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Social foraging and habitat use by a long-distance passerine migrant, Whinchat *Saxicola rubetra*, at a spring stopover site on the SE Adriatic coast

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Abstract The preference for foraging in groups and the effect of physiognomic factors of a habitat on its use by foraging Whinchats (*Saxicola rubetra*) was studied during spring migration stopover in a mosaic cultural landscape at the SE Adriatic coast. Every record of spatially distinct Whinchats, either a solitary individual or a group, was referred to as a Whinchat unit. The units were classified as intensively foraging, less intensively foraging or non-foraging and divided into four size classes. The effect of physiognomic habitat factors on use of habitat by foraging Whinchat units was modelled. All possible additive models using logit link function were constructed from five independent physiognomic variables: (1) natural perches (NP), (2) artificial perches (AP), (3) high herbal vegetation (HHV), (4) open bushes (OB) and (5) heterogeneity of vegetation types (HVT). Variables HHV and OB were included simultaneously in the models. Models that were substantially supported by the data were selected according to second order Akaike's information criterion AIC_c. Two such models contained variable(s) (1) NP and (2) NP + AP. The relative importance weights of physiognomic variables NP, AP, HVT, HHV and OB were 1, 0.38, 0.24, 0.13 and 0.13, respectively. Perches were thus the most important physiognomic habitat factor affecting habitat use by Whinchats in a mosaic cultural landscape. The great majority of Whinchats foraged in groups and the proportion of intensively foraging Whinchat units increased with unit size, leading to the conclusion that

Whinchats preferred social to solitary foraging on the spring stopover at the SE Adriatic coast.

Keywords Whinchat (*Saxicola rubetra*) · Spring migration · Social foraging · Habitat use · Effect of physiognomic habitat factors

Introduction

Birds adapt their migration strategies mainly to minimise overall journey time, energy consumption or predation risk, or combinations of these (Alerstam and Lindström 1990).

Stopovers between migratory flights are essential for birds to refuel, take up water and rest (Newton 2008), but also account for the majority of time and energy spent on the entire migration (Hedenström and Alerstam 1997; Alerstam and Hedenström 1998; Wikelski et al. 2003). Stopover strategies that minimise these expenditures are therefore favoured in evolution. Behavioural responses such as social foraging (Ekman and Hake 1988; Szekely et al. 1991) and selection of high quality habitats (Schaub and Jenni 2000) are involved in successful accomplishment of a stopover.

Presence of competitors limits the amount of food available to an individual but it can still be favourable for birds to forage in flocks. Potential payoffs of social foraging for a bird on migration are improved searching for food, enhanced capture and consumption of food, reduced time and energy costs of foraging or increased protection from predators (Ekman and Hake 1988; Giraldeau and Caraco 2000). Whinchats (*Saxicola rubetra*) are territorial in the breeding season and on the wintering grounds, but in the post-breeding season they form mixed flocks of adults and juveniles (Bastian and Bastian 1996) and often forage

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in flocks during migration (Glutz von Blotzheim 1988). There is some evidence that the foraging efficiency of Whinchats on autumn migration stopovers is higher in larger groups (Draulans and van Vessem 1982), but it is unknown whether social foraging is advantageous and preferred to solitary foraging during spring migration, which is quicker than autumn migration (Bastian and Bastian 1996), and where an effective time and energy use is expected.

Selection of habitat by birds at migration stopover sites is a complex decision-making process affected by several factors (Hutto 1985a; Maccarone and Brzorad 2005; Chernetsov 2006). Food abundance is of crucial importance (Bibby and Green 1981; Martin and Karr 1986; Delingat and Dierschke 2000), but the physiognomy of a microhabitat may be equally important for species with specific morphological or behavioural constraints (Bairlein 1992; Block and Brennan 1993; Chernetsov 2006). Intra- and interspecific interactions, particularly predation risk (Suhonen 1993; Walther and Gosler 2001) and competition (Hutto 1985b; Martin and Karr 1986; Yong et al. 1998), often influence selection of foraging habitat. Whinchats select specific habitats at migration stopover sites in European cultural landscapes (Draulans and van Vessem 1982; Bairlein 1983; Duckworth 1994), but the specific environmental factors bearing on this selection are unknown.

