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Habitat segregation among the woodchat shrike, *Lanius senator*, the red-backed shrike, *Lanius collurio,* and the masked shrike, *Lanius nubicus,* in NE Greece

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A b s t r a c t We studied habitat selection of the woodchat *Lanius senator*, red-backed *Lanius collurio*, and masked *Lanius nubicus* shrikes in NE Greece, where they occur sympatrically. During the breeding season the masked shrike is most distinct, but woodchat and red-backed shrikes highly overlap in their habitat use. Multivariate discriminant analysis revealed the best separating variables from a set of 13 vegetation variables measured around perch sites. For axis one the best separating variables were identified as the woodland character, and the shrub character for axis two. By the help of the multivariate discriminant analysis the habitat selection in these avian species can be separated with high probability (64%, 64%, and 86% for the woodchat, red-backed and masked shrikes, respectively).

Key words: shrikes, sympatry, habitat selection, multivariate analysis

Introduction

Although shrikes (Laniidae) are medium-sized songbirds, they hunt for large insects and small vertebrates, combining the insectivorous and carnivorous mode of feeding (C a d e 1995). In Europe most of the species show a severe decline and regional extinction in several countries (T u c k e r & H e a t h 1994, Yosef 1994, Y o s e f & L o h r e r 1995, H a g e m e i j e r & B l a i r 1997). Extreme examples are those of the red-backed shrike *Lanius collurio* that disappeared from Britain in 1989 (P e a k a l l 1995), and the lesser grey shrike *L. minor*, which is almost extinct in France (L e f r a n c 1997). In Europe there are five breeding shrike species, namely the red-backed shrike, the lesser grey shrike, the great grey shrike *L. excubitor*, the woodchat shrike *L. senator*, and the masked shrike *L. nubicus*. Additionally, the southern subspecies of the great grey shrike *L. e. meridionalis*, inhabits southern France and the Iberian peninsula, and is treated by certain authors as a separate species *L. meridionalis* (L e f r a n c 1995, L e f r a n c & W o r f o l k 1997). The coexistence of these small predators in the same geographical area is affected by habitat preference and interspecific competition. Generally, there is a diversity of factors that affects habitat use of avian species, and even ecologically similar species segregate by fine tuned differences in habitat use (C o d y 1985a). Earlier in the last century, in Europe there were more places where three or four shrike species occurred sympatrically, like the woodchat, red-backed, great grey and lesser grey shrikes in SE Gemany (U l l r i c h 1971). The latter three species still breed sympatrically in Slovakia (K r i š t í n , in litt.). In recent years the multispecies shrike assemblages tend to disappear because of the strong decline of some shrike species (Y o s e f 1994). At present NE Greece is almost the only area in Europe where

the breeding range of four shrike species, namely that of the woodchat, the red-backed, the lesser grey and the masked shrikes, overlap. This "hot spot" area for shrikes partly extends to the southern part of Bulgaria and northern-western Turkey. The masked shrike has only a limited range in Europe, and is concentrated in the north-eastern part of Greece, including a few islands in the Aegean Sea. It also occurs along the western cost of Turkey, and the island of Cyprus (Lefranc & Worfolk 1997), and extends to Israel (Inbar 1995). Although the Greek population has declined considerably, its population is stable in Bulgaria. However, the Bulgarian population is small, and contains no more than 100 pairs, but appears to be increasing (Tucker & Heath 1994). Unfortunately, no data are available whether these species coexist in the same breeding habitats, and the type of specialization on habitat structure that is to be found at the regional or the local spatial scales.

The aim of the present study was to examine how the three sympatric shrike species breeding in NE Greece are separated by habitat requirements. We analyse how vegetation structure affects habitat occupancy pattern of the three shrike species. We wanted to determine which habitat variables separates them.

Study Area and Methods

The study was conducted in the surroundings of the town Alexandroupolis, NE Greece (40°50'–41°10'N, 25°55'–26°15'E), in the vicinity of the villages Avas, Lefkimi, Dadia, and Loutros during 6 and 13 June, 1997. This period coincides with the breeding season for all of the studied species. No fledglings were observed at that time, but several nests had well-developed chicks. Although some of the habitats in the study area seemed to be similar to the breeding habitat of the lesser grey shrike in central Europe (Krištín 1995, Krištín et al. 2000, Lovászi et al. 2000), we observed only one lesser grey shrike, so this species was excluded from the analysis. Therefore we sampled habitat parameters of the woodchat, red-backed and masked shrikes.

