ORIGINAL ARTICLE

Habitat structure versus food abundance: the importance of sparse vegetation for the common redstart *Phoenicurus phoenicurus*

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Abstract As many other birds breeding in agricultural areas, the common redstart declined strongly in many Central European countries over the last 60 years. The destruction of traditionally managed orchards, an important breeding habitat in Central Europe, is a relevant cause. An additional factor for the decline of this species could be the intensified management of the ground vegetation in orchards through reducing food availability and lowering prey detectability and accessibility. In this study we examined the importance of surfaces with sparse vegetation for the location of redstart territories and for foraging. To validate the results of these field studies we made habitat-choice experiments in aviaries with captive birds. Territories occupied by redstarts in orchards of northwestern Switzerland contained a significantly higher proportion of surfaces with sparse vegetation than unoccupied control sites. Redstarts made almost five times more hunting flights into experimentally established ruderal vegetation strips than into adjacent unmown meadows. No difference was observed when the meadow was freshly mown. Vegetation height and the proportion of open ground surface correctly predicted the vegetation type for hunting in 77% of the cases. Experiments in aviaries offering two types of sparse vegetation and a dense meadow supported the results of the field experiments. Even a four-fold increase of the food abundance in the meadow did not lead to a noticeable change in preference for the sparse vegetation types. For the conservation of the common redstart, not only traditionally managed orchards with tall trees with cavities should be preserved but also areas with sparse vegetation should be favored.

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Introduction

The intensified management of farmland over the last 50 years is responsible for the decline of many bird species breeding in agricultural areas all over Europe (Bauer and Berthold 1996; Donald et al. 2006; Wretenberg et al. 2006). A bird that suffered a strong decline in several European countries is the common redstart (Zbinden et al. 2005; BirdLife International 2006). This species depends on open and savannah-like woodland and was common in traditionally managed orchards with trees that have high trunks and cavities in Switzerland (Schmid et al. 1998). In Switzerland, orchards even became the main habitat for redstarts after open woodland disappeared. In the course of

the mechanization of agricultural management practices, many of these orchards have disappeared.

Another presumed reason for the decline is a worsened detectability and accessibility of prey in the meadows of the orchards due to intensified farming practices such as fertilizer input (Donald et al. 2001; Vickery et al. 2001). Fertilizer input leads to denser and higher vegetation (Jacquemyn et al. 2003). Intensively managed meadows may also have a reduced density and diversity of inverte-brates (Britschgi et al. 2006). Detecting prey in high and dense grassland takes much more time than detecting the same prey in sparse vegetation of low height (Butler et al. 2004). Additionally, it is more difficult to reach and catch a prey item in dense and high vegetation (Jakober and Stauber 1987; Schaub 1996; Atkinson et al. 2005). In the context of optimal foraging theory (Krebs et al. 1977), a bird should therefore prefer sparse vegetation for foraging. The common redstart is a sit-and-wait predator that hunts from vantage points (Menzel 1971) and catches about 50% of all prey on the ground (Sedlácek et al. 2004). Therefore the changes of the ground vegetation of orchards due to their intensification could be an important reason for the decline of the common redstart.

Agri-environment schemes are used all throughout Europe to counteract negative effects of farmland intensi-fication (Kleijn and Sutherland 2003). In Switzerland, a nationwide agri-environment scheme was launched in 1993 and the first results show that it indeed seems to have a moderately positive effect on farmland birds (Birrer et al. 2007). Among several agri-environment measures in Switzerland, there is one that pays farmers for each orchard tree with a high trunk they cultivate (Bundesamt für Landwirtschaft 2007). The aim is to stop the destruction of orchards. Orchards, however, are still destroyed and the population of the common redstart did not stabilize since agri-environment schemes exist in Switzerland (Zbinden et al. 2005). While trees with nesting sites may be pre-served, there is no suitable management of the soil vege-tation under the trees. The actual measures for orchard trees therefore are likely to be only half of what is needed for the preservation of the common redstart. An additional measure could be the establishment of sparse vegetation plots within orchards to facilitate foraging for the common redstart. Other endangered bird species living in orchards, e.g.; woodchat shrike *Lanius senator*, Eurasian hoopoe *Upupa epops* and wryneck *Jynx torquilla* also catch a large proportion of their prey on the ground in sparse vegetation (Bauer and Berthold 1996; Schaub 1996). Thus, their populations might also benefit from new management measures in orchards.

To find new and effective management measures for redstarts and other ground-hunting bird species in orchards we first studied whether sparse ground vegetation is an important character of common redstart territories in orchards. Secondly, we studied the degree of preference of sparse ground vegetation for foraging within the territory. Thirdly, we studied whether a high prey density could compensate for missing sparse vegetation within the for-aging site of the common redstart.

Specifically we tested the following three main predic-tions: (a) The proportion of sparse vegetation is higher in occupied redstart territories than in unoccupied control sites in orchards with potential nest sites. (b) Sparse veg-etation within territories is important for foraging. Red-starts make disproportionately more hunting flights into sparse vegetation types. (c) Very high prey densities would be needed to compensate for unsuitable structural qualities of a vegetation type. We tested these hypotheses by com-paring occupied territories with unoccupied control sites and by performing direct observations of wild redstarts, field experiments with newly installed ruderal vegetation plots and experiments in aviaries.