The Whinchat breeds in the major part of Europe and northwest Asia and it winters in sub-Saharan Africa (Bastian and Bastian 1996). Migration through southeast Europe is largely unknown. Birds passing this region in spring are most probably travelling directly from northern Africa to the eastern part of the species' breeding range (Glutz von Blotzheim 1988). West, central and some east European populations of Whinchats have declined substantially in the past decades (BirdLife International 2004). Loss of breeding habitats is recognised as the main cause for the decline, and attempts have been made to mitigate this process (Müller et al. 2005; Britschgi et al. 2006; Horch et al. 2008). Loss of high quality habitats at important stopover sites can substantially reduce the

success of migration (Moore et al. 1995) and therefore add to the decline of populations. Basic information on habitat selection and life-history characteristics throughout the Whinchat's range is therefore needed for long-term conservation of the species (Moore et al. 1995; Donovan and Thompson 2001).

The aim of our study was (1) to test whether Whinchats favour social foraging during the spring migration stopover and how flocking affects their foraging activity in heterogeneous environment, and (2) to assess the importance of physiognomic habitat factors in Whinchats' foraging habitat selection in the mosaic cultural landscape on the SE Adriatic coast.

Methods

Study area

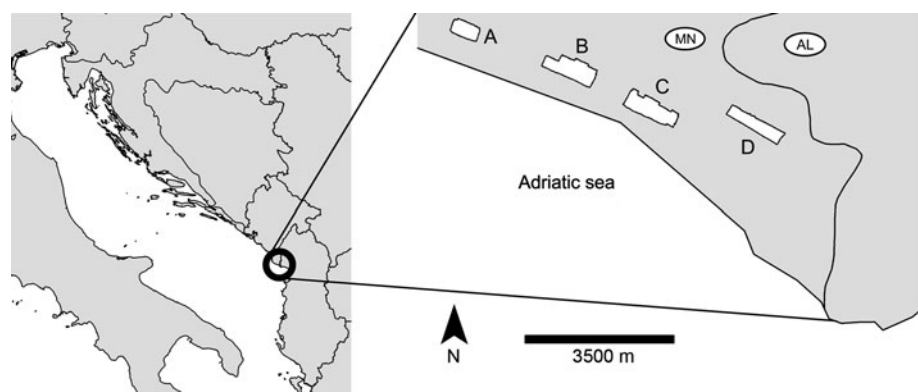
The study area was located in the mosaic cultural landscape of the Montenegrin coast in the hinterland of Velika plaža, a sandy beach extending 10 km south-eastwards from the city of Ulcinj (41.89°N, 19.30°E) (Fig. 1). The area is a part of the delta of the Bojana-Buna river, recently recognised as an area of great ecological value with an extraordinarily rich bird community (Schneider-Jacoby et al. 2006). Among 237 bird species recorded, 52 are regular passage migrants, including the Whinchat. The weather during the study period was rather constant, the majority of days being sunny with moderate winds and midday temperatures between 22 and 27°C.

Foraging and use of habitat by migrating Whinchats were studied at four plots, sized 14, 24, 31 and 31 ha (Fig. 1). Aerial distances between adjacent plots were 1.3, 0.7 and 0.8 km.

Whinchat censuses

The censuses of Whinchats were carried out between 5 and 24 April 2007, during the first half of the passage of the

Fig. 1 *Left* Adriatic region and location of the study area (circle). *Right* Part of the delta of Bojana-Buna river and positions of study plots (A–D)



species through the region (Štumberger, personal communication). A total of 54 complete plot censuses were carried out, starting between 0600 and 1800 hours and lasting 30–160 min at a single plot. The starting time of the censuses at each plot was varied in order to avoid time bias. The birds were counted and their sex determined from distances of at least 100 m, to avoid disturbance. Observations were made with 8 × 50 binoculars and a 20–60× spotting scope. We refer to every record of spatially distinct Whinchats, either a solitary individual or a group, as a Whinchat unit. The Whinchat units were classified according to the number of individuals in the unit as (1) solitary birds, (2) small groups (2–3 individuals), (3) medium groups (4–10 individuals) and (4) large groups (≥11 individuals). Every Whinchat unit was observed for 5 min. Its activity during this interval was recorded and the exact area that it used was mapped (scale 1:3,000). The unit was classified as *foraging* if all individuals in the unit foraged within this interval or as *non-foraging* if none of the individuals foraged during this interval. No groups were encountered in which only some individuals foraged within the observation interval, although the intensity of foraging in some groups differed between individuals. We estimated overall foraging intensity of foraging units on ordinal scale: 1: less intensively foraging; 2: intensively foraging. The areas used by Whinchat units were digitised using GIS software ESRI ArcView 3.1. Three zones were defined within the study area, pooled for all observations: (1) the *foraging zone*, used by Whinchat units for foraging, (2) the *non-used zone* where no Whinchat units were registered at any time of the censuses (forest fragments within the study plots were excluded) and (3) the *non-foraging*

zone, used by non-foraging Whinchat units. During the observation interval some foraging Whinchat units moved across the habitat from one foraging patch to another, during which time their foraging activity ceased (see “Discussion”). These transient areas were included in the non-foraging zone. The non-foraging zone comprised only 1% of total study area and was not included in further analysis.