The study area is characterised by hills (up to 300 m), covered mainly by bushy pastures, scrubs, and small woodlands. Riverine forests and agricultural areas occur in the valleys, but closed forests were found only at higher elevations. In the field we characterised each shrike site by the main habitat type. This is not easy because shrikes occupy habitats that exhibit relatively fine-grain patchiness at the scale of individual territories (Yosef & Grubb 1992), and they are often a mixture of two or more habitat types (e.g. cereal field and olive grove). All of the sites were recorded on video tape for later identification. We characterised six habitat types: (1) Forest edge: edge of broad-leaved forest (*Quercus* spp.), sometimes with scattered pines (*Pinus* spp.), with thorny shrubs, or with small patches of grassland; (2) Olive, almond, and walnut groves, or the mixture of them (generally old, but rarely young stands); (3) Cereals: cereal fields with hedges or sparse trees; (4) Bushy pasture and scrub (xerophytic): dense scrub on hillside, or small patches of thorny shrubs, occasionally Junipers, or scattered trees; (5) Bushy pasture and scrub (mesophytic): patches of shrubs with scattered trees, mainly in the valleys; (6) Riverine woodland: dense wooded vegetation with well-developed bushes along the streams in the valleys, occasionally with old *Platanus* trees.

Following the guidelines for habitat description (James & Shugart 1970, Noon 1981), we measured 13 habitat variables in the field within a 25 m radius circle around the perch sites of the shrikes: percent foliage cover (%), mean height of trees (m), mean diameter of tree canopies (m), mean distance between tree canopies (m), mean diameter of

tree trunks at breast height (m), mean distance between tree trunks (m), percent bush cover (%), mean height of bushes (m), mean bush diameter (m), mean distance between bushes (m), percent grass cover (%), mean height of grass (m), percent bar ground cover (%). When tree or bush cover was 0% at a sampling circle, variables mean distance between tree canopies and mean distance between tree trunks, were set up as the diameter of the sampling circle (50m). The same value was given to variable mean distance between bushes if bush cover was 0%. By this recalculation we avoided giving the same value (zero) to two separate extreme cases: (i) when distances between canopies, tree trunks or bushes were zero because of the high density of trees or bushes, and (ii) when these variables were not measurable because of the lack of trees or bushes within the sampling circles. Variables deviating from the normal distribution were transformed (Dunn 1981). All percentage variables were arcsine transformed (Zar 1984).

Although we did not colour-ring the populations, we measured only one set of habitat variables within a territory in order to avoid pseudoreplication in the data set. Then we moved on until we found a new territory.

Overlap in habitat selection was calculated by the Petraitis formula (Petraitis 1979). The main advantage of this likelihood measure is that a significance test is available for it (Petraitis 1985). The computer program SPOVRLAP was used for calculation (Ludwig & Reynolds 1988).

The multivariate discriminant analysis (MDA) is a suitable technique for evaluating the best discriminator variables between the species and to test the separation among the populations within the canonical space (Morrison et al. 1997). Different variants of MDA have already been applied to compare niche partitioning of closely-related avian species (Cody 1985b), to compare habitat selection during migration and breeding (Moskát et al. 1993), or the habitat use of taxonomically different species, like the loggerhead shrike *Lanius ludovicianus* and the American kestrel *Falco sparverius* (Gawlik & Bildstein 1995). MDA was performed with SPSS/PC+ (Norusis 1990). Both discriminant function coefficients and discriminant loadings are used to explain the relationships between the discriminant functions and the original variables, but discriminant loadings offer a more appropriate approach for interpretation because of the potential multicollinearity between variables (Morrison et al. 1997, Sharma 1996).

Results

Altogether 117 samples on the vegetation structure around perch sites were collected. Woodchat shrikes and red-backed shrikes were common in pastures, but the masked shrike was found only in special habitats, like olive groves and orchards, in valleys with patchy but well-developed vegetation, and generally along streams. Vegetation samples were collected at 56 sites for woodchat shrikes, 33 for red-backed shrikes, and 28 for masked shrikes.

