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Redistribution of songbirds within a migratory stopover site as a response to sylviid warbler song playback

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Assessing habitat quality is critical for migrating birds, with implications for fuel loading, predation risk and timing of departure. To efficiently distribute within stopover sites, migrants rely on various cues that facilitate habitat quality assessment. In this study, we conducted a playback experiment at a mid-route stopover site to test the effects of vocal cues, specifically bird songs, on habitat redistribution during spring migration. To estimate the effect of bird songs on bird abundance we mist-netted and ringed birds for 60 days on alternating playback treatment (playing songs of three sylviid warbler species) and no playback (control) days. A nearby site was used to control for fluctuations caused by migration waves. Overall, total bird abundance was significantly increased by the playback treatment. This increase resulted from the attraction of conspecifics (species whose songs were played) rather than of other species – sylviids or others. Correspondingly, species richness was seemingly unaffected. To investigate the relationship between internal-state factors and the attraction to playback in the most abundantly attracted species, Eurasian Blackcap *Sylvia atricapilla*, we tested associations with age, sex and body condition index but found no significant effects, possibly because of the limited sample size. Our findings challenge established ideas regarding heterospecific attraction and contradict previous studies. Attraction to bird song is discussed in the context of geographical location, timing and internal drivers. Vocal cues, specifically bird songs, may affect micro-habitat selection by migrating songbirds during stopovers. Consequently, we call for consideration of the influence of the acoustic environment on birds during migratory stopover in future studies, habitat management and conservation efforts.

Keywords: bioacoustics, Eurasian Blackcap, habitat selection, migration, stopover ecology.

The search for suitable environments has driven remarkable sensory and behavioural adaptations, enabling informed habitat selection by birds (Hutto 1985, Moore & Aborn 2000, Caspi *et al.* 2022). Selecting a food-rich habitat could have direct fitness consequences because habitat-specific food intake rates influence the physiological condition and behaviour of birds (Lindström & Alerstam 1992), probably affecting survival and reproduction (Both & Visser 2001, Norris & Taylor 2006). Habitat quality is particularly important during migration because it can influence foraging efficiency, fuel loading and time of departure (Bairlein 1983, Lindström & Alerstam 1992, Deppe & Rotenberry 2008, Mukhin *et al.* 2008, Domer *et al.* 2021). Consequently, and especially while crossing large ecological barriers (e.g. the Sahara Desert), habitat selection decisions during migratory stopover are essential for long-distance migrants (Biebach *et al.* 1986, Moore & Aborn 2000).

The role of vocal or visual cues in breeding site selection has been well established (see reviews by

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Stamps 1988, 1991, Nocera & Betts 2010, DeJong *et al.* 2015, Buxton *et al.* 2020). For example, Eurasian Blackcap *Sylvia atricapilla* song rate provides information regarding breeding habitat quality (Hoi-Leitner *et al.* 1995). Specifically, the role of vocal cues upon migrants' arrival at their breeding grounds has been studied (Ahlering *et al.* 2010, Szymkowiak *et al.* 2017, Valente *et al.* 2021), with potential implications for conservation (Ward & Schlossberg 2004, Ahlering *et al.* 2010, Valente *et al.* 2021). However, less is known in the context of stopover site selection, even though it similarly relies on both visual (Hutto 1985, Moore *et al.* 1995, Moore & Aborn 2000) and vocal (Herremans 1990a, Chernetsov 2006, Mukhin *et al.* 2008) cues, including songs and calls. When birds alight, habitat quality information can be gathered from other individuals in the habitat, enabling rapid habitat quality assessment (Németh & Moore 2007, 2014), which is critically important for migratory birds that occupy unfamiliar environments during their journeys (Hutto 1985, 1998, Moore & Aborn 2000, Chernetsov 2006).