Methods

Sparse vegetation in territories and unoccupied sites

Study design and study sites

To test the hypothesis that the proportion of sparse vege-tation is higher in redstart territories than in unoccupied control sites, we compared redstart territories with unoc-cupied control sites in the same orchard, both with poten-tial nest sites available. In April and May 2006, 24 territories were mapped in ten traditionally managed orchards in NW Switzerland, known to hold breeding populations of common redstarts from earlier work (Biber et al. 1996). As control sites, we selected sites that were not occupied by a redstart pair but offered potential nest sites (free and suitable nest boxes or natural cavities). For each territory one out of all potential control sites occurring in the same orchard but at least 150 m away from the nest was randomly chosen.

Habitat description

Between May and July 2006 the habitat was mapped on a circular area with a radius of 50 m (7,850 m^2), which corresponds to the size of a redstart territory (1,400–5,000 m^2, Menzel 1971; up to 10,000 m^2, Glutz von Blotzheim 1988). For territories with known nest sites, the nest was taken as circle center, for territories with unknown nest sites the center of the "paper territory" (based on 5–11 observations), and for control sites an unoccupied nest site. Within each circle roads, trees and parcel borders were

Table 1 The 16 different vegetation types that occurred in territories and in control areas and the four and two habitat types they were classified into

all vegetation types	4 habitat types	2 habitat types
dense meadow low intensity meadows lawn	dense vegetation	dense
pasture maize fields potato fields mustard fields vineyards	large surfaces with sparse vegetation	sparse
woods forest	forest	
vegetable garden non-asphalted roads ruderal vegetation strips small sparse vegetation patches	small surfaces with sparse vegetation	
cereal fields asphalted roads	not considered	

mapped. A standardized photograph of 1 m^2 vertically from above was taken of all different vegetation types occurring in the area to assign them to one of the vegetation types listed in Table 1. The 16 vegetation types were grouped into four habitat types and for further analysis into two habitat types ("dense vegetation" and "sparse vegetation"; Table 1).

Statistical analysis

The percentage of each vegetation type in the circular "territory" or control area was determined with a grid of 2,500 points. Habitat composition of territories and the corresponding control sites was compared with a compositional analysis (Aebischer and Robertson 1992, 1993) including Wilk's Lambda test using the Microsoft Excel Macro Compos Analysis Vers. 6.2 (Smith 2006). Zeros in the matrices were replaced with 0.001.

Importance of sparse vegetation plots within territories

Study design and vegetation

To test the hypothesis that disproportionately more hunting flights are made into sparse ground vegetation than into dense vegetation, we artificially created plots with sparse vegetation cover (ruderal vegetation strips) next to a normal meadow within redstart territories. Ten ruderal vegetation strips measuring approximately 2.5 × 40 m were established in a large orchard (80 ha) in NW Switzerland with a rotary harrow in March and April 2006. The strips were not sown. Along the border between the created plot and the adjacent meadow we installed posts (1.5 m tall)

every 5 m. Thus, using them as vantage points, redstarts had the choice to catch prey in sparse or dense vegetation. We then observed whether foraging redstarts preferred either the ruderal vegetation strip or the meadow. In order to compare the results with the available prey density, we caught insects and spiders using pitfall traps in both vegetation types.

Standardized photographs of 1 m^2 from above were taken and the height of the vegetation was measured at the level below which about 80% of the vegetation was estimated to be growing (following Hodgson et al. 1971; Stewart et al. 2001) every 2 weeks in the ruderal vegetation strips and the adjacent meadow. The percentage of open ground in both vegetation types was estimated from the photographs using a grid of 2,500 points.

Arthropod abundance

Pitfall traps catch mainly ground-dwelling arthropods, e.g., spiders and beetles (Cooper and Whitmore 1990), which represent an important prey of the common redstart (Menzel 1971). On each ruderal vegetation strip that was located inside a redstart territory we randomly chose two collecting points. For the ruderal vegetation strips without nearby redstart pair we randomly chose one collecting point instead of two. At each collecting point, three plastic cups (diameter = 7 cm) with a cover to prevent rain from filling the cup and containing 4% formalin were burrowed 1 m apart in a row. The same number and distribution of traps that was put in the ruderal vegetation strips was put in the adjacent meadow, 1 m from the ruderal vegetation. We set the traps on May 25, June 16, and July 7, for a period of 72 h. All arthropods were conserved in 70% ethyl alcohol and

classified into eight different taxa and five size classes (<2, 2–5, 5–10, 10–20, >20 mm). Only insects and spiders measuring 2–20 mm were used for further analysis, because it is unlikely that smaller and larger prey items are an important part of the diet of the common redstart (Sedlácek et al. 2007). Lepidoptera larvae >20 mm, which may be an important prey for nestlings, were only exceptionally caught in the pitfall traps (three individuals in total). We estimated the potential prey biomass according to the relationship weight = length^3 × a (coefficient a: Arachnida = 0.076, Orthoptera = 0.046, Coleoptera (without Staphylinidae) = 0.070, Staphylinidae = 0.035, Diptera = 0.032, Hymenoptera = 0.042, Lepidoptera = 0.040, Auchenorrhyncha = 0.040, own unpubl. data).