None of the species were found in all of the six habitat categories, but the woodchat and the red-backed shrikes were observed in five habitats. The masked shrike showed the narrowest range and occurred in only four habitats (Table 1). More than half of the woodchat shrikes (53.6%) were found in open xerotherm bushy pasture or woodlands. This habitat was also preferred by the red-backed shrike (42.4%) in addition to the forest edge habitat (36.4%). No masked shrike occurred in the xerotherm open bushy pasture or woodland habitat, but preferred the olive grove and orchard habitat (53.6%), the mesophil

Table 1. Habitat distribution of the woodchat shrike, red-backed shrike and masked shrike in NE Greece (percentages and total number of observations).

Habitat	Woodchat Shrike	Red-backed Shrike	Masked Shrike
Forest edge	14.3	36.4	3.6
Olive grove or orchard	10.7	3.0	53.6
Cereals	8.9	6.1	0
Bushy pasture and woodland (xerotherm)	53.6	42.4	0
Bushy pasture and woodland (mesofil)	12.5	12.1	21.4
Riverine woodland	0	0	21.4
N	56	33	28

Table 2. Specific pairwise overlap (SO) of habitat distribution of the woodchat, red-backed, and masked shrikes in NE Greece, calculated by the Petraitis formula.

Pairs of shrike species		SO	U	df
woodchat	- red-backed	0.848	18.509**	5
red-backed	- woodchat	0.839	11.569*	5
woodchat	- masked	0.000	1295.234***	5
masked	- woodchat	0.007	275.215***	5
red-backed	- masked	0.000	632.579***	5
masked	- red-backed	0.004	305.257***	5

* = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$

Table 3. Wilks' Lambda (U-statistic), univariate F-ratio with 2 and 114 degrees of freedom, standardized discriminant coefficients, and correlations between dicriminating variables and canonical discriminant functions (discriminant loadings) (PFC: percent foliage cover (%), MHT: mean height of trees (m), MDTC: mean diameter of tree canopies (m), MDBTC: mean distance between tree canopies (m), MDT: mean diameter of tree trunks at breast height (m), MDBTT: mean distance between tree trunks (m), PBC: percentage bush cover (%), MHB: mean height of bushes (m), MBD: mean bush diameter (m), MDBB: mean distance between bushes (m), PGC: percentage grass cover (%), MHG: mean height of grass (m), PBGC: percentage bare ground cover (%)).

Habitat variable	Wilks' Lambda	F	Standardized discriminant coefficients		Discriminant loadings	
			Function 1	Function 2	Function 1	Function 2
PFC	0.891	6.992**	0.277	0.262	0.427	-0.070
MHT	0.787	15.450***	0.288	0.222	0.637	-0.081
MDTC	0.765	17.490***	-0.010	0.070	0.672	-0.148
MDBTC	0.907	5.864**	-0.697	1.798	-0.394	0.031
MDT	0.789	15.25***	0.140	-0.520	0.595	-0.289
MDBTT	0.949	3.052	0.567	-1.964	-0.272	-0.108
PBC	0.862	9.112***	0.109	0.701	0.038	0.629
MHB	0.883	7.551***	0.434	0.195	0.257	0.470
MBD	0.906	5.942**	0.006	0.239	0.074	0.500
MDBB	0.927	4.493*	0.275	0.029	0.034	-0.441
PGC	0.795	14.740***	-0.133	0.070	-0.596	-0.244
MHG	0.923	4.739*	0.512	0.284	0.348	0.090
PBGC	0.937	3.839*	0.407	0.107	0.290	-0.171

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

bushy pasture or woodland (21.4%), and the riverine woodland habitats (21.4%). Pairwise comparison of the three shrike species in habitat overlap revealed a higher similarity between the woodchat and red-backed shrikes ($0.839 < SP < 0.848$), and a much lower overlap with the masked shrike ($0.000 < SP < 0.007$; Table 2.), when the value of the general overlap (GO) was 0.717. Although all of the differences in habitat occupancy of any pair of shrikes were statistically significant ($P < 0.05$ for all), the differences between the masked shrike and the woodchat or red-backed shrikes proved to be the widest ($P < 0.001$).