Understanding the spatial scale of habitat selection during migration is fundamental for recognizing the role of range-limited acoustic cues. Habitat selection involves, first, stopover site selection and, secondly, redistribution within the selected site (micro-habitat selection; Fransson *et al.* 2008, Chernetsov 2012). The first is at the scale of kilometres, but the second is seemingly limited to only several hundred metres (Ktitorov *et al.* 2010). For Eurasian Blackcaps, the movement range is less than 150 m, similar to their ranges during other parts of the year (Chernetsov 2002, Preiszner & Csörgő 2008). This may allow the detection of vocalizing individuals during redistribution, as the transmission distance of bird song is of a similar spatial scale (Dooling *et al.* 2000). Although the scientific literature seldom distinguishes between these two stages of habitat selection, the similar distance range of micro-habitat selection and vocal cue distribution suggests that vocal cues may influence decisions within stopover sites (e.g. Fransson *et al.* 2008), expanding beyond traditional studies of acoustic cue effects on site selection.

Current knowledge of the impact of acoustic cues on migratory birds is based mainly on playback experiments where different playback timings can provide information regarding different stages of habitat selection. In most site-selection studies, songs are primarily played overnight to attract actively migrating birds (e.g. Herremans 1989, 1990a, 1990b, Weller 1995, Schaub & Jenni 1999, Mukhin *et al.* 2008, Alessi *et al.* 2010, Panov 2011). In fewer studies, diurnal tape luring has been used to investigate habitat redistribution within sites (Arizaga *et al.* 2015, de la Hera *et al.* 2017, Sebastianelli *et al.* 2020). Both types of experiments usually use specific vocalizations (particularly bird songs), were limited to a single species and focus on conspecific attraction (but see Mukhin *et al.* 2008, Panov 2011, de la Hera *et al.* 2017, Sebastianelli *et al.* 2020), and largely reveal increased bird abundance in response to playback (Buxton *et al.* 2020). To account for natural daily fluctuations in bird migration and to obtain a more robust estimation of effect size, several studies also included a control site without playback (Mukhin *et al.* 2008, Arizaga *et al.* 2015, de la Hera *et al.* 2017).

In previous studies, higher bird abundance in playback sites resulted from a stronger response of either juveniles (Borras & Senar 1986, Brotons 2000, Ward & Schlossberg 2004) or adults (Mukhin *et al.* 2008, Panov & Chernetsov 2010), but not both. A stronger response of either females (Weller 1995) or males (Herremans 1989, Lecoq & Catry 2003) of the same species or among species was also documented in some studies. In addition, birds in poorer physiological condition tended to respond more frequently to vocal cues than birds in better condition (Figuerola & Gustamante 1995, Brotons 2000, Panov & Chernetsov 2010, Arizaga *et al.* 2015). This variability suggests that internal state may shape responses to acoustic cues, and may do so differently at different locations, times of day and periods of the annual cycle.

Our understanding of how vocal cues shape the spatiotemporal redistribution of birds during migratory stopovers remains incomplete. Still, little is known about how vocal cues from individual species influence transient community composition, same-species abundance at migratory stopovers, or the role of internal factors like age, sex and physiological condition in micro-habitat selection. In this study, we aimed to help fill this knowledge gap by examining the effects of diurnal sylviid warbler playback on these factors during spring migration stopover at the edge of an ecological barrier, thereby advancing our understanding of this complex puzzle. Specifically, we predicted that individuals from species whose songs were played would redistribute in the site, showing attraction and resulting in higher abundance in the vicinity of the playback area (Buxton *et al.* 2020), and that closely related sylviid warblers, whose songs were not played, would also show greater attraction than other unplayed species, based on overlaps in habitat requirements (Mukhin *et al.* 2008, Panov 2011). Secondly, we predicted that based on their experience, adults would be attracted to playback more than juveniles (i.e. second calendar year birds; hereafter '2CY'), shifting the age structure of the population (Mukhin *et al.* 2008, Panov & Chernetsov 2010). Thirdly, we predicted that the population structure would skew towards a higher proportion of females in response to the playback treatment, as females will be more attracted than males to songs during our springtime study period (Weller 1995). Lastly, we predicted that leaner birds would be more attracted to playback than birds in better physiological condition. Poorer condition might result from inefficiency in locating food or from recent arrival from an exhausting migratory journey. Consequently, leaner birds would be expected to rely on conspecific cues to a greater extent (Figuerola & Gustamante 1995, Brotons 2000, Panov & Chernetsov 2010, Arizaga *et al.* 2015).

