

Acoustic information as a distant cue for habitat recognition by nocturnally migrating passerines during landfall

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During migration, birds must fly over suboptimal habitats differing from those selected during breeding and wintering. Nocturnally migrating passerines need to assess the suitability of potential stopover habitats during landfall. Before actual landfall, distant cues may play a significant role in habitat selection. In this paper, we studied the possibility that migrant songbirds use acoustic information as distant cues for habitat selection when ceasing flight. We also investigated differences between habitat generalists and specialists in their use of acoustic cues by comparing the proportion of species killed at lighthouses with those captured in mist nets using song playback in both suitable habitats and suboptimal stopover habitats during spring and fall migratory seasons. Our observations showed that during twilight landfall, birds may respond to acoustic cues, especially when visual cues are reduced or absent. This was true for habitat specialists (Eurasian reed warblers and sedge warblers) whose songs are also more attractive to conspecifics and other birds of wetland habitats than to habitat generalists (pied flycatchers and redwings). Adult Eurasian reed warblers had a tendency to be more attracted by acoustic cues than juveniles. This finding suggests that previous experience may play a role in habitat recognition using acoustic stimuli. *Key words:* heterospecific attraction, lighthouses, song playback. [*Behav Ecol*]

Rapid selection of high-quality habitat makes it possible for migrants to gain access to resources at stopover sites ahead of conspecific competitors. Two possible strategies of habitat assessment can be used: birds either sample the suitability of the habitat on their own (direct sampling) or use cues from other birds that are already present in a particular habitat (cue using according to Mönkkönen et al. 1999). Cue use allows birds to assess habitats from a distance without sampling, thus making the process more rapid. Individuals gain a larger benefit when they make the correct habitat assessment quickly (Thomson et al. 2003; Mettke-Hofmann and Gwinner 2004). Therefore, we hypothesize that initial assessment of landfall habitats occurs when birds are still aloft. During landfall, birds may assess a habitat on the basis of both visual (Hutto 1985; Moore et al. 1995; Moore and Aborn 2000) and acoustic cues. The acoustic environment created by any terrestrial habitat could give the birds additional cues regarding its quality. One such cue could be vocalizations made by conspecifics and heterospecifics already present at a particular site. For example, loudly singing species of wetland birds could be markers of their respective habitat, and their songs could play a role in habitat assessment by avian migrants from different taxa (Herremans 1990a, 1990b; Schaub et al. 1999).

Using conspecific and heterospecific song playbacks, we investigated the following hypotheses:

- I. During landfall, acoustic cues may play an important role in habitat assessment. This might be especially true for nocturnal migrants ceasing flight in the morning

twilight or deep in the night (Cochran et al. 1967) when the use of visual cues might be impaired.

- II. Habitat specialists use acoustic markers (both conspecific and heterospecific) for habitat selection, whereas habitat generalists do not. Specialists, especially those using patchy environments (e.g., wetlands), are under strong selection to choose the correct habitat. Therefore, these species may use a broader array of characters to select habitat (but see Dall and Cuthill 1997). For generalists, fine-tuned habitat selection during migratory stopovers may be less critical.
- III. Age will influence the responses of migrating birds to acoustic cues. Adult birds may be more strongly attracted by song playback than juveniles because of their prior experience and familiarity with songs of conspecific and heterospecific breeders in suitable habitats. Alternatively, young naive birds, on their first migration, might be expected to use every possible cue to help them land in an appropriate habitat.

We propose that association of acoustic stimuli (species-specific songs) with particular habitats on the ground could provide critical cues regarding habitat quality for transient migrants.

MATERIALS AND METHODS

To test our hypotheses, we analyzed data sets from 2 trapping sites on the Courish Spit of the Baltic Sea (55°00'–09'N, 20°34'–51'E) and from birds killed at lighthouses in Denmark (Figure 1).

Trapping sites

- I. First, we conducted tape-luring experiments during the spring and fall migratory seasons 1999–2003 at a specially