Habitat data

Eight habitat types were defined and mapped at the study plots. Their areas were obtained in GIS (Table 1). Forty-three non-overlapping sampling squares with 30-m sides were placed at random in the study area using GIS. According to the case–control design (Hosmer and Lemeshow 2000; Keating and Cherry 2004), 16 sampling squares were placed within the foraging zone and 27 within the non-used zone. The following physiognomic variables of habitat were mapped within the sampling squares between 25 and 28 April: (1) natural perches (NP), (2) artificial perches (wire fence) (AP) and (3) vegetation types. Three distinct vegetation types were recognised: high herbal vegetation (HHV), low herbal vegetation (LHV) and open bushes (OB). Maps were digitised in GIS, and surface areas of vegetation types and lengths of wire fence were obtained.

The physiognomic variables were used in microhabitat analysis as independent (predictor) variables. The variable NP was quantified as the abundance of outstanding plant stems and small individual isolated bushes (at least 30% above the rest of vegetation). The abundance was estimated

Table 1 Definitions, general characteristics, areas and proportions of the habitat types at the study plots

Habitat type code	Habitat type	Definition	General characteristics	ha	%
EXME	Extensive meadow	Mown once a year, no mineral fertilisers	Abundant natural perches, high diversity of plant species	8.3	8
INME	Intensive meadow	Mown more than once a year, mineral fertilisers	No or very few perches, low diversity of plant species	4.2	4
EXPA	Extensive pasture	Pasture with low grazing density (cattle, sheep or both)	High physiognomic heterogeneity, natural perches present in low to high abundance	12.8	13
INPA	Intensive pasture	Pasture with high grazing density (cattle, sheep or both)	Very low vegetation (grazed), physiognomic homogeneity, no or very few perches	29.8	30
ARLA	Arable land	Ploughed field	No plants, bare ground—soil	1.2	1
OPED	Open edge	30-m-wide band on the borders between pastures and/or meadows	Wire fences or hedgerows, high physiognomic heterogeneity	21.3	21
FOED	Forest edge	30-m-wide band along forest patches	Immediate proximity of forest	17.5	18
FOFR	Forest fragment	Patch of forest inside cultivated area	Deciduous tree species	4.0	4

in the field according to the following ordinal scale: 0: no natural perches; 1: some natural perches; 2: considerable amount of natural perches; 3: many natural perches. The variable AP was quantified as the length of wire fence inside a sampling square. The lengths were classified to six length classes: 0: 0 m; 1: 1–10 m; 2: 11–20 m; 3: 21–30 m; 4: 31–40 m; 5: 41–50 m. The vegetation types (HHV, LHV, OB) were quantified as surface areas in square metres. HHV was defined as herbal vegetation which was generally higher than 20 cm, LHV as herbal vegetation which was generally lower than 20 cm and OB as herbal vegetation overgrown with bushes which covered at least 25% of the patch surface. When the bushes were isolated and covered less than 25% of the patch surface, they were classified as natural perches (NP) within HHV or LHV.

Data analysis

Using χ^2 test, we tested whether time of the day, date, habitat type or unit size affected a Whinchat unit's foraging activity (no foraging/less intensive foraging/intensive foraging). Furthermore, using the Cochran–Mantel–Haenszel test, we tested whether there was a difference in the proportion of foraging units between solitaries and groups, after controlling for habitat type. The data used in the test were: foraging (yes/no) and habitat type as control factors, and unit size (solitary/group) as an additional control factor. Three habitat types where 85% of the Whinchat units foraged (OPED, EXPA and INPA), and two classes of units: (1) solitary and (2) group (joint size classes 2–3, 4–10 and 11–29) were used in the analysis.

