményessége kistermetû énekesmadarak vizsgálatakor

A 25 mm szemnagyságú függönyhálók fogási eredményességét értékeltük direkt megfigyelésekkel két élőhelyen az Ócsai Tájvédelmi Körzetben. A madarak aktivitása szignifikánsan különbözött a nádas, illetve száraz nádas élőhelyeken. Az előbbiben 0,85 madár/háló×óra aktivitást, az utóbbiban csak 0,28 madár/háló×óra aktivitást figyeltünk meg. Az aktivitás hálózsebek magassága szerinti eloszlása szignifikánsan egyenlőtlen volt mindkét élőhelyen és egymástól is szignifikánsan különbözött. Mindösszesen, a hálóba került madarak 37%-a szökött meg az óránkénti ellenőrzés megérkezte előtt. A két élőhely között nagy különbséget találtunk: a nádasban a hálók a beléjük került madarak átlagosan 70%-át tartották vissza, míg a száraz nádban csak átlagosan 30%-ot. A legkevesebb madár a négy zsebes háló két középső zsebéből szökött meg. Ezek a zsebek a belekerült mada-

rak 67-75%-át visszatartották. A legalsó zseb a belekerült madarak 75%-át visszatartotta a nádasban, de csak 33%-ukat a száraz nádas élőhelyen. A legfelső zsebek mindkét élőhelyen kevésbé voltak hatékonyak, mint a középsők, de az élőhelyek közötti különbség itt kisebb volt (53% a nádasban, illetve 42% a száraz nádban).

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All EOU members as well as other ornithologists are invited to participate in the EOU 2003 conference. Contribution of posters, oral paper presentations and whole symposium sessions are very welcome. They should follow the spirit of the conference and present new results of ornithological research linking two or more scientific fields, present comparative reviews of research running in parallel in different countries, or present joint projects of research groups from different European countries. Invited plenary speakers will give links and perspectives of population biology, behavioural ecology, life history, biogeography, evolution and large scale projects in ornithology. The 4th International Shrike Symposium will be integrated in the EOU conference. Please refer to the EOU homepage **http://www.eou.at** for all conference details. Interested persons without internet access may contact the Secretary of the EOU, Dr. Wolfgang Fiedler, Max Planck Research Centre for Ornithology, Vogelwarte Radolfzell, Schlossallee 2, D-78315 Radolfzell, Germany.

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Daily changes in body mass of incubating Kentish Plovers

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We investigated the daily body mass changes in incubating female Kentish Plovers *Charadrius alexandrinus*. We found that the body mass of females decreased over the day. The change in body mass was significant both from morning to midday (median decrease: 3.36%), and from morning to afternoon (8.40%). We suggest two reasons for this decrease: depletion of fat reserves and the evaporation of water from body tissues. These changes may either indicate a physiological cost of incubation, or they may be the result of a strategic body mass regulation.

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1. Introduction

One of the key issues in behavioural ecology is how animals allocate time and energy to various activities (Cuthill & Houston 1997). Since resources are often limited, there must be trade-offs between various life-history components. For example, parent birds may enhance their current reproductive value by spending time and energy on incubating their clutch and raising their young, although these behaviours may reduce their residual reproductive value (Roff 1992, Kosztolányi & Székely 2002a). Such trade-offs are often interpreted as acting directly through the depletion of body reserves, i.e. it may indicate a cost of reproduction (Jones 1988, Kacelnik & Cuthill 1990). For example, low body reserves may reduce the chance of initiating a new clutch either in the same breeding season or in future

years, or they may reduce the chances of parent's survival until future breeding seasons (Hemborg 1999).

Mass loss during breeding is often interpreted as an indicator of physiological stress. For example, a significant mass loss during incubation has been detected in several Passerines (Moreno 1989, Halpern *et al.* 1997). Furthermore, a positive relationship was observed between mass loss of females and their reproductive effort, whereas the females' ability to allocate energy to self-maintenance decreased with mass loss (Merilä & Wiggins 1997).