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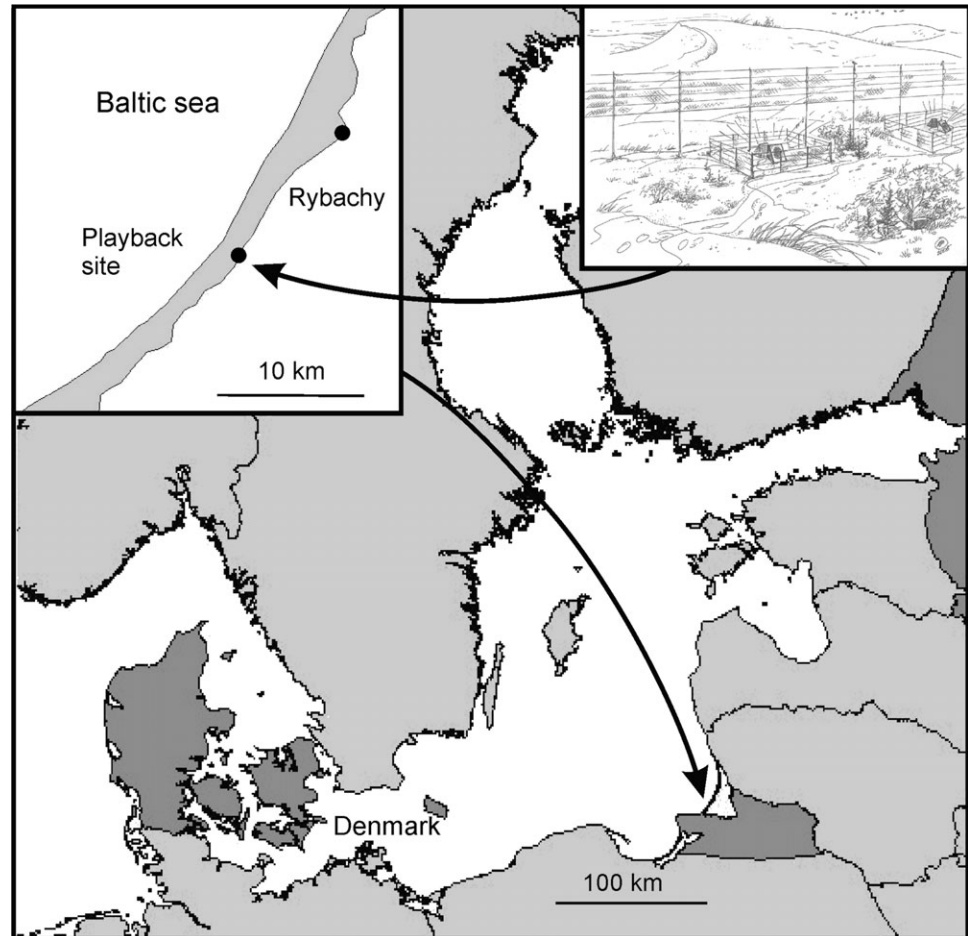


Figure 1
Map of study sites and
sketch of tape-luring setup.

selected playback site situated in the transition gap between pine plantations and high sand dunes partly covered by willow scrub. The nearest reed stands were located 4 km to the southwest and 10 km to the northeast of the study site. We considered the dunes where the song playback experiment was performed as a suboptimal habitat for *Acrocephalus* species whose songs we played (Table 1) 1) because only 175 Eurasian reed warblers and 190 sedge warblers (*Acrocephalus schoenobaenus*) had been captured in stationary funnel traps located 150 m away (for a description of the traps, see Payevsky 2000) over a 45-year period (Mukhin, Chernetsov, and Kishkinev 2005). These long-term trap data indicate that this site is rarely used by wetland birds, in particular by *Acrocephalus* warblers, under natural conditions; 2) because of recapture rate of Eurasian reed and sedge warblers at this site (see Results).

The birds were captured in mist nets positioned in rectangles with the acoustic systems in the center (Figure 1). Additionally, high mist nets (upper edge 7 m above the ground) (described in Bolshakov et al. 2000) were set between the 2 rectangles. The nets were open at sunset and closed 30–40 min after sunrise (1999) or 20 min before sunrise (2000–2003). The acoustic systems included 2 car tape players with 30 W loudspeakers (frequency range 50–20 000 Hz) directed toward the northeast and southwest.

If songs of 2 species were played during the same trapping session (Eurasian reed warbler and sedge warbler, Eurasian reed warbler and pied flycatcher, Table 1), both songs were played simultaneously by 2 different acoustic systems. Depending on the weather, we guess that migrants could hear

the playback at a distance varying between several hundred meters and 1 km.

After sunset, we checked the nets on an hourly basis throughout the night. All birds captured at night were released 250 m from the capture site after sunrise. Data collected at this playback site were assigned to 1 of 2 data sets: the first consisted of birds that were caught more than 2 h before sunrise (i.e., during “deep night”) (data set 1) and the second consisted of birds that were caught during morning twilight (data set 2).

II. Our second trapping site was the Rybachy field station on the Courish Spit, 11 km northeast of the playback site. The data collected at the Rybachy study plot formed our third data set (data set 3). Birds were captured here using 73 mist nets located in reed stands and scrub. These birds made natural landfall without additional acoustic stimuli. We considered this site as a highly suitable habitat.

