SHORT COMMUNICATION

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Scale-dependent habitat selection in migratory frugivorous passerines

Abstract Frugivorous migrants may select fruit-rich habitats en route to attain high food rewards, yet their stopover behavior may also be shaped by other considerations, such as predation risk. During 1996–2001 we investigated autumn stopover habitat use of three *Sylvia* warblers (sylviids; *S. hortensis*, *S. atricapilla* and *S. curruca*) and three Turdidae chats (turdids; *Cercotrichas galactotes*, *Oenanthe hispanica* and *Phoenicurus phoenicurus*) in planted groves of the fruiting tree *Pistacia atlantica* in Lahav Forest, Israel, which is located at the edge of a desert. We used fecal analysis, a constant-effort trapping scheme and field observations to estimate the extent of frugivory, and bird habitat and microhabitat selection with regard to natural fruit and foliage densities. We also measured bird microhabitat selection in a set of fruit-manipulated trees. We trapped a total of 2,357 birds during the course of the study. Although sylviids exhibited higher frugivory level than turdids, both species groups exhibited a similar significantly positive correlation between bird and fruit densities at the habitat scale. However, at the microhabitat scale, sylviids selected densely foliated trees, whilst turdids were randomly distributed among trees. Our findings suggest that both species groups selected fruit-rich stopover habitats to take advantage of the high food availability before the demanding migration journey. No other mechanism except predation avoidance can explain the sylviids' microhabitat selection; the migrants used foliage cover to reduce bird detectability by raptors. We conclude that en route passerines may use staging habitats in a sophisticated manner, by adopting scale-related behavior with regard to the availability of food and refuge cover.

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Introduction

Time, energy, and safety from predators are probably the most crucial selective forces affecting staging migratory birds. Since behavioral decisions regarding food acquisition and safety from predators during stopover can have direct ramifications on bird survival, and since the interplay between these two factors often results in trade-offs (Metcalfe and Furness 1984; Ydenberg et al. 2002), examination of bird habitat selection during staging periods can provide information on the ways in which migratory birds respond to environmental heterogeneity that is likely to affect bird fitness (Moore and Aborn 2000).

During migration, bird decision-making may differ between different spatial scales. The most relevant scales for birds that alight during migratory flights are the between-habitat scale, in which the bird selects or avoids certain habitats, and the within-habitat scale, in which the bird selects or avoids certain vegetation structures such as trees and shrubs within the habitat (hereafter, habitat and microhabitat scales, respectively; Hutto 1985). The behavioral response of birds to environmental heterogeneity at these two scales comprises the birds' habitat selection. Yet, the notion of geographic scales during stopover has seldom been explicitly addressed in studies of bird migration.

Migratory birds are good model organisms for studying trade-offs between safety from predators and foraging, especially prior to crossing wide barriers. In such areas not only do birds have to deposit large amounts of fuel,

but they are also at a high risk of predation as a result of both high foraging intensity (Dierschke 2003) and high fuel mass (Ydenberg et al. 2002).

The total number of cross-Sahara migrants that fly over Israel each autumn is about 500 million (Shirihai 1996), and the desert edge comprises their last opportunity to re-fuel before entering the 1800 km-wide desert (Biebach et al. 1986). We investigated how passerine migrants respond to habitat and microhabitat heterogeneity in terms of food and refuge availabilities. Specifically we address the following questions: (1) Does en route fruit-based habitat and microhabitat selection depend on the species' frugivory level? (2) Does predation risk affect bird behavior while staging en route? (3) Does bird behavior change in relation to the geographic scales (sensu Hutto 1985)?

Materials and methods

Migrants were studied during autumn 1996–2001 in three groves of *Pistacia atlantica* located within 1.5 km of each other in the mainly coniferous Lahav Forest, Israel (31°20′N, 34°50′E): the western grove (area of 3 ha, hereafter WG), the eastern grove (also 3 ha, hereafter EG) and the small grove (0.5 ha, hereafter SG); all groves had similar tree densities and were of the same age. We studied the three most abundant species in each of the two following taxonomic groups of migratory passerines: *Sylvia* warblers (Orphean warbler, *S. hortensis*, blackcap, *S. atricapilla*, and lesser whitethroat, *S. curruca*; hereafter sylviids) and Turdidae chats (rufous bush-chat, *Cercotrichas galactotes*, black-eared wheatear, *Oenanthe hispanica*, and redstart, *Phoenicurus phoenicurus*; hereafter turdids).