Two types of body mass variation have been reported during incubation. Firstly, the mass of the incubating parent decreased in those species in which incubation was carried out by a single parent and/or nest attentiveness was very high (Moreno 1989, Hegyi & Sasvári 1998). This change may be due to the fact that the incubation metabolic rate (IMR) is often elevated above the metabolic rate of non-incubating birds, e.g. by 19-50% in Passerines (Williams 1996). Secondly, body mass did not show any trend over the course of incubation in those species in which both parents incubated the clutch and/or in which the nest was attended for a low percentage of time (Moreno 1989, Hegyi & Sasvári 1998).

The reproductive stress hypothesis, which argues that the mass loss of breeding birds is due to the increased energetic expenditure, has been frequently criticised. For example, mass loss may simply be due to degeneration of the reproductive organs (Ricklefs & Hussel 1984), or the loss of body mass may be an adaptive adjustment to reduce energetic cost of flight during brood rearing when the demands of the offspring increases (Nornberg 1981). Finally, low body mass reduces wing loading and enhances the take-off ability and flying performance, and thus reduces the risk of predation (Witter & Cuthill 1993).

Although shorebirds Charadrii have an immense annual variation in their body mass due to migratory fattening (Piersma 1994), only few body mass changes are documented during the breeding season. Nevertheless, these studies would be particularly important in shorebirds, since it has often been hypothesised that the changes in their body mass (and body condition) should influence their mating and parental behaviours (Ashkenazie & Safriel 1979, Erckmann 1983). Also, many shorebirds breed on the ground, and thus the cost of keeping the eggs within the required temperature range, e.g. on the frozen tundra (Piersma & Morrison 1994) or on desert sand, may have significant consequences on the body mass of incubating parent(s). In line with this argument the body mass of several subarctic shorebirds tended to decrease during reproduction (Soloviev & Tomkovich 1997), possibly due to their elevated metabolism.

The objective of our study was to investigate the daily changes in body mass of female Kentish Plovers Charadrius alexandrinus. Kentish Plovers are small ground-nesting shorebirds. Their incubation period is about 25 days and their chicks are precocial. Both the male and the female incubate the clutch (Kosztolányi & Székely 2002b), although shortly after hatching of the eggs one parent commonly deserts the brood (Paton 1995, Székely & Cuthill 2000). Males typically incubate at night, whereas females incubate mostly during the daylight period (Kosztolányi & Székely 2002b).

2. Study area and methods

Field work was carried out in May 1999 in Southern Turkey, near the village of Tuzla $(36^{\circ}42'N 35^{\circ}03'E)$. The study site was a salt marsh between Lake Tuzla on the south and arable land on the north. The size of the breeding population of Kentish Plover was about 1000 pairs (Székely *et al.* 1999).

Females were caught on their nest by a funnel-trap, and ringed with a metal ring and an individual combination of colour rings. Each female was captured three times: in the morning (06.00 h-09.00 h, local summer time, i.e. GMT+3 hours), at midday (11.00 h-14.00 h) and in the afternoon (16.00 h-19.00 h). At every capture their body mass was measured (± 0.1 g).

Captures of the same female were carried out on different days. We randomised the sequence of captures for each female to eliminate carry-over effect. The interval between first and second captures was 1.11 ± 0.20 days (mean \pm SE), and between the second and third captures was 2.00 ± 0.53 days. Only nests with three eggs (modal clutch size, Székely *et al.* 1994), and those incubated for more than three days were investigated. Further details of field methods are given elsewhere (Székely *et al.* 1999, Székely & Cuthill 2000, Kosztolányi & Székely 2002b).

The distribution of body mass was not normal, thus we used non-parametric tests such as Friedman two-way ANOVA (factor: time of the day, block: individuals). Comparisons between groups were conducted using Wilcoxon matched-pairs signed-rank tests. In the latter analyses we corrected the significance level for multiple comparisons by sequential Bonferroni adjustment (Chandler 1995). We used SPSS for Windows for statistical analysis. Values are given as median (lower quartile – upper quartile), and we provide the exact two-tailed probabilities. In all analyses the sample size was nine females.