Foraging behavior of redstarts

The foraging behavior of the parental birds feeding their young in the nest was observed from May 18 to July 29, 2006, from a point at the edge of each territory from which the ruderal vegetation strips and the posts were well visible. If possible, both parents were observed simultaneously for at least 1 h per day. All hunting flights were recorded with vantage point and target vegetation. As it was difficult to observe redstarts in trees, we only used the hunting flights directed to the ground for further analysis. For one-third of the observation time we enhanced prey density with mealworms *Tenebrio molitor* on a 1-m-wide part of the ruderal vegetation strips and on a 1-m-wide part of the adjacent meadow along the border with the installed posts between these two vegetation types. We threw four mealworms on each m^2.

In total, four pairs of common redstarts bread next to experimentally established ruderal vegetation strips and one unpaired male was established over a longer period. Hunting flights were observed of seven individuals, five males and two females. Out of a total of 2,359 observed hunting flights, 644 started from the installed posts between the ruderal vegetation strip and the meadow, 607 of these hunting flights were directed towards the ruderal vegetation strip or the meadow. All six redstarts (without the solitary male) preferred posts as vantage points which were nearer to the nest than the average distance of available posts from the nest (χ^2 test, p-values for all individuals <0.001).

Statistical analysis

For each sampling period, we used paired *t*-tests in Microsoft Excel to test for differences in potential prey biomass between ruderal vegetation strips and meadow vegetation. To test whether birds preferred the posts as vantage points that were nearest to the nesting site we compared the observed proportion of hunting flights from the available posts with the expected proportions for each individual with an χ^2 test.

To assess the preferences of the birds for habitat types we used a generalized linear mixed model with a logit-link function and binomial error distribution using the statistical software R. As the dependent variable, we constructed a binary variable indicating for both habitat types (ruderal vegetation strips and meadow) whether it was used by the bird or not during one hunting flight. In this way, one hunting flight gave two observations (pair of observations), one for the ruderal strip and one for the meadow of which one has the value 1 and the other 0 depending on where the bird hunted (1 = bird was present; 0 = bird was absent). Vegetation type (ruderal strip or meadow), vegetation height, arthropod biomass, proportion of open ground and mealworm treatment were included as fixed factors in the model, while the pair of observations nested in individuals were included as random variables to account for the interdependence of observations. To find the optimal model, we started with all variables and excluded them stepwise based on their BIC-value. We used the BIC because it seems to perform better than AIC in mixed models (Verbeke and Molenberghs 2000). Interactions were not considered in the model. To construct the model, 70% of all hunting flights directed towards the ruderal vegetation strips or the adjacent meadow were randomly chosen (overall $n = 607$). The model was then tested with the remaining 30%. In a second step, we tested each of the variables named before singly.

During the observations, we also recorded hunting flights of five individuals from other vantage points besides those made from the posts installed. We therefore could record all hunting flights they made during the observations and compare hunting frequency in different vegetation types with their availability within 50 m around the nest. According to the null-hypothesis that all vegetation types are used for foraging in relation to their availability, the proportions of vegetation types used for hunting flights corresponded to the surface percentage of each vegetation type. Only hunting flights that were recorded during periods without mealworm treatment were used. Due to the small number of observed individuals, we could not use compositional analysis. We therefore used binomial tests (Holm corrected, Holm 1979) for each individual to compare the expected hunting flight proportions into the sparse vegetation types with the observed values.

Foraging in aviaries depending on ground vegetation structure and food abundance

Study design and vegetation plots

To test the hypothesis that very high prey densities would be needed to compensate for bad structural vegetation
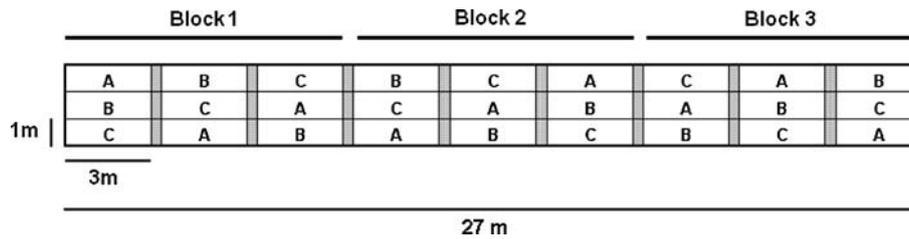
Fig. 1 Experimental plots for the aviary experiments. Each plot measured 3 × 3 m with three 1-m-wide vegetation strips. There is one strip of each vegetation type in each plot. To avoid effects of exposition, side preference and other factors, the vegetation strips were arranged differently. *A* meadow, *B* wild flower strip, *C* ruderal vegetation strip

quality, we performed habitat-choice experiments in aviaries with two sparse and one dense vegetation type and with a variable density of mealworms.