We examined bird diet of all species except the rufous bush-chat (insufficient sample size) during autumn 1998 in the WG, following Jordano (1988). In addition we observed individual birds during morning hours for variable time periods (range: 12–220 s) and recorded their consumption of arthropods and *P. atlantica* fruits.

We estimated fruit density in two spatial scales: fruit per grove (habitat scale) and fruit per tree (microhabitat scale): in autumn 1998 we counted fruit crops of 30 randomly selected trees and used this count to estimate both per tree and per grove densities throughout the study. We classified the trees into five classes of fruit abundance and calculated each class's average fruit crop. We estimated the total per grove fruit abundance during the years 1998–2001 by assigning each tree in each grove into one of the fruit abundance classes, and then summed the per tree fruit abundance

estimates. During earlier years (1995–1997) Shochat et al. (2002) used a different method of estimation, which was found to positively correlate with ours based on 1998–2001 data (Spearman's correlation, r_s=0.96, n=7, P<0.001); hence, we also used earlier years' data. We assigned the total fruit number per grove in a certain year into three categories of fruit abundance (high, medium and low; see Table 1).

We manipulated fruit density during autumn 1998 at the WG in 12 trees that featured approximately 70,000 fruits/tree by creating four artificial fruit density classes (0, 10,000, 20,000, 40,000 fruits/tree; 3 trees/class). During 1998–2000 we also used non-manipulated trees (18 in 1998 and 30–35 in 1999/2000), assigned into six fruit density classes (0, 10,000, 20,000, 40,000, 70,000, 100,000 fruits/tree; 3 trees/class). We estimated tree foliage density by averaging the number of leaves counted in an 8,000 cm^3 cube placed on four randomly selected branches facing the four main compass directions.

Bird habitat selection was measured by bird trapping, which took place in the WG during each of 1996–2001 autumns and in the EG during 1996, 1998 and 2000 autumns. Thirteen to twenty-five constant-effort trapping days per season were conducted in each grove. The daily species density is the sum of all individuals trapped during a period of 4 hours starting from first light in eight 12×2.5 m lined mist nets. We defined for each species a main period of migration, in which it was present at the study area consistently across all years of the study and arbitrarily defined the period between 15 August and 15 October as the main migration period for all turdids and sylviids (pooled across all species). Bird microhabitat selection, with regard to the tree foliage and fruit densities, was measured in the WG during autumns 1998–2000 and in the SG during autumn 1999, by observing each tree for 2 min during the first two morning hours on several different dates. The order of the observations was randomized across the different trees (and treatments in 1998), and took place at least 2 days apart to avoid re-counting the same birds.

Results

During autumns 1996–2001, we trapped a total of 2,357 birds of the six studied species (see Table 1 for species totals). All species consumed, to variable extents, both *P. atlantica* fruits and arthropods. No differences in the proportion of fecal fruit remains across species within each group was found (sylviid species: Kruskal-Wallis test $\chi^2_{(2)}$=3.27, P=0.2; turdid species: Mann-Whitney U test, U=1412, n_1=86, n_2= 32, p=0.82), but while fruits comprised 69% of the sylviids' fecal volume, it com-

Table 1 Densities (constant mist-netting efforts) of bird species with respect to the habitat's fruit abundance (Low fruit yield: 0.09–0.17 million fruits/habitat, EG in 1996, 1998 and 2000; medium: 0.56 million fruits/habitat, WG in 2000; and high: 5.5–9 million fruits/habitat, WG during 1996–1999 and 2001). One-way ANOVA tests followed by Bonferroni post-hoc tests on the natural logarithm of bird densities