3. Results

Body mass of females decreased during the day from 41.8 g (41.0 g-43.5 g) in the morning to 40.3 g (39.8 g-42.7 g) at midday, and 39.8 g (37.9 g-40.4 g) in the afternoon (Fig. 1.). Thus the body mass of females decreased by 3.36%(2.81%-4.98%) from morning to midday, by 3.72% (2.11%-6.77%) from midday to afternoon, and by 8.40% (1.69%-10.56%)



Fig.1. Body mass of incubating female Kentish Plovers over the day (N=9 females in all three periods). The thick horizontal line indicates the median; the bottom and the top of the box are lower (Q1) and upper quartiles (Q3), respectively. The whiskers indicate the lowest and highest observation, within the range defined by Q1-1.5×(Q3-Q1) and Q3+1.5×(Q3-Q1). An outlier is indicated by a circle.

from morning to afternoon. We estimated that females lost about 0.33 g/hour (0.07 g/hour–0.45 g/hour) of their body mass from morning till afternoon.

The mass change between morning, midday and afternoon was highly significant (Friedman test, $\chi^2=9.314$, df=2, P=0.007). The difference in body mass was also significant both between morning and midday (Wilcoxon matched-paired signed-ranks tests, Z=2.549, P=0.008), and morning and afternoon (Z=2.310, P=0.020), whereas the mass change was not significantly different between midday and afternoon (Z=0.980, P=0.383).

4. Discussion

Our results show that incubating female Kentish Plovers lose mass during the day. This result was unexpected, since females often interrupt their incubation by either spending a few minutes in the vicinity of nest and then resuming incubation, or being relieved by their mate for a variable period of time (Kosztolányi & Székely 2002b). In these recess times the females typically forage. Thus the total loss in body mass would have been larger if the females were to incubate constantly during the investigated daytime periods.

We suggest two ways for the observed loss in body mass: depletion of stored body fat and evaporation of water. Depletion of fat stores can be the result of the increased energetic demands of incubation or starvation. For example, it is probably costly to maintain the egg-temperature within the range in which the embryonic development is normal (i.e. between 30 to 40 °C, Purdue 1976). Female Kentish plovers relieve their incubating mate at dawn (Kosztolányi & Székely 2002b), when the ambient temperature is low. At this time of the day an increased metabolic rate may be required to keep the egg temperatures in the optimal range. At midday, when the ambient temperature is high, the parent has to cool the eggs. Thus, at midday the parents often shade the eggs and they may themselves lose a considerable amount of water by evaporation (Hinsley & Ferns 1994). Also, cooling the eggs may elevate the energy expenditure of the parents, for instance an increase of 1.3 BMR was shown in sandgrouse (Hinsley & Ferns 1994). So both cooling and keeping the eggs warm may be costly for the incubating parent, and thus they may result in depletion of fat reserves. The significant decrease in body mass between morning and midday suggests that heating the eggs may be more demanding than cooling in the Kentish Plover.

While the parent is restricted to sitting on its nest, it cannot replenish the lost reserves by feeding. For example, one reason why female Kentish Plovers stop incubating in the evening may be that they have to replenish their body reserves (Purdue 1976, Paton 1995). The other possibility is that nighttime incubation is more demanding than incubation during daytime, and thus if females are exhausted by egg laying (Monaghan *et al.* 1998) then the males are in a better position to carry out nighttime incubation. Future studies, preferably experimental manipulations, are required to identify how the various costs and benefits of incubation vary over the day.