Lighthouse data

Our fourth data set (data set 4) was obtained from birds killed at night at lighthouses in Denmark during migratory periods from 1886 to 1939 (Hansen 1954). Twenty species of long-distance passerine migrants were included in the analysis. We assume that relative numbers of these species among birds killed at lighthouses are representative of their proportions in the flow of passerine migrants in the southern Baltic area and therefore provide a reasonably good indication of the

Table 1
Time schedule of songs played

Species	1999	2000	2001	2002	2003
Reed warbler	22 July to 11 September	30 April to 17 October	30 April to 23 September	27 July to 11 September	
Marsh warbler	22 July to 11 September				
Sedge warbler			12 May to 23 September		
Pied flycatcher		30 April to 9 September			
Redwing				7–28 May	
Garden warbler					27 July to 18 September

composition of birds aloft. Although the lighthouse data were gathered more than 60 years ago, 550 km from our study site, and relative abundances could very well have changed over this period, we have nevertheless used this data set because it is the only large data set available on relative numbers of different passerine species aloft during nocturnal migration in this part of the world. Any captures on the ground are necessarily biased with respect to the sampling habitat.

Comparison of data

As we used 3 different methods to collect our data, variation in the number of mist nets at different sites and between the years of study does not allow us to compare relative abundance of migrants between sites/data sets on the basis of trapping rates. However, the number of mist nets and trapping design are unlikely to influence the relative proportions of common species regularly caught/collected within each site. Therefore, 20 passerine species among those captured at each site and found dead at lighthouses were selected for analysis, most of them long-distance migrants. Their relative proportions were compared by Yates-corrected chi square.

To investigate hypothesis I (the importance of acoustic cues)

- The composition of birds attracted by playback during morning twilight (i.e., 2 predawn hours) that could use both visual and acoustic stimuli (data set 2) were compared with captures of long-distance passerine migrants at Rybachy (data set 3). During landfall at the latter, suitable habitat, migrants had to rely primarily on visual cues because no additional acoustic cues were provided. For the purpose of our comparisons, only birds captured within the first 2 h after sunrise in Rybachy were included. We assume that the proportion of migrants captured during this period is more representative of their proportions at landfall because it is less biased by the differential mobility of preexisting migrants that have already become established at the stopover (Chernetsov and Mukhin 2006).
- Birds tape lured in the deep night (data set 1) were compared with birds killed at lighthouses in Denmark (data set 4). We assume that for individuals attracted by playback during the deep night, visual cues were not easily available for habitat assessment.

To investigate hypothesis II (specialists vs. generalists)

- We played the songs of species that could be associated with wetland habitats (habitat specialists like Eurasian reed warbler and sedge warbler), as well as those of species whose association with such habitats is much weaker (garden warbler *Sylvia borin*). We also played those of species that do not normally occur in wetland habitats (habitat generalists like the pied flycatcher, *Ficedula hypoleuca*, and the redwing, *Turdus iliacus*).

- We carried out choice experiments between conspecific and heterospecific acoustic stimuli. We analyzed the distribution of Eurasian reed and sedge warblers captured along the high mist net line relative to 2 song playback sources: 1) Eurasian reed warbler—pied flycatcher (2000) and 2) Eurasian reed warbler—sedge warbler (2001), located 68 m from each other in 2000 and 51 m from each other in 2001. The difference was tested by Spearman rank correlation. As the number of high nets varied between the years of study, data from 2000 and 2001 were analyzed separately. The null hypothesis was that the number of Eurasian reed and sedge warblers captured by the high mist nets did not depend on the distance to any of the acoustic sources. Significance was tested by comparison with the critical value of the sample rank correlation (T_{crit}) for $P = 0.05$ with rank correlation coefficient (ds). If $T_{crit} > ds$, then H_0 cannot be rejected (no significant differences), and if $T_{crit} < ds$, then H_0 can be rejected.

To examine hypothesis III (adults vs. juveniles)

We compared the proportions of adult Eurasian reed warblers (the most numerous species) at the playback site (considered as a suboptimal habitat) and in the suitable habitat in Rybachy without playback.

All years when the Eurasian reed warbler song was played are analyzed together. Data obtained during playback of garden warbler and redwing songs are discussed separately.

RESULTS

Estimation of habitat quality

To prove our estimation of chosen sites, we used a number of recaptured individuals trapped on subsequent days. Of the 116 Eurasian reed warblers captured using song playback in spring, none was recaptured at the same site on subsequent days. During the same period, 6.5% of birds mist netted in Rybachy without playback were subsequently recaptured ($n = 792$, Yates-corrected $\chi^2 = 6.91$, $P = 0.009$). The respective figures for the sedge warbler were 0% of recaptures at the song playback site ($n = 49$) and 2.0% in Rybachy ($n = 408$, Yates-corrected $\chi^2 = 0.17$, $P = 0.68$). A similar pattern was observed in the fall: 0% of recaptures at the playback site in Eurasian reed warblers ($n = 242$) compared with 29.0% of recaptures in Rybachy ($n = 1287$, Yates-corrected $\chi^2 = 91.2$, $P < 0.0001$). The respective figures for the sedge warbler were 0% ($n = 147$) and 15.6% ($n = 942$, Yates-corrected $\chi^2 = 25.2$, $P < 0.0001$).