The aviary experiments were carried out at the Research Institute for Organic Agriculture FiBL in Frick between August and September 2006. In April and May 2006, we set up nine plots of 9 m² each on a flat meadow that contained all possible combinations of three vegetation types in strips measuring 1 × 3 m (Fig. 1). Besides the already existing dense meadow, we created ruderal vegetation by removing the existing meadow, and wild flower strips by removing the meadow and sowing a wild flower seed mix and planting seedlings of several herbs. Before the start of the experiments in August, we weeded the ruderal vegetation and the wild flower strip, removing individuals of *Potentilla reptans*, *Echinochloa crus-galli* and *Chenopodium album*. Vegetation height and the percentage of open ground were estimated every second week in the same way as for the field experiments by direct measurement of the vegetation height (Stewart et al. 2001) and by analyzing standardized photographs using a grid of 2,500 points.

Aviaries and birds

Two mobile aviaries covering a plot of 9 m² with a height of 2 m were constructed and two 1.5-m-tall posts serving as vantage points put between the borders of the three vegetation types. Nine common redstarts, born in captivity in spring 2006, were kept indoors in individual cages (100 × 50 cm and 50 cm high) under artificial light following the natural light–dark cycle. The redstarts received water, dried food for insectivores and mealworms ad libitum, and every second day dead insects caught with an UV trap. Before the experiments, food was removed for 6–12 h.

Experiments and mealworm treatment: For a first set of experiments, we put 20 mealworms in each of the three vegetation types. For a second set of experiments, we put 60 mealworms in the meadow and only 15 mealworms each in the wild flower strip and in the ruderal vegetation.

Redstarts were put into the mealworm-treated aviaries and observed for 1–2 h. Each individual was used for 6–9 experiments of the first set and for 2–5 experiments of the second set. Between experiments, individuals had at least 1 day off. For each hunting flight we recorded vantage point, target vegetation of the hunting flights as well as whether a mealworm, another prey or nothing was caught. Only hunting flights with mealworms caught (89.8% of all hunting flights observed) were used for analysis.

Statistical analysis

To analyze whether the proportion of hunting flights directed to the three vegetation types differed significantly from expected values, we used χ^2 tests in Microsoft Excel. Because the three vegetation types occupied the same surface in the aviaries, 0.33 was the expected value for each vegetation type. Individuals with less than 15 hunting flights were not included in the analysis, because the expected value per vegetation type would be <5. Because the different individuals were observed repeatedly, we adjusted the significance with the Holm correction (Holm 1979) using the statistical software R.

Results

Proportion of sparse vegetation in territories
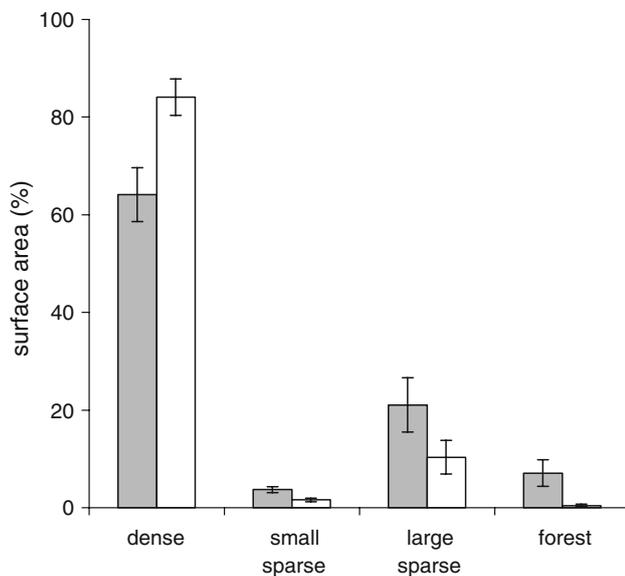and unoccupied sites

The proportion of vegetation types differed significantly between occupied territories and their nearby control sites (Table 2). Territories contained 0.7 times less surface covered with dense vegetation than nearby control sites (64.1 vs. 84.1%), 2.3 times more surface of sparse vegetation distributed in small plots (3.7 vs. 1.6%), 2.0 times more surface of sparse vegetation distributed in large plots (21 vs. 10.3%), and 17.8 times more surface covered with forest (7.1 vs. 0.4%) (Fig. 2).