Although we have limited information on the other potential explanations for the observed daily mass loss (such as the degeneration of reproductive organs and strategic body mass regulation), we make the following inferences. Firstly, it is unlikely that the loss of body mass was due to degeneration of reproductive organs (Ricklefs & Hussel 1984), since female body mass changed in a short, i.e. daily basis. Secondly, the strategic adjustment of body mass seems more plausible (Moreno 1989, Witter & Cuthill 1993, Thomas 2000), and we encourage researchers to consider the explanation that reducing body mass may be advantageous for requiring low cost of self-maintenance and/or for reducing the risk of predation. Nevertheless, we do not see any apparent reason why such mass loss would be adaptive only between morning and midday in the Kentish Plover.

In conclusion, our results show that the body mass of female plovers decreases during the day. This decrease may indicate a cost of incubation in terms of depletion of fat reserves and evaporation of water, although we cannot rule out the alternative explanation that body mass regulation is strategic.

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Összefoglalás

Széki lilék napi tömegváltozása a kotlás alatt

Széki lile tojók napi tömegváltozását vizsgáltuk a dél-törökországi Tuzla-tónál 1999 májusában. Az általunk vizsgált kilenc tojó mindegyikét három alkalommal fogtuk be és lemértük a tömegüket: reggel (06.00-09.00 h), délben (11.00-14.00 h) és délután (16.00-19.00 h). Mivel a befogások nem azonos napon történtek, ezek sorrendjét randomizáltuk.

Kimutattuk, hogy a tojó széki lilék tömege szignifikánsan csökken a nap során a kotlási periódus alatt. A madarak tömege 41.8 g (medián) volt reggel, 40.3 g délben és 39.8 g délután. Mind a reggeltől délig, mind a reggeltől délutánig történő tömegcsökkenés szignifikáns volt, míg déltől délutánig a madarak tömege nem változott szignifikánsan.

A vizsgálatunkban megfigyelt testtömeg csökkenésnek két okát feltételezzük. Az egyik a szülői zsírtartalékok leépülése, a másik a párologtatás során bekövetkező vízvesztés. A zsírtartalékok leépülése feltehetően a kotlás megnövekedett energetikai igényeinek a következménye, ami különösen nagymértékû lehet a reggeli órákban, amikor a tojásokat melegíteni kell az embriók normális fejlődéséhez (szignifikáns tömegcsökkenés reggeltől délig). A tojók vízvesztését a tojások evaporatív hûtése okozhatja a meleg déli órákban. Ráadásul amíg a szülők kotlanak a fészken csak korlátozott mértékben tudják táplálkozással és ivással pótolni a készleteiket. A tömegcsökkenés tehát utalhat a kotlás költségeire, ugyanakkor nem zárhatjuk ki azt sem, hogy stratégiai szabályzás eredménye. Ennek tisztázására további vizsgálatok szükségesek.

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Short communications - Rövid közlemények

Changes in the frequency of hunting techniques in the Red-backed Shrike Lanius collurio during the breeding season

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Shrikes (Laniidae) are sit-and-wait predators, often seen on twigs of trees, on the top of bushes, sticks or fences, looking for prey on the ground or in the air. Although aerial chase is one of the hunting techniques in the foraging repertoire of shrikes, they usually catch food on the ground. For example, in Taiwan, ca. 90% of the foraging attempts by Brown Shrikes (Lanius cristatus) were oriented toward the ground from the perch (Severinghaus & Liang 1995). The frequency of aerial chase increased to 30% in tall, 1.5-2 m high grass for the Loggerhead Shrike (Lanius ludovicianus) in Florida (Yosef & Grubb 1993), whereas the proportion of aerial hunts decreased through the season in the Lesser Grey Shrike (Lanius minor) in Slovakia (Wirtitsch et al. 2001). On the other hand, Great Grey Shrikes (Lanius excubitor) were able to select foraging sites with higher food availability (Fuisz & Yosef 2001).

The Red-backed Shrike (*Lanius collurio*) is a common bird species during the breeding and post-breeding seasons in Hungary (Tucker & Heath 1994, Schmidt 1998, Fuisz & Yosef 1998). In the present study the hunting behaviour of Redbacked Shrikes was studied in a dense population in Hungary. I describe a case when aerial chase was observed in an unusually high rate (>90%), and demonstrate the change of the frequency of hunting techniques during the breeding season. Besides these, the observations set up a few questions and possible explanations on the causes of aerial chase.