Birds that respond to song playback

A total of 2607 birds belonging to 42 species were captured using song playback. In all years, the most common species of

long-distance migrant was the Eurasian reed warbler (1999, 41%; 2000, 49.8%; 2001, 50.6%; and 2002, 59.4%), followed by sedge warblers (11.3%, 14.1%, 15.9%, and 16.7%, respectively), garden warblers (15.6%, 2.9%, 4.4%, and 11.7%, respectively), blackcaps (*Sylvia atricapilla*, 6.8%, 2.2%, 2.1%, and 1.8%, respectively), and grasshopper warblers (*Locustella naevia*, 5.7%, 3.2%, 3.7%, and 0%, respectively). The proportions of other species were negligible. Of nonpasserines, a water rail (*Rallus aquaticus*), 2 spotted crakes (*Porzana porzana*), and a common sandpiper (*Actitis hypoleucos*) were captured. However, if we exclude those birds caught 2 h before sunrise, only 17 species of passerines were captured in 1999–2002. These species were captured during the deep night and were thus most likely lured by song playback, rather than during their morning movements (Mukhin, Chernetsov, and Kishkinev 2005).

Response to song playback in spring

Song of habitat specialists: Eurasian reed warbler and sedge warbler
Tape luring took place during the spring migratory periods of 2000–2001 when songs of the Eurasian reed warbler, sedge warbler, and pied flycatcher were played (Table 1). The proportion of Eurasian reed warblers in captures during the deep night (data set 1) exceeds 90%, whereas among migrants killed at lighthouses (data set 4), this species comprised only 0.31% (Table 2). Several species commonly sampled in the flow of migrants, for example, the pied flycatcher, northern wheatear (*Oenanthe oenanthe*), common redstart (*Phoenicurus phoenicurus*), whinchat (*Saxicola rubetra*), and whitethroat (*Sylvia communis*), were virtually absent from song playback captures.

Comparison of twilight tape-luring captures (data set 2) with morning captures in standard mist nets (data set 3) during the same period showed that the proportion of Eurasian reed warblers was significantly lower in the suitable habitat than in the suboptimal habitat with song playback (Table 3). The same was true for the sedge warbler. In 2 species (the common redstart

and the blackcap), a reverse pattern was observed: these were more common in the suitable habitat without song playback.

Song of habitat generalists: pied flycatcher and redwing

Playback of the pied flycatcher song along with the Eurasian reed warbler song in the spring 2000 did not result in the capture of any pied flycatchers. Playback of the redwing song in spring 2002 (between 7 and 25 May, i.e., during the passage of long-distance migrants) attracted just 9 individuals: 3 lesser whitethroats (*Sylvia curruca*), 2 red-backed shrikes (*Lanius colurio*), a marsh warbler, a Eurasian reed warbler, a European robin (*Erithacus rubecula*), and a whinchat. Only 3 birds were captured more than 2 h before sunset.

Response to song playback in the fall

Song of habitat specialists: Eurasian reed warbler and sedge warbler

Proportions of 4 *Acrocephalus* species were significantly higher in song playback captures (data set 1) than in the nocturnal flow of migrants (data set 4) during the 4 years (1999–2002) when Eurasian reed warbler song was played (Table 4). As in the spring, the pied flycatcher, northern wheatear, common redstart, and willow warbler (*Phylloscopus trochilus*) were significantly underrepresented in captures. Proportions of other species in captures were not significantly different from their proportions in the flow of long-distance nocturnal migrants.

As in the spring, proportions of Eurasian reed and sedge warblers captured in standard nets in the suitable habitats during the first 2 daylight hours (data set 3) were significantly lower than in the sand dunes with song playback (data set 2). Other long-distance migrants occurred less frequently in tape-lure captures (redstart, willow warbler, blackcap, and spotted flycatcher) or the difference was not significant (Table 5).