With only two vegetation classes (sparse, dense, see Table 1), sparse vegetation occupied 2.5 times more surface

Table 2 Composition analysis comparing the proportion of different vegetation types in territories and in nearby control areas

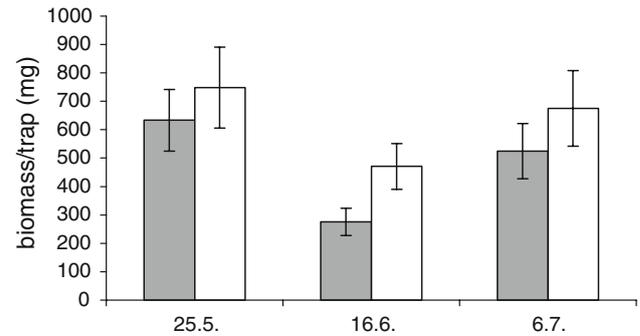|	Forest	Small sparse	Large sparse	Dense vegetation	Rank
Forest		0.244	1.403	1.787	3
Small sparse	−0.244		1.159	1.542*	2
Large sparse	−1.403	−1.159		0.383	1
Dense vegetation	−1.787	−1.542*	−0.383		0

Total significance: $\lambda = 0.582$, $p < 0.01$. The matrix of *t*-values comparing all vegetation types against each other with indication of their significance ($p < 0.05$) is given. A significantly positive *t*-value indicates that the vegetation type in the first column is preferred over the vegetation type in the first line. In the last column, the ranking of vegetation types according to abundance in territories is given, the highest rank indicating the most preferred vegetation type

Fig. 3 Mean biomass (±SE) of spiders and insects measuring 2–20 mm of all ten sites where we established ruderal vegetation strips. Only in the second sampling period the difference between meadow (*white columns*) and ruderal vegetation (*grey columns*) was significant (paired *t*-test; $p_1 = 0.39$, $p_2 = 0.01$, $p_3 = 0.33$)

Fig. 2 Proportions of different vegetation types (mean value ± SE) in all 24 territories (*grey columns*) and 24 control areas (*white columns*)

in territories than in nearby control sites (31.8 vs. 12.3%; compositional analysis: total significance: $\lambda = 0.625$; $\chi^2 = 11.28$, df = 1; $p < 0.001$, randomized $p = 0.001$).

Importance of sparse vegetation within territories

Mean vegetation height (±SE) of the ten ruderal vegetation strips between May and July 2007 was 5.9 ± 0.6 cm with a maximum of 14.9 cm and a minimum of 2.3 cm. The meadow vegetation adjacent to the ten strips increased from 24.1 ± 2.6 cm in early May up to 43.9 ± 4.4 cm in early June. Most meadows were mown in early June; mean vegetation height in the week after mowing was 10.7 ± 2.5 cm and did not exceed 20 cm up to the end of the observation period. During the time when parents fed

their young, open ground covered $28.9 \pm 7.3\%$ of the four ruderal vegetation strips in territories (range 10–53.5%). Before mowing meadows had no open ground visible from above, while after mowing open ground covered $25.4 \pm 11.8\%$ in the four meadows inside the territories (range 0–47.9%).

A total of 783 ± 102 spiders and insects 2–20 mm long were collected in the pitfall traps during each of the three sampling periods in the ruderal vegetation plots and 900 ± 113 spiders and insects 2–20 mm long were collected in the pitfall traps during each sampling period in the adjacent meadows. Insect and spider biomass was significantly lower in the ruderal vegetation strips than in the nearby meadows in the June sample (paired *t*-test: $t = 3.494$, df = 7, $p = 0.01$, Fig. 3). In the two samples from May and July, no significant differences were observed (paired *t*-test: May: $t = 0.90$, df = 8, $p = 0.39$; July: $t = 1.03$, df = 8, $p = 0.33$; Fig. 3) although biomass was again higher in the meadow than in the ruderal vegetation strips.

Redstarts perched on posts between the ruderal vegetation strip and the meadow clearly preferred the ruderal vegetation strip for foraging when the adjacent meadow was higher than 20 cm: 90% of all hunting flights from the vantage points between ruderal vegetation strip and adjacent meadow ($n = 4$ individuals, 355 hunting flights, with and without mealworms treatment combined) were made into the ruderal vegetation. This preference was no longer observed when the meadow was freshly mown and shorter than 20 cm: Only 39% of all hunting flights from the vantage points between ruderal vegetation strip and adjacent meadow ($n = 5$ individuals, 286 hunting flights, with and without mealworms treatment combined) were made into the ruderal vegetation.

The mixed-model analysis revealed that the choice of foraging vegetation was best explained by the proportion of

Table 3 Generalized logistic linear mixed model table for testing the relationship between habitat characteristics and the probability of the habitat being used by the birds

	Estimate	SD	χ^2	df	p-value
Intercept	0.361	0.73			
Vegetation height	−0.097	0.015	44.65	1	<0.001
Bare ground	5.799	1.864	8.53	1	0.004

The best model (i.e., the one with the lowest BIC value) is shown. χ^2 with its df and significance are given for the likelihood test

bare ground and by vegetation height (Table 3). This model had the lowest BIC value, while the other variables (vegetation type, arthropod biomass and mealworm treatment) did not explain much additional variance. When the variables where tested singly, vegetation height correctly assigned 76.5% of the 182 cases not used to construct the model ($\chi^2 = 511.7$, $p < 0.001$). This is almost the same proportion as obtained with the best model (77.8%, Table 3). The proportion of bare ground tested singly correctly assigned a smaller, but still significant, part of the 182 cases not used to construct the model (69.3%, $\chi^2 = 475.6$, $p < 0.001$). When the vegetation of the meadow was high, there was almost no bare ground visible from above. Therefore, bare ground was almost as predictive of foraging habitat as vegetation height. Arthropod biomass predicted habitat choice in 69.3% of the cases ($\chi^2 = 283.1$, $p < 0.001$), and birds preferred the habitat with less biomass (i.e., the ruderal vegetation strip). The supply of mealworms had no significant effect on foraging habitat choice and did not correctly assign a higher proportion of cases than by chance (50%).