The foraging behaviour of male Redbacked Shrikes was studied at the beginning and at the end of their breeding season (22-28 May and 2-18 July, 1997). The study was carried out in the Medvesplateau, in the surroundings of the town Salgótarján, in northern Hungary (48°10'N; 19°50'E). In this area shrikes were found in bushy pastures and at forest edges. Main bush species in the area are dog rose (Rosa canina) and blackberry (Rubus fruticosus), but blackthorn (Prunus spinosa) and hawthorn (Crategus monogyna) are also present. In the study area the first eggs of the Red-backed Shrikes are usually found in mid-May, but a high proportion of the nests is usually lost to predation or rain. Replacement clutches proved to be more successful. In early July most pairs fledged juveniles in their territories. Although these young birds already have the ability to forage

Habitat:	ungrazed	ungrazed	ungrazed	grazed	ungrazed
Grass height:	moderate	high	high	low	high
Nesting period:	incubation	nestling	fledging	fledging	post-fledging
Time:	May	July	July	July	July
Foraging method:					
ground hunting	56 (93%)	33 (92%)	3 (5%)	35 (70%)	2 (8%)
aerial chase	4 (7%)	3 (8%)	52 (95%)	15 (30%)	22 (92%)
n	60	36	55	50	24

Table 1. The frequency of foraging tactics in ungrazed old pasture and grazed pasture habitats, in different nesting stages.

individually, parents usually feed them, and juveniles often beg for food from their parents. (I refer to this stage as "fledging stage".) After 1-2 weeks juveniles mainly forage individually, and the boundaries of the territories disappear, families move around in the area ("post-fledging stage") (Moskát unpubl.).

Perch height, foraging type and flying distances were registered in 12 territories. Hunting bouts of shrikes were observed once in the nesting stage within each territory for 30 minutes. While hunting on the ground was almost the exclusive foraging technique during the incubation and nestling periods (93% and 92%, respectively), aerial chase played a more important role during the fledging and postfledging periods (95% and 92%, respectively) (Table 1). Just the opposite tendency was observed in the Lesser Grey Shrike in Slovakia (Wirtitsch et al. 2001). Pairwise comparisons of Red-backed Shrikes' hunting techniques in successive breeding periods by a chi-square test of independence (Norusis 1986) showed no significant differences between the incubation and nestling stages, or between the fledging and post-fledging stages $(\chi^2=0.092, df=1, P=0.761, and \chi^2=0.234,$ df=1, P=0.629, respectively). However, a significant difference was detected between the nestling and fledging stages in the ungrazed habitat (χ^2 =67.63, df=1,

P<0.001). Aerial chase dominated ground hunting in sites where no grazing occurred, such as old pastures and forest edges, whereas in areas where cattle grazing was important, ground hunting was more frequently observed in the fledging period (70%). The difference in the frequency of hunting techniques between grazed and ungrazed habitats proved to be significant during the fledging stage $(\chi^2 = 47.24, df = 1, P < 0.001)$. Although birds had difficulties with foraging on the ground in high grass late in the season, only a few aerial chases were observed (8%) during the nestling period at late nests. If shrikes were to fly far from the perch site (>15 m), they often missed their prey and in this case they hovered close to the ground (ca. in 0.5-1 m height). Hovering is an energy-consuming behaviour (Yosef & Grubb 1983). For this reason the shrikes preferred hunting on the bare ground of a small road crossing the territories. In these territories ca. 40%-75% of all ground huntings were done on these narrow roads. Because the frequency of aerial chase was low (8%) in the nestling period and high (95%) in the fledging stage at different nests within the same season, area and habitat, only the stage of breeding can explain the difference. Aerial chase is a visible hunting type, which possibly increases the risk of predation by Sparrowhawks (Accipiter *nisus*), the main aerial predator of Redbacked Shrikes in the study area. The behaviour of the parent birds is rather shy during the nestling period, which may be related to why aerial chase is not an advantageous hunting tactic at that time.