METHODS

Study site

We collected data during spring 2014 at the International Birding and Research Center Eilat, located north of Eilat, Israel (29°34′N, 34°58′E; Fig. 1a), which covers approximately 25 hectares. Although most of the region is extremely arid (14.1 mm mean annual precipitation; Ginat *et al.* 2011), the park, once part of a unique salt marsh habitat, is densely vegetated and includes a brackish water lake. Consequently, many passerines that migrate through the Sahara Desert use the park for stopovers.

Bird capturing was carried out at two sites within the park using mist-nets. The first was the experimental site (hereafter – ES; Fig. 1b), where the playback was applied on alternating playback treatment and 'no playback' (control) days (see Experimental protocol section below). Additional nets were positioned in a second site of similar habitat, between 330 and 370 m away from the ES (about twice the movement range of our focal species during stopover; Chernetsov 2002, Preiszner & Csörgő 2008, Ktitorov *et al.* 2010). This control site (hereafter CS; Fig. 1b) served as a baseline sampling site without playback. Mist-nets 42 m long and 3 m high were deployed at ES, and 54-m long mist-nets (also 3 m high) were used at CS. The difference in net length between the two sites was addressed in the statistical analyses. At both sites (ES and CS), nets were placed within the sparse scrub, composed mainly of *Salvadora persica*, *Suaeda monoica* and small *Vachellia* (previously *Acacia*) trees ranging from 80 to 150 m from the park's brackish water pond.

Study species

We used playback songs of three sylviid warbler species that migrate through the Middle East and specifically through Eilat during spring: Eurasian Blackcap *Sylvia atricapilla*, Rüppell's Warbler *Curruca ruppeli* and Eastern Subalpine Warbler *Curruca cantillans*, an abundant, an uncommon and a rare species, respectively (Shirihai *et al.* 1996). Bird songs from these species were used in the playback because they are known to sing during spring migration (Shirihai *et al.* 2001) and because bird songs were used in similar studies that tested the response of migrating warblers to vocal cues (e.g. Herremans 1989, Weller 1995, Sebastianelli *et al.* 2020), allowing qualitative cross-study comparisons. As we captured only 18 Rüppell's Warblers during the entire study period (below), our analysis of this species' data was limited (see Data analysis section below). The Subalpine Warbler is not included in the analysis because we did not capture any during the study.

Experimental protocol

We captured birds daily between 1 March and 29 April 2014 (60 consecutive days). Mist-nets were opened for 5 h daily, starting 30 min before sunrise (first light). We avoided playback during the hours of darkness to minimize vocally induced landfall, which could disrupt passerines' nocturnal migratory patterns (Harper 1994; see also Supporting Information Appendix S1). Throughout the experiment, we positioned an MP3 audio device (Sandisk, China) equipped with a 20-W speaker (model PA-815 M, Pro-audio, China) at the same location by the ES nets. Days without playback served as 'control' days. Every other day, on

Figure 1. (a) A regional map covering the range from the over-wintering areas in tropical Africa, through the Sahara Desert to the south of the Mediterranean Sea, and some of the European and Asian breeding grounds in the north and showing the landscape that birds were crossing before and after their arrival at the experimental site. Image sourced from Google Earth. The black dot is enlarged in (b). (b) The International Birding and Research Centre park, located north of Eilat, Israel (29°34′N, 34°58′E), where the experiment took place. Mist-netting sites are marked with their abbreviations: experimental site, where playback was broadcast every other day with playback days defined as 'treatment' days and days without playback defined as 'control' days (ES; speaker on icon), and control site, used as a treatment-free baseline (CS; speaker off icon). We used 12-m nets (orange) and 18-m nets (red). Image sourced from govMap: www.govmap.gov.il.