Vegetation variables were tested by the univariate Wilks' Lambda statistic. It tests the differences in the means of the three species for each habitat variable (Table 3.). Except for the variable mean distance between tree trunks, all of the variables measured showed significant differences among the three groups. Multiple discriminant analysis of the habitat variables grouped for the three shrike species revealed highly significant differences between the groups (Table 4). In the case of the first discriminant function the highest positive loadings were for the variables mean height of trees, mean diameter of tree canopies, mean diameter of trunks, percent foliage cover and the highest negative loadings were for percent grass cover and mean distance between tree canopies. In the case of the second discriminant function the highest positive loadings were found for the variables percentage bush cover, mean bush diameter, mean height of bushes, and the highest negative loading were get for mean distance between bushes. So we can interpret axis one as the woodland character, and axis two as the bush character. The classification probability (i.e. the probability that a habitat sample that belongs to a given shrike species can be classified correctly) was 86% for the masked shrike and 64% for both the woodchat and the red-backed shrikes (Table 5).

Table 4. Statistical properties of the discriminant functions.

	Function 1	Function 2
Eigenvalue	0.6606	0.4021
Percent of variance	62.16	37.84
Cumulative pct of variance	62.16	100.00
Canonical correlation	0.6307	0.5355
Wilks' Lambda	0.4295	0.7132
Chi-square	91.272	36.500
df	26	12
Significance	$P < 0.001$	$P < 0.001$

Table 5. Results of classification derived from discriminant analysis showing actual and predicted species (group) membership for woodchat shrike, red-backed shrike and masked shrike based on vegetation structural data around perch site within territories.

	Predicted group membership		
	woodchat shrike	red-backed shrike	masked shrike
woodchat shrike	64%	18%	18%
red-backed shrike	21%	64%	15%
masked shrike	7%	7%	86%

Discussion

Segregation mechanisms on the local scale play an important role in the coexistence of related species. Including the much rarer lesser grey shrike, four *Lanius* species coexist in NE Greece, and this overlap is restricted to a limited area around Alexandroupolis. At present the masked shrike sparsely inhabits Greece and occurs only east of Asprovalta (Handrinos & Akriotis 1997). It shows a higher frequency in the Alexandroupolis area, but earlier it was a regular breeder along the east coast between Thessaloniki and Athens. On the Turkish side of the border these species also overlap locally. In the Alexandroupolis area we found that masked shrikes separated well from the woodchat and red-backed shrikes by habitat, using riverine and mesophil bushy woodlands and bushy edges of forests. We found a high overlap between the woodchat and the red-backed shrikes in the Alexandraoupolis area, but the woodchat shrike showed a tendency to use xerotherm bushy pastures, and did not avoid cereal fields when some bushes were present. The red-backed shrike showed a greater tendency to occupy forest edges, mesophil bushy pastures and woodlands. This is similar to the habitats in Central Europe where this species is found.

In central Italy Guerrieri et al. (1995) studied the habitat selection of three coexisting shrike species, namely the woodchat shrike, the red-backed shrike, and the lesser grey shrike. The latter species was rare and was found in only 2.6% of the 10x10 km quadrates. Shrikes were segregated mainly by vegetation characteristics. The lesser grey shrike preferred habitats with scattered low shrubs and reduced arboreal components. The red-backed shrike occurred in each habitat type, but preferred edges of dense arboreal and shrubby formations. The woodchat shrike overlapped with the other shrike species, especially the red-backed shrike.

Some altitudinal differences can be observed in the distribution of shrike species in Greece (Handrinos & Akriotis 1997). The woodchat shrike occurs mainly on the coastal plains, and in the lower foothills, up to 500 m a.s.l., but occasionally goes up to 1000 m. The red-backed shrike breeds mainly between 500–1500 m, but sometimes up to 1700 m. Locally, as in our study area, it is also found at sea level and in the lower hills. The lesser grey shrike is restricted to altitudes from sea level to 1000 m. We found most of the woodchat and red-backed shrikes in NE Greece at lower elevations, from the coastal plains up to 300 m, because xerotypic pastures mainly occur in the lower elevations. The masked shrike was found in the lower parts of the valleys, and the coastal lowlands in olive groves and orchards. We do not consider elevation as a separating factor among the shrike species, because the availability of suitable habitats changes with elevation. At higher elevations the closed forest is generally not suitable for shrikes. The red-backed shrike shows the greatest affinity to small open patches with bushes and young trees in the mountains. Fuisz & Yosef (1997) showed the preference of post-breeding red-backed shrikes for forest edges and pastures in Hungary, but they did not find red-backed shrikes in closed broad-leaved forests. Our results explain this by higher preference of this species for denser vegetation than the woodchat shrike.