Grass height is important in shrike foraging, because tall grass limits the visibility of prey (Rothhaupt 1995). Grass height increased considerably during the breeding season. In late May grass height was only ca. 10 cm, but in early July the average grass height increased to ca. 50 cm. Grass was mainly composed of Agrostis tenuis. Scattered Festuca pratensis of ca. 100-120 cm height formed another, but less dense grass layer above the former one. In pastures the grazed grass was only ca. 5 cm high. Prey were superabundant in the study area in July. Especially in tall grasslands, Orthopterans offered easily catchable and valuable prey for the shrikes, however, shrikes preferred aerial food in the fledgling stage, when Breezeflies (Tabanus bovinus) were common in the area. I observed Red-backed Shrikes chasing and catching Breeze-flies several times. By mid-July fledglings in most territories learned to forage individually, but parents still fed them sometimes. At this time of the season males preferred to choose the top of high trees (up to 25 m) as perch sites, which they rarely, if ever, used in the earlier parts of the breeding period. One possible reason for this is that by mid-July territory boundaries more or less disappeared, and males were free from territorial and breeding behaviour, so they could choose unusual perch sites if it was advantageous for them to do so. In earlier stages of nesting the shrikes would waste a lot of time and energy flying up to the high perch sites. I also suppose that

parent birds tried to avoid the begging of the fledged juvenile birds. When males sat up on high trees, at 15-25 m height, they hunted only by aerial chases, and they rarely fed fledglings. I observed only one case when a juvenile bird flew up to 22 m to beg the male parent for food, and once a male flew up to 15 m to feed a juvenile bird. Another important aspect of aerial chases from high perches is that in the post-fledgling period families wander around in the area, and sometimes they get into the territories of late breeders. One such wandering family was observed to forage without any difficulties, but the male was suddenly attacked by the territory holder male when he went down from the top of the trees to the bush layer. No attack was observed against foreign juveniles foraging mostly in the bush layer.

Higher perch sites allow shrikes to overlook a larger hunting area around the perch site. Moskát et al. (2000) found a strong positive correlation between height of the perch site and foraging distance in the Bull-headed Shrike (Lanius bucephalus) in Japan. In contrast, Brandl et al. (1986) reported that Red-backed Shrikes prefer pastures because lower grass height allows better access to prey. Bohall-Wood (1987) and Yosef & Grubb (1993) found similar results for the Loggerhead Shrike in Florida and Wirtitsch et al. (2001) for the Lesser Grey Shrike in Slovakia. Foraging in high vegetation needed more energy, because shrikes flew more as a consequence of the higher frequency of aerial chase.

Although this study was based on a small sample size, the results demonstrate some basic tendencies or generate new hypotheses to explain the increase in aerial chase of Red-backed Shrikes at the end

of their breeding season: (1) There is a general tendency of shrikes to forage more frequently in the air when valuable aerial food (e.g. Breeze-flies) becomes more readily available during the breeding season. In the early fledging period aerial chase is an effective way to collect food for feeding juvenile birds (Seasonal effect). (2) Aerial chase can also be an alternative hunting technique to ground hunting when foraging on the ground is limited by vegetation structure (Effect of habitat or visibility of prey). (3) In the post-fledging period aerial chase from high perch sites may give a chance for the parent birds to escape from the begging juveniles (Escape from fledglings). (4) Because aerial chase was rare in the nestling stage when the parent birds are shy, aerial chase is likely to involve higher risks of predation than ground hunting (Predation risk on foraging). (5) Aerial chase from high perch sites also offers a possibility for a temporary, vertical sharing of the territory between a wandering family and the territory owners that usually forage on the ground (Territory sharing). I suggest future studies to reveal the explanation for the increase in the frequency of aerial chases during the breeding season in the hunting behaviour of Red-backed Shrikes.

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