Song of habitat generalists: pied flycatcher and garden warbler

Playback of pied flycatcher song induced the same number of captures of this species in both the fall and the spring. Playback of the garden warbler song in the summer and fall of 2003

Table 2
Responses to song playback in spring: comparison with birds killed at lighthouses

Species	Playback (data set 1)		Lighthouse (data set 4)		Chi square	P
	Number (n)	Proportion (%)	Number (n)	Proportion (%)		
Great reed warbler	1	0.64	0	0.00	4.14	0.042*
Marsh warbler	1	0.64	1	0.03	1.63	0.20
Sedge warbler	4	2.56	162	5.61	2.1	0.15
Reed warbler	142	91.03	9	0.31	2564	<0.0001*
Tree pipit	0	0.00	39	1.35	1.2	0.27
Bluethroat	0	0.00	11	0.38	0.01	0.93
Icterine warbler	0	0.00	5	0.17	0.24	0.62
Red-backed shrike	3	1.92	15	0.52	2.86	0.09
Grasshopper warbler	0	0.00	2	0.07	1.63	0.20
Pied flycatcher	0	0.00	414	14.34	24.7	<0.0001**
Spotted flycatcher	0	0.00	19	0.66	0.24	0.62
Wheatear	0	0.00	528	18.28	33.2	<0.0001**
Redstart	1	0.64	523	18.11	30.5	<0.0001**
Willow warbler	1	0.64	734	25.42	48.2	<0.0001**
Whinchat	0	0.00	177	6.13	9.06	0.003**
Blackcap	0	0.00	31	1.07	0.79	0.37
Garden warbler	0	0.00	36	1.25	1.05	0.31
Whitethroat	1	0.64	135	4.67	4.74	0.029**
Lesser whitethroat	1	0.64	44	1.52	0.3	0.58
Barred warbler	1	0.64	3	0.10	0.45	0.50

Number (n), real number of trapped or found birds; proportion (%), their relative proportion. Scientific names in bold are habitat specialists.

* Significant overrepresentation at the playback site.

** Significant underrepresentation at the playback site.

Table 3

Responses to song playback in spring: comparison with birds mist netted at the suitable habitat in Rybachy

Species	Playback (data set 2)		Rybachy (data set 3)		Chi square	P
	Number (n)	Proportion (%)	Number (n)	Proportion (%)		
Great reed warbler	4	1.90	1	0.26	2.73	0.0990
Marsh warbler	2	0.95	60	15.35	29.00	<0.0001
Sedge warbler	49	23.33	48	12.28	12.30	0.0004*
Reed warbler	116	55.24	122	31.20	27.40	<0.0001*
Tree pipit	1	0.48	1	0.26	0.09	0.7700
Bluethroat	1	0.48	1	0.26	0.09	0.7700
Icterine warbler	1	0.48	1	0.26	0.09	0.7700
Red-backed shrike	0	0.00	1	0.26	0.10	0.7500
Grasshopper warbler	6	2.86	15	3.84	0.15	0.7000
Pied flycatcher	2	0.95	15	3.84	3.15	0.7600
Spotted flycatcher	1	0.48	5	1.28	0.26	0.6100
Wheatear	0	0.00	1	0.26	0.10	0.7500
Redstart	0	0.00	21	5.37	10.15	0.0014**
Willow warbler	4	1.90	5	1.28	0.06	0.8000
Whinchat	7	3.33	11	2.81	0.01	0.9200
Blackcap	1	0.48	35	8.95	15.90	0.0001**
Garden warbler	1	0.48	9	2.30	1.78	0.1800
Whitethroat	8	3.81	25	6.39	1.30	0.2500
Lesser whitethroat	6	2.86	14	3.58	0.05	0.8200
Barred warbler	0	0.00	0	0.00	—	—

Number (n), real number of trapped or found birds; proportion (%), their relative proportion. Scientific names in bold are habitat specialists.

* Significant overrepresentation at the playback site.

** Significant underrepresentation at the playback site.

attracted only garden warblers and grasshopper warblers. Captures of Eurasian reed and marsh warblers and common redstarts and willow warblers were significantly less common (Table 6).

Adults versus juveniles

Adult Eurasian reed warblers were more attracted by song playback than juveniles. In 1999–2001, adults comprised 15.6% of

all birds of this species tape lured after 1 August ($n = 546$), when the numbers of self-sustaining juveniles performing migratory and premigratory nocturnal flights (Mukhin 2004; Mukhin, Kosarev, and Kitorov 2005) were already high. During the same period, adults comprised only 6% of mist net captures without acoustic cues in Rybachy ($n = 801$), a significantly lower proportion ($\chi^2 = 33.4$, $P < 0.0001$). Adult Eurasian reed warblers migrate earlier than juveniles (Chernetsov

Table 4

Responses to song playback in the fall: comparison with birds killed at lighthouses