Species	No. of birds (no. of trapping occasions) [dates range]	Mean bird density (±SE) in each habitat			F
		Low fruit yield	Medium fruit yield	High fruit yield	
Orphean warbler	292 (70) [13/8–20/9]	2.5 (±0.5)	0.9 (±0.4)	5.7 (±0.7)	$12.8_{2,67}$***a
Blackcap	487 (98) [19/8–24/10]	1.9 (±0.3)	3.6 (±0.8)	6.6 (±0.7)	$19.4_{2,95}$***b
Lesser whitethroat	491 (93) [17/8–11/10]	0.7 (±0.2)	2.2 (±0.7)	7.9 (±0.6)	$62.7_{2,90}$***a
Rufous bush-chat	94 (52) [13/8–8/9]	0.6 (±0.2)	1 (±0.3)	2.9 (±0.5)	$9.7_{2,49}$***b
Black-eared wheatear	761 (76) [23/8–14/10]	0.3 (±0.2)	3 (±1.1)	16.3 (±2.1)	$81_{2,73}$***
Redstart	232 (37) [24/9–31/10]	2.1 (±1)	2.8 (±0.9)	7.9 (±1.1)	$6.4_{2,34}$**b

**P*<0.01, ****P*<0.001
[a] Bird density is not significantly different between the low fruit yield and the medium fruit yield habitats
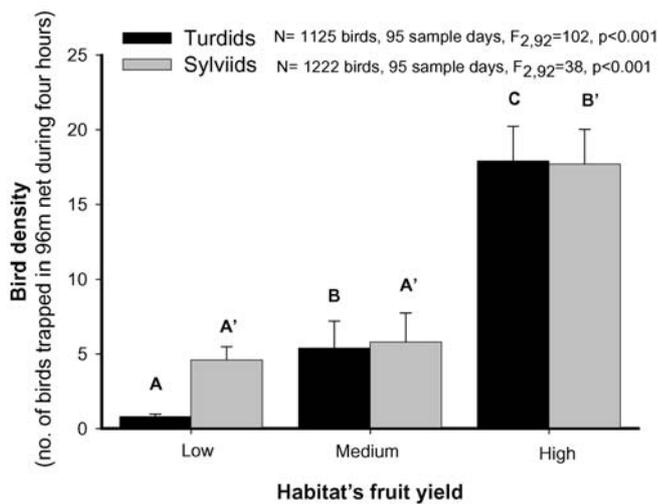[b] Bird density is only significantly different between the low fruit yield and the high fruit yield habitats

Fig. 1 Densities (constant mist netting efforts; means ± SE) of sylviids and turdids (pooled across all species in each group) trapped in three habitats, characterized by different fruit abundance between 15 August to 15 October during 1996–2001 in the study area (for habitat descriptions see Table 1). Different letters above bars (*A*, *B*, *C* for turdids and *A′*, *B′* for sylviids) indicate significant differences within bird group (one-way ANOVA followed by Bonferroni post-hoc test for each species group on natural-logarithm-transformed densities)

prised only 28% of the turdids' fecal volume (Mann-Whitney U test, U=2892.5, n_1=120, n_2=118, P<0.001), indicating a significant difference in the extent of frugivory between these two groups. We observed 50% of the sylviid individuals (10 out of 20) but only 14% of the turdid individuals (6 out of 42) feeding on fruits, while 35% of the sylviids were observed feeding on arthropods, compared with 48% of turdids (Fisher's exact probability test on the frequency of fruit feeding between the groups after sample size and observation time corrections, n=62, P=0.0009). Average ± SE consumption rates of all the observed individuals: sylviids 1.19±0.01 and turdids 0.71±0.39 fruits/minute; sylviids 0.49±0.003 and turdids 1.22±0.31 arthropods/minute.

Significantly more birds were trapped in fruit-rich habitats than in fruit-poor habitats. This was evident in each of the six bird species and also in the pooled per-group densities (Table 1, Fig. 1). We found that fruit crop and foliage density of *P. atlantica* trees were negatively correlated (Pearson correlation on square-root-transformed fruit quantity, r=−0.73, n=43, P<0.0001). We

could not find any evidence for microhabitat selection in the manipulated trees (ranging between 0 and 40,000 fruits/tree), with regard to both fruit and foliage densities (logistic regression analyses, P>0.05). It should be noted that the manipulated trees were originally fruit-rich trees, and thus featured a rather low foliage density. Among the non-manipulated trees, sylviids selected microhabitat (a single tree) based on foliage density (Table 2): densely foliated trees were utilized more often by sylviids than sparsely foliated trees. This pattern was consistent in three different years and at two different groves (Table 2). Nevertheless, when the effect of fruit density was examined, either a non-significant (P>0.05, 1999 SG and 2000 WG) or negatively significant (1998 and 1999 WG) relationship was found, with the latter result being probably a consequence of the negative fruit–foliage relationships. Similar analyses on turdids data were not significant (P>0.05 in all).