playback treatment day, the device played iteratively the songs of the three sylviid warbler species. Each species' song was played for 3 min, including at least two different sub-songs for each species (*sensu* Kroodsma *et al.* 2001). Bird song recordings were taken from Schulze and Dingler (2007). The songs of the three species played consecutively on a loop, repeating every 9 min (3 min per species) during the 5 h daily session. The playback was audible to the people who worked in the field site up to approximately 200 m from the speakers, meaning that focal species presumably heard it only when approaching closer than this distance (Dooling & Popper 2007) and not near the CS.

All captured birds were measured and marked using uniquely numbered aluminium leg rings. We registered the following data for each individual: date and time of capture, species identity, age, sex, visual fat score (0–8 following Kaiser 1993), maximum wing chord length (± 0.5 mm), tail length (for wing length validation; ± 0.5 mm) and body mass (± 0.1 g). By dividing body mass by wing length, we calculated body condition index, following previous studies on small migratory passerines (ratio of body mass/wing length; Benson & Winker 2005, Seewagen 2008). The birds were released back to the wild 300 m away from the ES and 70 m from the CS. To prevent pseudoreplication, we used only data from the first capture for any bird captured more than once.

Data analysis

Variables

Species composition of captures, bird abundance, and age and sex structures showed high spatial and temporal variation throughout the experiment, so we used two variables to account for this. First, to account for seasonal variation in both bird assemblage and micro-habitat quality at the site, we included the experiment day (1–60) as an independent continuous covariate in all models. Secondly, to account for the possible effect of bird migration waves, which cause high daily fluctuations in abundance throughout the migration period, we included the corresponding daily value of the specific variable (i.e. species richness, daily abundance, age or sex ratio) from the CS in each model (see below).

Because the playback used may affect multiple bird species (either directly or indirectly), our abundance response variable expressed the daily abundance of all species summed (Table S2). In addition, we considered three specific bird abundance categories: (1) sylviid warbler species whose songs were played, (2) sylviid warbler species whose songs were not played and (3) all other species. We used relative abundance variables, which were the proportion of birds captured at ES out of the total number of birds captured on that day at both ES and CS. We did the same for species richness (i.e. the proportion of species number at ES out of all species captured that day in both ES and CS; models 1–3 and 5 in Table 1). We also used Fisher's α index (Fisher *et al.* 1943, Rosenzweig 1995; R package vegan; Dixon 2003) to correct species richness for the daily number of individuals sampled (model 4 in Table 1), and used this measure as a response variable. Similarly, to test our predictions for higher attraction of adults than 2CY birds, and females than males, we calculated the daily proportion of each age group and each sex group in the ES out of that at both sites (ES + CS) as response variables in the same way (models 6 and 7 in Table 1). Finally, to test our prediction of higher playback attraction of birds in poor physiological condition, we used the body mass/wing length ratio as a response variable (Benson & Winker 2005, Seewagen 2008; model 8 in Table 1; for fat scores see Appendix S4).

Statistical modelling

We analysed the data using R version 3.4.4 (R Core Team 2022) in RStudio (RStudio Team 2022) with the packages lme4 (Bates *et al.* 2015) and lmerTest (Kuznetsova *et al.* 2017). For all analyses, we used generalized linear models (GLMs) to test whether song playback treatment significantly affected the response variable of interest. To test the effect of the treatment, we used likelihood ratio tests, each time comparing a null model including only covariates (see Variables section above) with a model including both the covariates and the song playback treatment as a categorical factor with two levels (playback or no playback; Zuur *et al.* 2009; Table 1). Only when the insertion of the playback treatment variable (or its interaction with the variable of interest) significantly improved the model compared with the null model (as implied by the likelihood ratio test; Zuur *et al.* 2009, Alday 2016) did we report the results of GLMs. When an interaction term was significant, we used estimated marginal means to compare the pairs within it (Lenth *et al.* 2022). We employed two-tailed tests to assess both attraction to and deterrence from song playback, as both are possible outcomes (Mukhin *et al.* 2008). In all analyses, we used a significance level of α = 0.05.