Species	Playback (data set 1)		Lighthouse (data set 4)		Chi square	P
	Number (n)	Proportion (%)	Number (n)	Proportion (%)		
Great reed warbler	3	0.84	1	0.02	21.5	<0.0001*
Marsh warbler	5	1.40	7	0.13	19.9	<0.0001*
Sedge warbler	27	7.56	142	2.66	26.2	<0.0001*
Reed warbler	224	62.75	62	1.16	2645	<0.0001*
Tree pipit	0	0.00	135	2.53	8.2	0.004**
Bluethroat	2	0.56	9	0.17	1.02	0.31
Icterine warbler	0	0.00	68	1.28	3.59	0.058
Red-backed shrike	1	0.28	16	0.30	0.19	0.66
Grasshopper warbler	2	0.56	16	0.30	0.13	0.72
Pied flycatcher	0	0.00	751	14.08	56.7	<0.0001**
Spotted flycatcher	0	0.00	17	0.32	0.32	0.57
Wheatear	0	0.00	765	14.35	57.9	<0.0001**
Redstart	1	0.28	1178	22.09	95.6	<0.0001**
Willow warbler	0	0.00	757	14.20	57.2	<0.0001**
Whinchat	2	0.56	50	0.94	0.19	0.66
Blackcap	22	6.16	267	5.01	0.70	0.40
Garden warbler	61	17.09	854	16.02	0.21	0.65
Whitethroat	4	1.12	163	3.06	3.75	0.053
Lesser whitethroat	2	0.56	59	1.11	0.50	0.48
Barred warbler	1	0.28	15	0.28	0.26	0.61

Number (n), real number of trapped or found birds; proportion (%), their relative proportion. Scientific names in bold are habitat specialists.

* Significant overrepresentation at the playback site.

** Significant underrepresentation at the playback site.

Table 5

Responses to song playback in the fall: comparison with birds mist netted at the suitable habitat in Rybachy

Species	Playback (data set 2)		Rybachy (data set 3)		Chi square	P
	Number (n)	Proportion (%)	Number (n)	Proportion (%)		
Great reed warbler	3	0.47	1	0.38	0.14	0.7100
Marsh warbler	10	1.56	10	3.82	3.38	0.0660
Sedge warbler	147	22.97	33	12.60	12.5	0.0004*
Reed warbler	242	37.81	61	23.28	17.6	<0.0001*
Tree pipit	2	0.31	1	0.38	0.22	0.6400
Bluethroat	5	0.78	5	1.91	1.35	0.2600
Icterine warbler	1	0.16	1	0.38	0.02	0.9000
Red-backed shrike	1	0.16	0	0.00	0.21	0.6400
Grasshopper warbler	59	9.22	7	2.67	10.8	0.01*
Pied flycatcher	4	0.63	7	2.67	4.88	0.0270
Spotted flycatcher	1	0.16	6	2.29	8.4	0.038**
Wheatear	3	0.47	0	0.00	0.22	0.6400
Redstart	8	1.25	17	6.49	17.04	<0.0001**
Willow warbler	7	1.09	29	11.07	45.7	<0.0001**
Whinchat	8	1.25	1	0.38	0.68	0.4100
Blackcap	49	7.66	55	20.99	31.1	<0.0001**
Garden warbler	81	12.66	23	8.78	2.74	0.0980
Whitethroat	6	0.94	0	0.00	1.26	0.2600
Lesser whitethroat	3	0.47	5	1.91	2.9	0.0890
Barred warbler	0	0.00	0	0.00	—	—

Number (n), real number of trapped or found birds; proportion (%), their relative proportion. Scientific names in bold are habitat specialists.

* Significant overrepresentation at the playback site.

** Significant underrepresentation at the playback site.

1998), and by 1 August, a larger proportion of adults than juveniles had already departed from the study area. However, because both samples were collected simultaneously, the difference between them is likely due to a stronger response to song playback by adults.

Response to conspecific and heterospecific songs by 2 habitat specialists

In both 2000 and 2001, Eurasian reed warblers were significantly more attracted by conspecific than heterospecific song

Table 6

Response to garden warbler song in fall

Species	Playback		Rybachy		Chi square	P
	Number (n)	Proportion (%)	Number (n)	Proportion (%)		
Great reed warbler	1	1.19	2	0.93	0.19	0.66
Marsh warbler	0	0.00	21	9.72	7.35	0.007**
Sedge warbler	4	4.76	25	11.57	2.48	0.12
Reed warbler	6	7.14	45	20.83	7.09	0.008**
Tree pipit	0	0.00	0	0.00	—	—
Bluethroat	0	0.00	0	0.00	—	—
Icterine warbler	2	2.38	0	0.00	2.21	0.14
Red-backed shrike	1	1.19	1	0.46	0.01	0.92
Grasshopper warbler	8	9.52	0	0.00	17.6	<0.0001*
Pied flycatcher	0	0.00	12	5.56	3.52	0.061
Spotted flycatcher	0	0.00	2	0.93	0.01	0.92
Wheatear	0	0.00	1	0.46	0.24	0.62
Redstart	0	0.00	20	9.26	6.91	0.009**
Willow warbler	0	0.00	29	13.43	11.0	0.0009**
Whinchat	2	2.38	1	0.46	0.73	0.39
Blackcap	17	20.24	28	12.96	1.97	0.16
Garden warbler	39	46.43	14	6.48	63.6	<0.0001*
Whitethroat	2	2.38	10	4.63	0.32	0.57
Lesser whitethroat	1	1.19	4	1.85	0.01	0.92
Barred warbler	1	1.19	1	0.46	0.01	0.92

Number (n), real number of trapped birds; proportion (%), their relative proportion.