Following Block and Brennan (1993), our study was carried out at macrohabitat and microhabitat spatial levels. At the macrohabitat level, we tested whether Whinchat units used habitat types according to their availability, using χ^2 test. Furthermore, we did all possible pairwise comparisons of habitat types according to use by Whinchat units, using χ^2 tests with Bonferonni correction. Only those habitat types which exceeded 10% of the total study area (OPED, FOED, EXPA and INPA) were included in this analysis.

At the microhabitat level, we modelled the use of a patch (represented by a sampling square) by foraging Whinchats in relation to physiognomic variables. Modelling was carried out in R software using the information-theoretic approach (Burnham and Anderson 2002) and was considered exploratory. Information in the data was modelled with logistic regression (logit link function) since the dependent variable (Ufor—use of a patch by foraging Whinchats) was binary (used/not used) and independent variables (physiognomic variables) were continuous and discrete (Tabachnick and Fidell 2001). Besides the five

physiognomic variables obtained in the field (NP, AP, HHV, LHV and OB), an additional independent variable Shannon–Wiener index was calculated from the proportions of vegetation types in a sampling square (Krebs 1999) and was used as index of heterogeneity of vegetation types (HVT). We calculated variance inflation factors (VIF)—scaled versions of the multiple correlation coefficients between each of the six variables and the rest of the independent variables—to detect potential multicollinearity between the independent variables. Where VIF was larger than 10 or the tolerance value was less than 0.1, the variable was excluded (Montgomery and Peck 1982; Neter et al. 1990; López-López et al. 2006). According to these criteria, the variable LHV was excluded from further analysis.

Using the five remaining independent variables (Fig. 2), all possible additive models and the null model (intercept only) were constructed. Both vegetation types (HHV + OB) were included simultaneously in models, thus 16 models were constructed (Table 2). All models were ranked according to the second-order information criterion AIC_c , since the ratio n/K was 8.6. Likelihoods and probabilities (w_i) were calculated for all models, and relative variable importance ($w_+(j)$) was calculated for each variable in the set of models. AIC_c differences (Δ_i), relative to the smallest AIC_c value in the set of models, were used as criteria for model selection and inference (Burnham and Anderson 2002; Johnson and Omland 2004).

Goodness-of-fit of the global model (Ufor \sim HHV + OB + NP + AP + HVT) was calculated using nonparametric bootstrap (Crawley 2007). The rank of deviance of the global model was determined in sorted deviances of simulated models (100 bootstraps) and proved a good model fit ($P = 0.22$) and justified inference from reduced models. Since we used a random case–control sampling

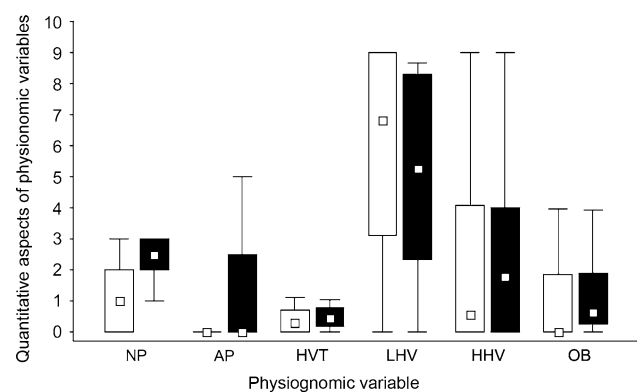


Fig. 2 Differences in physiognomic variables between the area used by Whinchats (*Saxicola rubetra*) for foraging (black boxes) and unused area (empty boxes). The boxes are quartiles, are whiskers minima and maxima, and the squares inside the boxes are medians. Units for LHV, HHV and OB are $m^2 \times 0.01$

Table 2 Logistic regression models with physiognomic variables as independent variables predicting use of a patch by foraging Whinchats (*Saxicola rubetra*)

	Model	<i>K</i>	AIC _c	Δ _{<i>i</i>}	Model likelihood	<i>w_i</i>
1	NP	2	46.255	0.00	1.000	0.41
2	NP + AP	3	47.180	0.93	0.630	0.26
3	HVT + NP	3	48.553	2.30	0.317	0.13
4	HVT + NP + AP	4	49.612	3.36	0.187	0.08
5	HHV + OB + NP	4	49.888	3.63	0.163	0.07
6	NP + AP + HHV + OB	5	51.273	5.02	0.081	0.03
7	HHV + OB + HVT + NP	5	52.355	6.10	0.047	0.02
8	HHV + OB + NP + AP + HVT	6	53.763	7.51	0.023	0.01
9	AP	2	58.375	12.12	0.002	0.00
10	Null	1	58.863	12.61	0.002	0.00
11	HVT	2	59.928	13.67	0.001	0.00
12	HVT + AP	3	60.165	13.91	0.001	0.00
13	HHV + OB	3	62.676	16.42	0.000	0.00
14	HHV + OB + AP	4	62.750	16.50	0.000	0.00
15	HHV + OB + HVT	4	64.644	18.39	0.000	0.00
16	HHV + OB + HVT + AP	5	65.133	18.88	0.000	0.00