We also analyzed all observed hunting flights (319 ± 47 hunting flights per bird) in the territories on days without mealworm treatment. All five redstarts made significantly more hunting flights into sparse vegetation than expected from the availability of the vegetation types in their territories (Fig. 4). On average, the redstarts made ten times more hunting flights into the sparse vegetation than expected from availability, and 24 times more into ruderal vegetation. These differences were highly significant for all five individuals (binomial tests, all p-values < 0.001).

Foraging in aviaries depending on ground vegetation structure and food abundance

In the aviaries, vegetation height was much lower and the proportion of open ground was much higher in the ruderal and wildflower strips than in the meadow (Table 4). In both sets of experiments (first set with 20 mealworms in each vegetation type, second set with 15 mealworms each in the ruderal and the wildflower strip, 60 mealworms in the meadow) the proportions of hunting flights directed to the three vegetation types differed significantly from expected values (Table 5). The proportion of hunting flights into each of the sparse vegetation types was almost 50 times higher than that into the meadow (98 vs. 2%) in the first and almost 30 times higher in the second set of experiments (96 vs. 4%).

Discussion

In territories of the common redstart there was a significantly higher proportion of surface with sparse vegetation and bare ground than in unoccupied control sites. This suggests that the common redstart is able to assess territory quality by using vegetation structure as predictor of food availability, as does the northern wheatear *Oenanthe oenanthe* (Tye 1992). Forests and woods were also much more frequent in territories than in control sites, probably because redstarts could access the bare ground under trees from the edge. This conclusion fits with results of other studies that found redstarts to prefer territories with mature and old open woodland (Taylor and Summers 2009) and to preferably occupy territories with higher proportions of trees when returning to their breeding patch (Sedlácek and Fuchs 2008).

Within territories, redstarts preferred sparse over dense vegetation. Our field experiments showed that newly established plots with sparse vegetation (ruderal vegetation strips) were readily accepted for foraging. From the vantage points, redstarts strongly preferred the ruderal vegetation strips with their sparse vegetation and bare ground or freshly mown meadows to forage. When redstarts hunted from the posts between unmown meadow and ruderal vegetation strips, they made 18 times more hunting flights into the ruderal vegetation than in the adjacent high meadow. As soon as the meadow was mown, the preference for ruderal vegetation strips disappeared. Then both vegetation types had a high proportion of open ground. Arthropod biomass as measured in pitfall traps was higher in the meadow than in the ruderal vegetation. Thus it was not prey abundance, but vegetation height and open ground that determined the preference for the sparse vegetation. Redstarts especially preferred small and patchily distributed sparse vegetation types. Small patches with sparse vegetation have a long borderline in relation to their size. Hunting along such borderlines between small patches of sparse vegetation and dense meadow offers benefits both from the higher detectability and accessibility of the insect prey in the sparse vegetation and from the higher prey biomass in the dense vegetation. A similar pattern was found in two avian predators of small mammals, the Eurasian kestrel *Falco tinnunculus* and the long-eared owl *Asio otus* (Aschwanden et al. 2005): Both species