* Significant overrepresentation at the playback site.

** Significant underrepresentation at the Rybachy site.

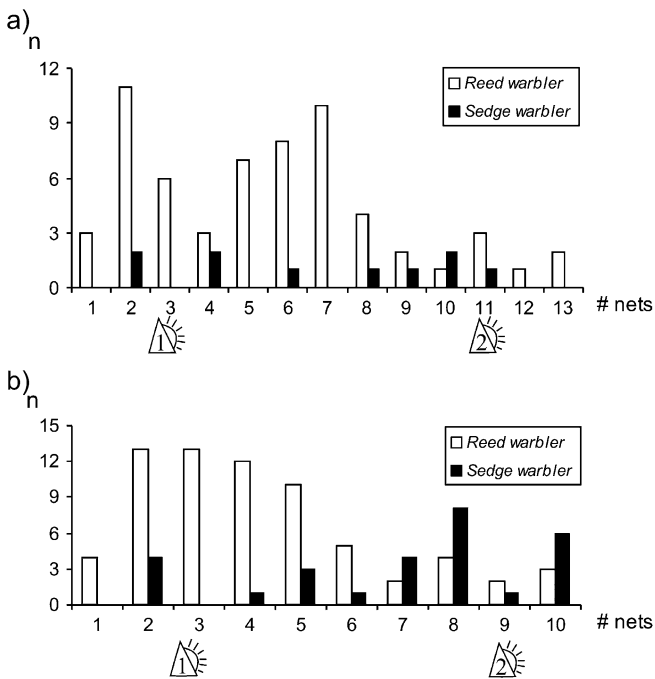


Figure 2
Acoustic choice experiment. The number of captured birds is plotted on the ordinal axis. The positions of acoustic stimuli (triangles with numbers) are shown under the abscissa. The numbers under the abscissa are the position of the mist nets during playback: (a) (2000)—source 1: reed warbler, source 2: pied flycatcher; (b) (2001)—source 1: reed warbler; source 2: sedge warbler.

(pied flycatcher: sample rank correlation, $d_s = 0.793 > T_{crit}$ for $P = 0.05 = 0.610$ in 2000 [H_0 is rejected]; sedge warbler: $0.780 > T_{crit}$ for $P = 0.05 = 0.724$ in 2001 [H_0 is rejected]; Figure 2).

A similar analysis of sedge warbler captures in response to conspecific (2001) and heterospecific (Eurasian reed warbler and pied flycatcher in 2000 and Eurasian reed warbler in 2001) song sources showed no significant patterns, suggesting that this species is not responding to acoustic cues as measured by the proximity of its capture to the positions of the loudspeakers, either when a conspecific song was played in combination with the Eurasian reed warbler song or when 2 different heterospecific songs were presented (sample rank correlation $d_s = 0.003 < T_{crit}$ for $P = 0.05 = 0.582$ in 2000 [H_0 cannot be rejected], $d_s = 0.417 < T_{crit}$ for $P = 0.05 = 0.679$ in 2001 [H_0 cannot be rejected]; Figure 2).

DISCUSSION

Because we performed our song playback experiment in a habitat atypical for wetland birds, there is little doubt that most tape-lured *Acrocephalus* warblers were indeed attracted by song playback. In stationary funnel traps located 150 m away, as few as 175 Eurasian reed warblers and 190 sedge warblers were captured over a 45-year period (Mukhin, Chernetsov, and Kishkinev 2005). In just 4 years, we captured by song playback 1176 Eurasian reed warblers and 341 sedge warblers. These 2 trapping mechanisms, funnel traps and mist nets, are not the same and may very well have different efficiencies, so a caveat for our conclusions is that our “experiment” did not have a proper control. Nevertheless, the difference in numbers of individuals netted using acoustic cues is so much greater than the number caught in funnel traps that the most parsimonious explanation for our results is that migrating Eurasian reed warblers and sedge warblers use acoustic cues to find suitable stopover sites.

Comparison of the proportion of captures in the suboptimal habitat during deep night with the proportions of those passing over (Hansen 1954) also strongly suggests that most Eurasian reed and sedge warblers were indeed lured by acoustic stimuli (Tables 2 and 4).