The models with substantial support from the data are in bold

K Number of estimable parameters in model, AIC_c a second-order Akaike’s information criterion, Δ_{*i*} AIC_c differences, relative to the smallest AIC_c value in the set of models, *w_i* Akaike weights *NP* natural perches, *AP* artificial perches, *HHV* high herbal vegetation, *LHV* low herbal vegetation, *OB* open bushes, *HVT* heterogeneity of vegetation types

design, we interpret parameter estimates of selected models in terms of odds ratios (Keating and Cherry 2004).

Results

We recorded 71 Whinchat units (47 foraging, 24 non-foraging). Percentages of solitary birds, small, medium and large Whinchat groups were 22, 30, 37 and 11%, respectively. The total number of observed Whinchats was 365 (261 males, 104 females). Minimum, maximum and average numbers of Whinchats in a unit were 1, 29 and 5.1 ± 0.6 (SD), respectively. A total of 96% of all observed Whinchats were members of groups of different sizes and 4% were solitaries, while 87% of all observed Whinchats belonged to foraging groups (7% to small groups, 46% to medium groups, 34% to large groups) and 1% were foraging solitaries, with 12% being non-foraging Whinchats, mainly solitaries and members of small groups.

There was a strong association between foraging activity of units and their size ($\chi^2 = 32.16$, *df* = 6, *P* < 0.001; Fig. 3). There was no association between foraging activity of units and hours ($\chi^2 = 15.40$, *df* = 22, *P* = 0.844) nor between foraging activity of units and days during the study ($\chi^2 = 33.5$, *df* = 30, *P* = 0.300). The selected habitat types did not differ significantly between intensively foraging, less intensively foraging and non-foraging

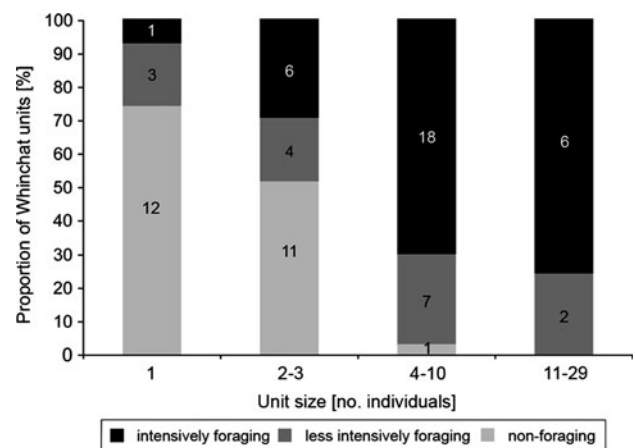


Fig. 3 Proportions of intensively foraging, less intensively foraging and non-foraging Whinchat units in relation to unit size. The numbers in the bars are the frequencies of observed Whinchat units

Whinchat units ($\chi^2 = 8.66$, *df* = 8, *P* = 0.371). There was a significant difference in the proportion of foraging units between the solitaries and groups, after controlling for habitat type ($\chi^2_{MH} = 15.210$, *df* = 1, *P* < 0.001). In each of the three habitat types (OPED, EXPA and INPA), the proportions of foraging to non-foraging solitaries were smaller than proportions of foraging to non-foraging groups.

Whinchats significantly selected particular habitats and avoided others ($\chi^2 = 42.06$, $df = 3$, $P < 0.001$; Fig. 4). The most preferred habitat type was open edge. Surface areas of the foraging, non-foraging and non-used zones were 6, 1 and 89 ha, respectively. The remaining 4 ha within the study area (100 ha) were forest islands.