Discussion

En route migratory passerines examined in this study exhibited scale-related habitat selection while staging at the edge of an ecological barrier. We suggest that bird behavior is an outcome of different risks and benefits concerning food (energy) acquisition and predator avoidance.

Given the high frequency of frugivory among temperate latitude migrants and the fruit-rich habitats found in temperate and Mediterranean zones, evidence for habitat selection by migrating frugivores is surprisingly limited (Parrish 2000, but see Blake and Hoppes 1986; Suthers et al. 2000). Fruit-based habitat selection was ubiquitous among our studied species (Fig. 1, Table 1) which consumed a mixed diet of arthropods and fruits. Despite being less frugivorous, it seems that the turdids exhibited a more fine-tuned habitat selection with respect to fruit abundance, by virtually avoiding the most fruit-poor habitat (Fig. 1).

It has been suggested that predation risk considerations may shape the way birds use en route habitats (Lindström 1990; Ydenberg et al. 2002). We suggest that the microhabitat selection of the sylviids (Table 2) is a consequence of these considerations, as foliage cover can reduce bird detectability and might also impose some physical difficulty for a raptor to capture a bird after it has been detected. The adaptive value of using densely foli-

Table 2 The effect of foliage density on bird presence on pre-measured sets of trees in different years and groves, analyzed by logistic regression. The variable tested in all analyses was the continuous variable foliage density (df = 1). The numbers of within-season replications are in parentheses

Location /year /treatment	Logistic model $Y=(1+\exp(\alpha+\beta*X))^{-1}$			Analysis results		Hosmer–Lemeshow goodness of fit test		
	α constant	β coefficient	n	Wald z	P	$\hat{C}$	df	P
WG 1998 (control)	−3.59	0.22	36 (2)	5.97	0.015	11.56	7	0.12
WG 1999	−2.41	0.08	120 (4)	7.18	0.007	25.43	8	0.001
SG 1999	−2.55	0.15	60 (2)	7.06	0.008	11.54	8	0.17
WG 2000	−4.53	0.15	70 (2)	9.07	0.003	6.39	7	0.49

ated trees could have evolved from other factors, such as radiation reduction considerations and food availability. The reduction of solar radiation intensity seems unlikely in our study since data were collected during early morning hours, when solar radiation was invariably low. In addition, neither arthropod (Sapir 2002) nor fruit densities positively correlate with foliage density.

Howe (1979) introduced a model to explain frugivory under risk of predation. This model assumes that a bird is attracted to a fruiting tree because of nutritional or energetic rewards, that the risk of predation is higher in fruiting trees than in nearby refuges, and that predation attempts occur at intervals that the frugivore cannot predict. Bird behavior was suggested to be a general response to the overall predation risk rather than a specific response to certain predator attacks. Howe's model can explain both sylviid behavior and the difference in microhabitat selection between the two groups of species. The sylviids' attraction to densely foliated trees is likely to be a general response to avoid predation, since the birds cannot predict the time of the next predator attack and under such conditions the overall probability of attack increases with time spent in the fruiting tree. Thus, to reduce predation probability, fruit processing should be made on neighboring densely foliated and fruit-poor trees. Conversely, the mainly insectivorous turdids are likely to devote only a fraction of their foraging time to fruit consumption and consequently their behavior is probably governed by a different set of behavioral rules than those of the sylviids, e.g., promoting detection of flying insects through the occupation of high perches where detectability conditions are the best. This may even facilitate early predator detection and thus may permit a quick response of the bird accordingly.

We suggest that the specific scale-related behavior enables the birds to assure high energetic rewards by selecting habitats characterized by high food availability, while reducing predation risks by selecting densely foliated trees that provide cover within these fruit-rich habitats. Thus, bird habitat selection decision-making during stopover is a complicated and hierarchical process (Hutto 1985). Detailed follow-up of individual birds may enable us in the future to evaluate the adaptive value of certain decisions taken by migratory birds during stopover.

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