Fig. 4 Comparison of the availability of ground vegetation types inside territories (*white columns*) and use for hunting flights (*black columns*; each summing up to 100%) of five individual common redstarts ($n_1 = 359$, $n_2 = 224$, $n_3 = 439$, $n_4 = 192$, $n_5 = 379$ hunting flights). *dense* dense meadow, *mown* mown meadow, *flat* flat grass, *ruderal vegetation* ruderal vegetation strip, *unpaved* non-asphalted road, *asph.* asphalted road, *sparse* small sparse vegetation types (without non-asphalted roads and ruderal vegetation strips), *forest ground* forest ground
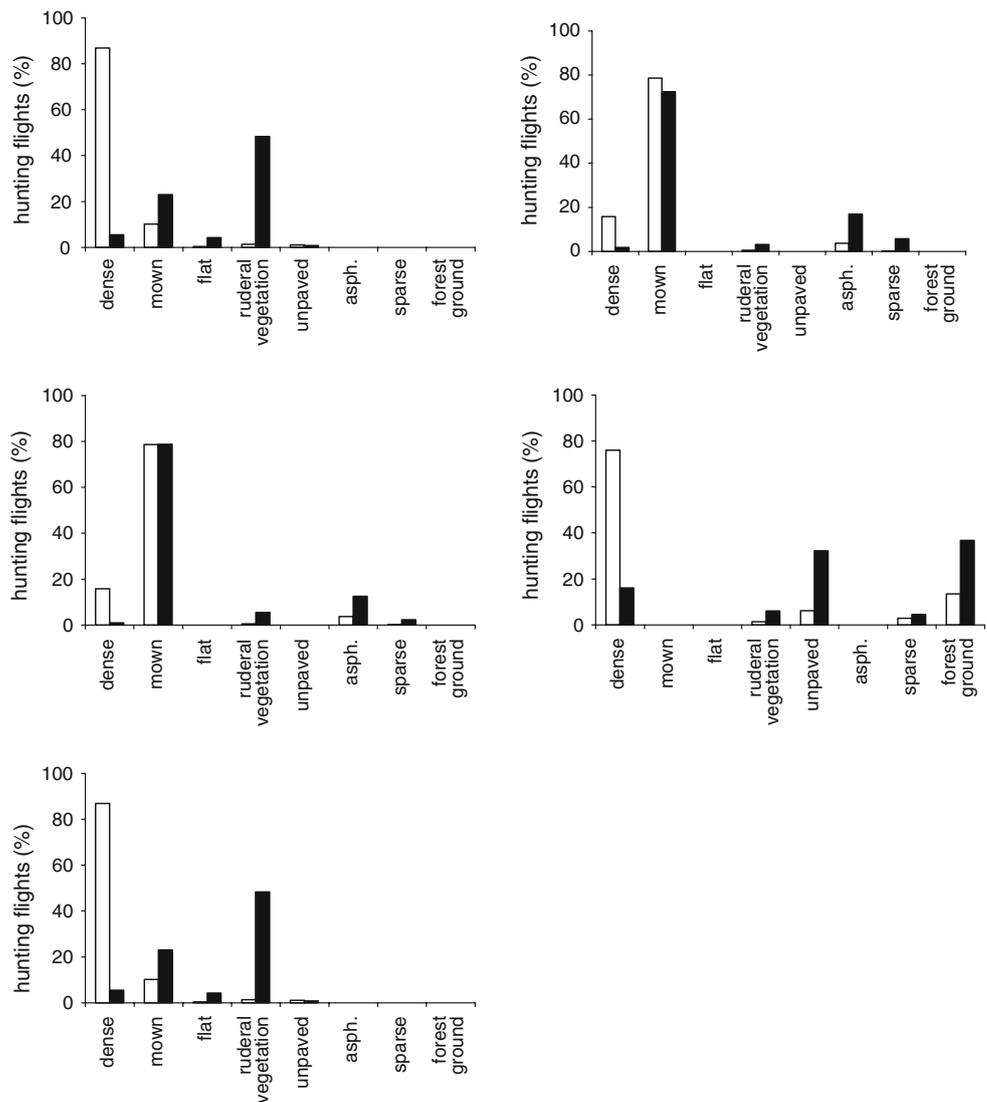

Table 4 Vegetation height and proportion of open ground in the three vegetation types in aviaries (means ± SE)

	Wild flower strip	Ruderal vegetation	Meadow
Vegetation height (cm)	4.2 ± 0.4	2.8 ± 0.5	18.5 ± 1.2
Proportion of open ground	0.2 ± 0.0	0.3 ± 0.1	0

preferably hunted on freshly mown meadows next to wild flower strips and therefore could benefit from the high density of small mammals in the wild flower strips.

The preference for low and sparse vegetation for hunting was confirmed with habitat choice experiments in aviaries. Redstarts caught mealworms almost exclusively in the sparse vegetation types. Even with a four times higher prey biomass in the dense vegetation of the meadow, we observed similar results. This shows clearly that habitat structure plays a more important role than prey abundance

for the common redstart. This is consistent with the finding that besides a high abundance of invertebrates (e.g., Britschgi et al. 2006; Atkinson et al. 2004), accessibility to the ground is of prime importance for many birds feeding on invertebrates on the ground.

Taking together the results from the analysis of vegetation structure in territories versus unoccupied sites, the preference for certain vegetation structures within territories, including newly established plots, and in aviaries, it appears that patches of sparse vegetation are very important for redstarts.

Implications for conservation

Atkinson et al. (2005) have already suggested that the higher and denser a vegetation type is, the less it is suited for ground-foragers feeding on invertebrates because the detectability and accessibility of prey decreases. In this

Table 5 Proportion of hunting flights into the three vegetation types in the aviaries of nine individuals (A) for situations when mealworms were added in equal density to all three vegetation types and (B) for situations when the mealworm density was four times higher in the meadow than in both other vegetation types

	Ind.	Obs. hunting flight proportion			χ^2-value	p-value	n
		Meadow	Ruderal vegetation	Wild flower strip			
A	1	0.1	0.4	0.6	7.18	0.03	17
	2	0.0	0.4	0.6	–	–	9
	3	0.0	0.6	0.4	–	–	5
	4	0.0	0.5	0.5	20.55	<0.001	41
	5	0.1	0.4	0.5	10.52	0.02	31
	6	0.1	0.6	0.3	17.89	<0.001	37
	7	0.0	0.7	0.3	28.23	<0.001	44
	8	0.0	0.6	0.4	14.89	0.002	27
	9	0.0	0.8	0.3	14.00	0.003	16
B	1	0.0	0.7	0.3	–	–	10
	2	0.0	1.0	0.0	–	–	1
	3	0.0	1.0	0.0	–	–	1
	4	0.0	0.9	0.1	41.41	<0.001	31
	5	0.1	0.6	0.3	13.31	0.001	29
	6	0.0	0.8	0.2	19.17	<0.001	17
	7	0.1	0.8	0.2	25.65	<0.001	32
	8	0.1	0.8	0.1	26.06	<0.001	28
	9	–	–	–	–	–	0