Of the physiognomic variables, the natural and artificial perches best predicted the use of a patch by foraging Whinchats. In the set of models, two were supported substantially by the data ($\Delta_i \leq 2$), five considerably less well supported ($2 < \Delta_i \leq 7$), and nine essentially not supported by the data ($\Delta_i > 7$) (Table 2). The predictor variables for the presence of foraging Whinchat units were, in order of importance, NP, AP, HVT, HV and OB, with relative importance weights 1, 0.38, 0.24, 0.13 and 0.13, respectively. Increase of the parameter value of the most important variable NP by one level means four times the odds that the habitat is selected by a Whinchat unit for foraging (Table 3).

Discussion

The great majority of Whinchats foraged in groups, indicating the preference for social foraging on spring migration. Small passerine birds travel at night solitarily or in very loose associations (Bruderer 1997). The groups of Whinchats observed on the Montenegrin coast had therefore most probably formed at the stopover site in order to forage socially. Most of the medium and large groups foraged intensively, while high proportions of solitaires and small groups foraged less intensively or did

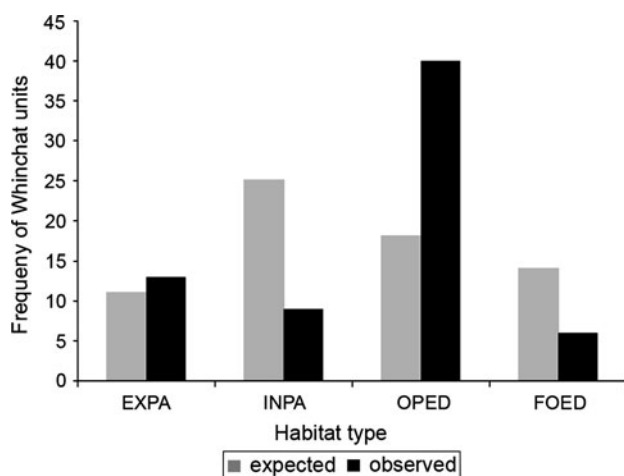


Fig. 4 Expected and observed use of habitat types by Whinchat units. Expected frequencies were calculated from proportions of available habitat types (see Table 1 for habitat type codes)

Table 3 Coefficients and odds ratios for models with substantial support from the data

Model	Variable in the model				Intercept
	NP		AP		
	β	exp (β)	β	exp (β)	
NP	1.471	4.35			-3.321
NP + AP	1.437	4.21	0.278	1.32	-3.523

not forage at all. These individuals were either less successful in finding a food-rich patch or were momentarily not motivated for foraging. Although the primary goal of birds on migration stopover is refuelling, they also spend time on other activities (e.g. resting, being cautious, defending temporary territories) (Dierschke et al. 2003). It is possible that the non-foraging solitaires and small groups in our study were the newcomers having a rest after a long non-stop flight (Schwilch et al. 2002) and which had not yet encountered their congeners to join for active foraging.

Draulans and van Vessem (1982) reported that foraging intensity of individual Whinchats was higher in larger groups in homogenous environment. They suggested that foraging Whinchats flush the insects which become available to other group members and this enhances their foraging intensity. Whinchats at the Montenegrin stopover tended to maximise foraging intensity through social foraging since most of medium and large groups foraged intensively. However, medium groups were much more common than large groups and more individuals were members of medium groups. If foraging intensity of the Whinchat groups in our study was dependent only on group size, like in the study of Draulans and van Vessem (1982), then Whinchats would tend to forage in large groups. Unlike the study of Draulans and van Vessem, our study was done in a heterogeneous environment. We suggest that, regarding the intensity of foraging, the optimal Whinchat foraging group size also depends on abundance and distribution of food in the environment. However, we do not have any data on insect abundance in our study sites to support this hypothesis. The groups can change in size during the stopover, since there are no tight bonds between individuals (Bastian and Bastian 1996).

Perches are used by Whinchats for singing and foraging and have been shown to be a limiting factor in the settlement of Whinchats on the breeding grounds (Labhardt 1988; Oppermann 1990; Bastian and Bastian 1996). Whether they also influence the distribution of Whinchats at migration stopover sites has, however, not been

determined. We argue that the intensive pastures at the Montenegrin coast were avoided due to lack of perches and not because of poor insect availability. Regular observation in this habitat type of other foraging migrating insectivore passerines (Northern Wheatears *Oenanthe oenanthe*, Yellow Wagtails *Motacilla flava*), which normally forage by pecking, suggests that the invertebrate food was also present on intensive pastures. Open edge and extensive pastures, both characterised by abundant perches, were selected preferentially by Whinchat units. We propose that the perches are an important cue for habitat selection and an important feature for habitat exploration by Whinchats within the stopover site. When the Whinchat groups moved across the habitat they consistently used perches. Some groups were observed moving across habitat in such a manner that individuals alternated in making short flights between natural perches or along the wire fence. From time to time some of them performed foraging flights which indicated scanning of the microhabitat for food. When the group encountered a suitable patch (probably assessed as high frequency of food items encountered), it stopped, started to forage intensively and stayed there for some time (even an hour or more).