For all response variables expressed as a proportion, we constructed a binomial error model (models 1–3 and 5–7 in Table 1). Model fits were visually checked with residual plots. We assessed treatment impact on species composition by constructing models for daily abundance across all species and for daily species richness (models 1 and 3, correspondingly, in Table 1). To test whether different species reacted similarly to playback treatment, we built a model with an interaction term between treatment and species category with three levels (sylviid warbler species whose songs were played, sylviid warbler species whose songs were not played and other (not-played) species; model 2 in Table 1). To examine the impact of playback specifically on the sylviid warbler species whose songs were played, we separately analysed data of Eurasian Blackcaps, the only species with a sufficient sample size (model 5 in Table 1). Similarly, we examined how internal state factors (age, sex and body condition) shaped the reaction to playback only for Blackcaps. To test for the possible effect of age on the response to the playback treatment, we compared the daily proportion of each age group at ES (2CY, adults; ES/(ES + CS)) by adding an interaction term between playback treatment and age with the two levels (2CY, adults; model 6 in Table 1). We did the same to test for the effect of bird sex on the response to the playback treatment (model 7 in Table 1). We did not include a model for age and sex three-way interaction with treatment because of our limited sample

Table 1. Statistical models structure.

	Model no.	Species		Response variable	Explanatory variables	Distribution	Link function	Comments	GLM, see in:	Figure
Abundance	1	All	Null	Daily ratio of bird number: ES/(ES + CS)	Day	Binomial	Logit		Table 2	2a
			Model		Playback treatment + Day					
Abundance (with spp. category)	2	All	Null	Daily ratio of bird number: ES/(ES + CS)	Playback treatment + spp category + Day	Binomial	Logit		Table 3	2b
			Model		Playback treatment: spp category + Day					
Species richness	3	All	Null	Daily ratio of species number: ES/(ES + CS)	Day	Binomial	Logit			
			Model		Playback treatment + Day					
Species richness corrected by sample size	4	All	Null	Daily Fisher's α value	Playback treatment + Site + Day	γ	Log	Site in two categorical groups: ES + CS		
			Model		Playback treatment: Site + Day					
Abundance	5	Eurasian Blackcap	Null	Daily ratio of bird number: ES/(ES + CS)	Day	Binomial	Logit		Table 4	2c
			Model		Playback treatment + Day					
Age	6	Eurasian Blackcap	Null	Daily ratio per age group: ES/(ES + CS)	Playback treatment + Age group + Day	Binomial	Logit	Age in two categorical groups: 2nd calendar year and adults		
			Model		Playback treatment: Age group + Day					
Sex	7	Eurasian Blackcap	Null	Daily ratio per sex group: ES/(ES + CS)	Playback treatment + Sex group + Day	Binomial	Logit	Sex in two categorical groups: female and male		
			Model		Playback treatment: Sex group					
Size-corrected for body mass	8	Blackcap	Null	Size-corrected body mass	Playback treatment + Site + Day	γ	Log	Site in two categorical groups: ES + CS		
			Model		Playback treatment: Site + Day					

'All' in the 'Species' column implies all captured species (Table S2). A colon represents interaction between variables, whereas a plus sign implies that these variables were included in the model without interaction. For a table with likelihood ratio test results please see Table S3. Abbreviations: CS, control site; ES, experimental site; GLM, generalized linear mixed model.

size (low number of individuals per day per each age and sex combination). For Fisher's α index and the ratio of body mass to wing length (body condition index) in Eurasian Blackcaps, we used γ distributions with log link function and compared a model with an interaction between site and playback treatment with its nested model (i.e. a model including these variables without an interaction; Zuur *et al.* 2009, Alday 2016) to test whether the playback treatment was associated with the difference in the response variable values between the ES and CS (models 4 and 8 in Table 1; see also Appendix S5).