Total number of hunting flights (n), χ^2-values and p-values are given for all individuals

study we provided evidence that this is true for the common redstart. The trees with cavities they need for nesting are just one limiting factor for this bird species. Besides the destruction of traditionally managed orchards by cutting the fruit trees, intensified management of the ground vegetation under the trees seems to play an additional important role for the observed decline of redstart populations. In order to preserve and possibly enhance populations of the common redstart, existing sparse vegetation patches have to be preserved and new patches should be created, e.g., sparsely vegetated tracks and embankments and ruderal vegetation strips. Another management measure would consist of mowing small plots of meadow over the entire breeding period of the redstart. This method has already been recommended as a management practice in orchards (SVS/BirdLife Schweiz 2006). The aim is to create patches of rich meadows with a high prey density next to newly mown meadow parts with optimal detectability and accessibility. Furthermore, this kind of management should also be suitable for other taxonomic groups, such as butterflies.

Current agri-environment schemes in Switzerland support low-intensity meadows, which are only mown after mid-June. This leads to high meadows at the time when the common redstart is feeding its young. Although low-intensity meadows often have a higher insect and spider diversity and biomass than intensive meadows (Di Giulio et al. 2001; McCracken and Tallowin 2004; Britschgi et al. 2006; Knop et al. 2006), it is difficult for redstarts to benefit from them, because the accessibility and detectability of prey is low as long as the meadows are not mown. The creation of sparse vegetation patches in or near low-intensity meadows close to potential breeding sites could offer better foraging possibilities, and they should be integrated in agri-environment schemes for low-intensity meadows. Extensive grazing is another possibility to produce heterogeneous sward heights (McCracken and Tallowin 2004).

Besides the common redstart, there are several other endangered ground-hunting bird species that should benefit from such measures, e.g., woodchat shrike *Lanius senator*, Eurasian hoopoe *Upupa epops* and wryneck *Jynx torquilla* (Bauer and Berthold 1996; Schaub 1996; Schaub et al. 2008).

Zusammenfassung

Habitatstruktur gegenüber Nahrungsdichte: die Bedeutung lückiger Vegetation für den Gartenrotschwanz

Wie viele andere, in Kulturlandschaften brütende Vogelarten, erlitt der Gartenrotschwanz innerhalb der letzten 60 Jahre einen starken Bestandsrückgang in vielen Ländern Mitteleuropas. Eine wichtige Ursache dafür ist die Zerstörung von traditionell bewirtschafteten Hochstammobstgärten, einem bedeutenden Bruthabitat des Gartenrotschwanzes in Mitteleuropa. Die intensivierte Nutzung der Bodenvegetation in den Obstgärten, welche möglicherweise dazu führt, dass die Entdeckungswahrscheinlichkeit und die Erreichbarkeit von Beutetieren erschwert wird, könnte eine weitere Ursache für den beobachteten Bestandsrückgang sein. In der vorliegenden Arbeit untersuchten wir die Bedeutung lückiger Vegetationsflächen bei der Revierwahl und beim Nahrungserwerb des Gartenrotschwanzes. Um die Ergebnisse dieser Feldexperimente zu validieren, führten wir mit Hilfe von Gefangenschaftsvögeln Habitatwahlexperimente in Volieren durch. Besetzte Gartenrotschwanz-Reviere in Obstgärten der Nordwestschweiz hatten einen signifikant höheren Anteil an lückiger Vegetation als nicht besetzte Kontrollflächen. Zudem unternahmen Gartenrotschwänze beinahe fünfmal mehr Fangflüge in experimentell erstellte Ruderalbrachen als in ungemähte Wiesen. Hatten die Gartenrotschwänze jedoch die Wahl zwischen den Ruderalbrachen und frisch gemähten Wiesen, konnte keine

Präferenz festgestellt werden. Mit Hilfe der Vegetationshöhe und des Anteils an offenem Boden konnte in 77% der Fälle korrekt vorhergesagt werden, wohin Gartenrotschwänze ihre Fangflüge unternehmen. Versuche in Volieren mit zwei lückigen Vegetationstypen und einer dichten Wiese als potenzielle Jagdhabitate bestätigten die Resultate aus den Feldexperimenten. Selbst bei vierfach höherer Futtermenge in der dichten Wiese, wurden die lückigen Vegetationstypen signifikant häufiger zum Nahrungserwerb genutzt. Förderprogramme für den Gartenrotschwanz sollten daher nicht nur traditionell bewirtschaftete Hochstammobstgärten erhalten, sondern in diesen Obstgärten auch Flächen mit lückiger Vegetation fördern.

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