The same conclusion is suggested by comparing tape-lure data with captures in the suitable habitat during morning twilight when visual stimuli could have also been used: song playback resulted in much higher proportion of *Acrocephalus* warblers in sandy dunes than in reed stands near Rybachy (Tables 3 and 5). This occurred in spite of the fact that reed stands are higher quality habitat for these species during migration, as reflected by a higher proportion of birds stopping over for more than 1 day in the fall. Conspecific song also appeared to be attractive to garden warblers—relative numbers of individuals tape lured in the fall were higher than those netted in the suitable habitat without acoustic stimuli.

What mechanism is behind the reaction to conspecific song? Warblers are known to migrate solitarily at night (Åkesson et al. 2001, 2002; Mukhin, Kosarev, and Kitorov 2005) and to give no calls, at least none audible to humans. No data are available suggesting that these species keep acoustic contacts between flying and grounded individuals as reported for the song thrush (*Turdus philomelos*, Bolshakov 1977).

Our data suggest that acoustic information plays an important role in recognition of habitat both during deep night and morning twilight as well as both in spring and (potentially) in fall. The more pronounced response by adults can possibly be explained by their previous experience in using acoustic cues for habitat assessment, whereas juveniles lack this experience because when they start their first fall migration, adults are no longer singing. Nevertheless, the responses of naive juveniles to acoustic lures may be explained by the existence of an innate mechanism of assessing habitat quality on the basis of acoustic cues.

We suggest that this mechanism (which we artificially induced in the fall and which is not normally working during fall migration) works during the spring arrival to breeding areas (Reed and Dobson 1993). The songs of early arrivals (Chernetsov 1999) might be a marker of suitable habitats for adult Eurasian reed warbler males. This mechanism may also function in the winter when juveniles could be using the singing of adults, both conspecifics and African reed warblers *Acrocephalus baeticatus* (whose song is very similar to the Eurasian reed warbler’s, Cramp 1992), to select a habitat. Playback of the Eurasian reed warbler song in the fall could trigger this mechanism and thus induce landfall.

Positive response to conspecific songs does not, however, answer the question as to whether the birds associate these songs with a particular habitat or are just attracted by species-specific song per se. It is noteworthy that the species with broader habitat preferences did not react to the conspecific song; playback of the pied flycatcher song did not result in trapping of pied flycatchers, either in spring or in fall.

In this respect, the heterospecific reaction is most interesting. During the 4 years of playing the Eurasian reed warbler song, 17 passerine species were tape lured at night (Mukhin, Chernetsov, and Kishkinev 2005). Song playback was attractive mainly for the species that benefit most from strict habitat selection, the *Acrocephalus* warblers. After the Eurasian reed warbler, the strongest response was shown by the sedge warbler, both in years when its own song was played and when not. The grasshopper warbler, though not overrepresented among tape-lured birds compared with the composition of migrants generally, was more common in the fall in the suboptimal habitat with song playback than in the suitable habitat without acoustic markers.

The comparison of captures from the suitable habitat versus those in the suboptimal habitat data does not allow us to claim

that other warblers also respond to heterospecific *Acrocephalus* species songs. It should, however, be stressed that we compared captures in the suitable habitat with those from a suboptimal habitat that also had song playback and not 2 suboptimal habitats. Therefore, the large proportion of garden warblers among the tape-lured birds in the fall, though not significantly higher than their proportion either in the migrant pool or in the captures in suitable habitat, suggests that the acoustic environment formed by the Eurasian reed warbler song might also attract garden warblers. Song playback may make a suboptimal habitat as attractive for garden warblers as the suitable one. The same can be said concerning the reaction of the blackcap to the garden warbler song: blackcaps comprised more than 20% of captures. Most impressive is the landfall of the water rail, spotted crane, and common sandpiper, which were captured in small numbers on sandy dunes when Eurasian reed and sedge warbler songs were playing.

Playing redwing song in the spring during the passage of long-distance migrants attracted just 9 individuals from 6 species. Long-distance migrants probably do not associate this song with a particular habitat.

We suggest that the difference in response of different warbler species to acoustic cues is the result of their varying habitat requirements. Using distant cues for stopover habitat assessment may be especially important for habitat specialists like *Acrocephalus* warblers that utilize wetland habitats during all stages of their life cycles. The sedge warbler responds equally well to conspecific and heterospecific (Eurasian reed warbler) acoustic stimuli, probably because songs of these 2 species are good markers of a wetland habitat. The lack of response shown by habitat generalists, such as the pied flycatcher, common redstart, and willow warbler, may be due to the fact that heterospecific acoustic cues containing information about wetlands (Eurasian reed and sedge warbler songs) are not sufficiently attractive because they carry no information regarding food and/or the availability of shelter for these species. It is also possible that even conspecific acoustic cues at landfall are generally not used by these species. Aerial feeders, like the pied flycatchers, do not care much about their exact landing location because they make comparatively long-range movements during stopovers, searching for local prey concentrations (Chernetsov et al. 2004).

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