RESULTS

Bird abundance and species composition

We captured and marked 2262 individual birds of 44 species during the 60 days of the experiment (Table S2). A further 145 re-capture events were excluded from all analyses to avoid pseudoreplication (after no significant pattern was found in relation to treatment type when exploring these data in preliminary analyses). The daily number (mean ± standard deviation (sd); here and throughout the text) of individuals captured in the ES during the playback treatment days was 21.5 ± 13.79 sd birds/day (total 645 birds), while 18.27 ± 15.37 sd birds/day (total 548 birds) were captured during no playback days, an increase of 17.7%. Bird abundance in the CS was similar during playback treatment (17.63 ± 10.44 sd birds/day; total 529 birds) and no playback (18.03 ± 11.35 sd birds/day; total 541 birds) days (with playback only at ES). We found that the proportion of all birds in the ES per day was significantly higher on playback days than on no playback days, with a 14.9% increase from 0.47 ± 0.17 sd on no playback days to 0.54 ± 0.16 sd during treatment (likelihood ratio test, $\chi^2_{(\mathrm{df}=-1)} = 5.83$, $P = 0.02$; model 1 in Table 1; GLM binomial distribution: $\mathrm{df}_{\mathrm{residual}} = 57$, Z value $= -2.41$, $P = 0.02$ for the effect of playback; Table 2; Fig. 2a). This increase resulted from a significant increase in the numbers of sylviid warbler individuals from species whose songs were played (likelihood ratio test, $\chi^2_{(\mathrm{df}=-3)} = 15.1$, $P = 0.006$; model 2 in Table 1; ANOVA for GLM binomial distribution: $P = 0.006$ for the interaction of playback treatment with species category; Tukey-adjusted comparisons: $P < 0.05$; Table 3; Fig. 2b), but no significant increase of sylviid warblers or other species whose songs were not played (Tukey-adjusted comparisons: $P = 0.2$ and $P = 1$, respectively; Table 3; Fig. 2b). Daily species richness was not significantly affected by playback treatment (likelihood ratio test, $\chi^2_{(\mathrm{df}=-1)} = 2.42$, $P = 0.1$; model 3 in Table 1) with a mean of 5.90 ± 2.07 sd species captured during playback

Table 2. Bird abundance model: in this model we explored how bird abundance (daily number of birds caught) was affected by sylviid warbler song playback.

	χ^2	df	P (> |z|)	
(a) Analysis of deviance				
Playback	6.0	1	0.02	*
Day	13.0	1	< 0.001	***

	Exp (estimate)	Estimate	se	z value	P (> |z|)	
(b) Generalized linear model						
Intercept	0.91	−0.10	0.10	−0.95	0.34	
No playback	0.81	−0.21	0.09	−2.41	0.02	*
Day	1.01	0.01	0.00	3.55	< 0.001	***

Two experimental phases are compared: 'playback' and 'no playback'. The model also included the day number (1–60) to account for possible temporal variation in the bird assemblage and habitat through the season. ES refers to the experimental site – where song playback was used on alternating days (playback and no playback days, respectively); CS refers to the control site – no song playback was used at the CS; se, standard error. The model was structured as follows: Daily bird number at ES/(daily bird number at ES + daily bird number at CS) ~ Playback treatment + Day. *Error distribution*: binomial. *Link function*: logit. Variables of special interest are highlighted in grey, variables in bold were found to significantly affect bird abundance, and the asterisks in the right-most column represent the level of significance: *$P < 0.05$, ***$P < 0.001$. (a) ANOVA table for the bird abundance model. (b) Generalized linear model results for bird abundance.