Specific vegetation types (HHV, OB) did not affect foraging patch selection. The type of herbal vegetation cover is important in Whinchats' choice of habitat during the breeding season, because it provides proper cover for the nest (Oppermann 1990; Denac 2007). We expected that the heterogeneity of vegetation types (HVT) would positively affect the selection of a foraging patch, because the abundance of grassland invertebrates is usually higher in heterogeneous than in homogenous herbal layers (Dennis et al. 1998; Britschgi et al. 2006). However, the models that contained this variable were less supported by the data and the importance of HVT relative to the most important variable (NP) was fairly low.

We conclude that Whinchats at the spring migration stopover site on the Montenegrin coast prefer social to solitary foraging. When they remain solitary or in very small groups, it is most probably because they have not encountered congeners. We also propose that perches are an essential habitat feature, substantially affecting habitat use and foraging patch selection by Whinchats in mosaic cultural landscapes on migration stopovers. Other physiognomic factors of open grasslands are likely to be important only to the extent to which they affect invertebrate abundance. The conservation efforts at Whinchat stopover sites should aim at preserving invertebrate rich habitat types with abundant perches and the presence of open edge. This can be achieved through extensive pasture characterised by low grazing density and small pastures lined off with wire fence and hedgerows.

Zusammenfassung

Soziale Futtersuche und Habitatnutzung bei einem langstreckenziehenden Sperlingsvogel, dem Braunkehlchen *Saxicola rubetra*, an einem Frühjahrs-Rastplatz an der südostadriatischen Küste

Die Vorliebe für die Futtersuche in Gruppen und der Einfluss physiognomischer Faktoren eines Habitats auf seine Nutzung durch futtersuchende Braunkehlchen (*Saxicola rubetra*) wurde während einer Rast auf dem Frühjahrszug in einer Mosaik-Kulturlandschaft an der südostadriatischen Küste untersucht. Jede Erfassung einzelner Braunkehlchen oder räumlich abgegrenzter Braunkehlchen-Gruppen wurde als eine Braunkehlchen-Einheit betrachtet. Die Einheiten wurden als intensiv nach Futter suchend, weniger intensiv nach Futter suchend oder nicht nach Futter suchend klassifiziert und in vier Größenklassen aufgeteilt. Der Einfluss physiognomischer Habitatfaktoren auf die Habitatnutzung durch futtersuchende Braunkehlchen-Einheiten wurde modelliert. Alle möglichen additiven Modelle, die eine Logit-Link-Funktion benutzen, wurden aus fünf unabhängigen physiognomischen Variablen erstellt: (a) natürliche Sitzplätze (NP), (b) künstliche Sitzplätze (AP), (c) hochwüchsige krautige Vegetation (HHV), (d) offenes Gestrüch (OB) und (e) Heterogenität der Vegetationstypen (HVT). Die Variablen HHV und OB wurden gleichzeitig in die Modelle aufgenommen. Anhand von Akaikes Informationskriterium zweiter Ordnung AICc. wurden die Modelle ausgewählt, die von den Daten am besten gestützt wurden. Zwei dieser Modelle enthielten die Variable(n) (a) NP und (b) NP + AP. Die relativen Gewichtungen der physiognomischen Variablen NP, AP, HVT, HHV und OB betragen 1, 0,38, 0,24, 0,13 und 0,13. Sitzplätze waren daher die wichtigsten physiognomischen Habitatfaktoren, welche die Habitatnutzung durch Braunkehlchen in einer Mosaik-Kulturlandschaft beeinflussten. Die große Mehrheit der Braunkehlchen suchte in Gruppen nach Futter, und der Anteil intensiv nach Futter suchender Braunkehlchen-Einheiten nahm mit der Größe der Einheit zu. Dies führte zu der Schlussfolgerung, dass Braunkehlchen am Frühjahrs-Rastplatz an der südostadriatischen Küste die soziale der individuellen Futtersuche vorzogen.

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