On Mount Hermon in Israel the woodchat, red-backed, and masked shrikes, and also the southern form of the great grey shrike ("meridionalis" group) occur sympatrically in the 300–1600 m elevational zone (Inbar 1995). The highest occurrence of shrikes is consistent with the distribution of bushes and tall trees. An obvious tendency for separation by habitat characteristics was described for the area. The great grey shrike preferred habitats with scattered thorny trees and bushes; the woodchat shrike inhabited areas with thorny bushes and shrubs, and also in sparse orchards; the red-backed shrike occurred in the steppe

forest with thorny bushes and trees in the elevational zone 1200–1600 m, and also at lower elevations; and the masked shrike was restricted to lower elevations, mainly to 1000m. This species preferred cherry and apple orchards.

On the local geographical scale, taxonomically similar species are separated by habitat. If they coexist in the same habitat, these species generally show divergent evolution, if not, they have become reproductively isolated (C o d y 1973). In our study only the masked shrike showed clear separation by habitat. Territorial behaviour, differences in morphology, diet and hunting techniques may also be important. Availability of high quality perch sites also has an importance for site occupancy (M o s k á t et al. 2000). Although shrikes are interspecifically territorial (C r a m p & P e r r i n s 1993), several studies have reported no territorial interactions among different shrike species (I n b a r 1995). Sometimes shrikes spread sparsely over the area, having a population density below the potential carrying capacity of the habitat (T e m p l e 1995). Although, in our study area at least, the woodchat and red-backed shrikes had generally neighbouring territories, we did not observe any interspecific conflict among any of the shrike pairs. However, one of the authors (C. M.) observed in northern Corfu a male woodchat shrike, which attacked and chased out of his territory an intruding lesser grey shrike. In the Kalahari desert, in Botswana, wintering lesser grey shrikes dominate overwintering red-backed shrikes in aggressive encounters (H e r r e m a n s 1998), and also in the breeding ground in Slovakia (H. H o i and A. K r i š t í n pers. com.). We suppose that interspecific conflicts are more severe at the beginning of the breeding season when boundaries of the territories are being established. In northern Japan, the bull-headed shrike *Lanius bucephalus* occupies the optimal habitats before the arrival of the brown shrike *Lanius cristatus* (T a k a g i & O g a w a 1995). There are other types of segregation mechanisms working on the time scale; e.g. the great grey shrike is a winter resident in Hungary, but the lesser grey shrike is a breeding species. They can never be seen simultaneously (K e v e 1984).

R e c o m m e n d a t i o n s f o r c o n s e r v a t i o n

Throughout Europe changes in land use and management seem to be the most important factors responsible for the decline of shrike species (T u c k e r & H e a t h 1994, L e f r a n c 1997). Multivariate analysis of the habitat structure proved to be helpful in finding the differences in the habitat selection on a fine-scale habitat level. Multiple discriminant analysis revealed the most important structural variables affecting habitat separation among the three sympatric shrike species. Most of the woodchat shrikes inhabited habitats containing bushy pastures, therefore sheep and goat grazing help to preserve these habitats from forest succession. The government in Greece subsidises this traditional farming method in order to maintain this habitat. Although this subvention is due to the black vulture *Aegipius monachus* population and for other raptor species in the surrounding of the WWF station in Dadia, this conservation management is also favourable for the woodchat shrike. The red-backed shrike population is not threatened in this area. It mainly breeds at forest edges and also in shrubby pastures, overlapping with the woodchat shrike. The masked shrike seems to be the most vulnerable shrike species in the area. As a considerable decline was recently shown in the species (T u c k e r & H e a t h 1994), nature conservation has to focus on this species in NE Greece. We do not expect that the masked shrike population can survive in the future without preserving old olive, almond and walnut groves, and additionally old *Platanus* trees along the streams.

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