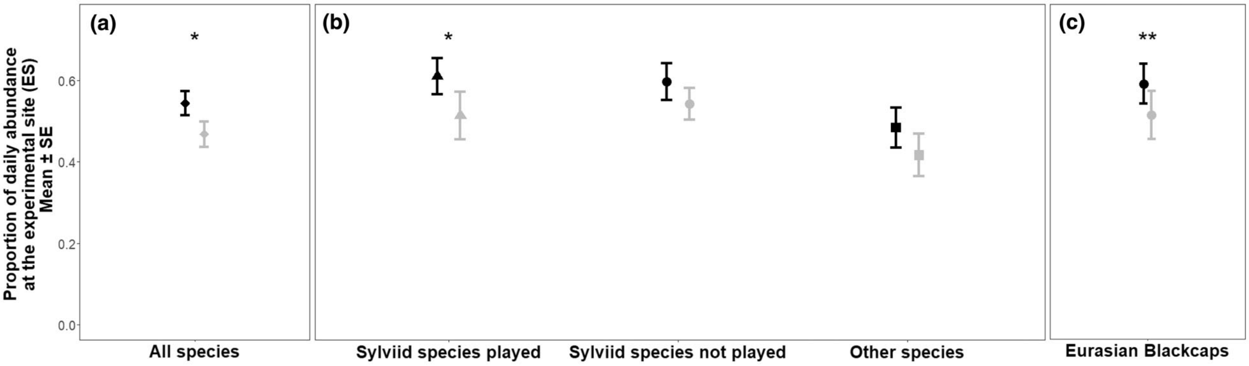

Figure 2. Proportion of daily bird abundance (mean ± standard error (se); *y* axis) at the experimental site (ES) for each experimental treatment phase (with playback – black, without playback – grey) according to species groups (*x* axis). Presented are the values for original data and not model outputs. (a) For all songbird species. The asterisk (*) indicates the level of significance ($P < 0.05$; Table 2). (b) For all songbird species divided into categories: sylviid warbler species whose songs were played (triangle), sylviid warbler species whose songs were not played (dot) and other not-played species (square). The asterisk (*) indicates the level of significance ($P < 0.05$; Table 3). (c) For Eurasian Blackcap. The asterisks (**) represent the level of significance ($P < 0.01$; Table 4).

days compared with 4.80 ± 1.88 sd species captured during no playback days at the ES. Similarly, species richness corrected for sample size, calculated using Fisher's α, was not significantly different between playback and no playback days (see independent samples *t* test in Appendix S5; likelihood ratio test, $\chi^2_{(\mathrm{df}=-1)} = 1.7$, $P = 0.19$; model 4 in Table 1).

The effects of song playback on species whose songs were played

Eurasian blackcaps

We captured 566 Eurasian Blackcaps during the study (Table S2). An additional 48 re-capture events were excluded from all analyses to avoid pseudoreplication. A mean of 5.77 ± 4.91 sd Blackcaps/day ($n = 173$) were captured in the ES during the playback treatment days, while 3.95 ± 4.29 sd Blackcaps/day ($n = 118$) were captured during no playback days, an increase of 46.1%. Blackcap mean abundance in the CS was similar during playback (4.40 ± 4.48 sd Blackcaps/day) and no playback (4.77 ± 5.81 sd Blackcaps/day) days (with playback only at ES). In total, the proportion of Eurasian Blackcaps captured in the ES significantly increased by 15.7%, from 0.51 ± 0.31 sd during no playback to 0.59 ± 0.25 sd during playback (likelihood ratio test, $\chi^2_{(\mathrm{df}=-1)} = 7.93$, $P = 0.005$; model 5 in Table 1; GLM binomial distribution, $\mathrm{df}_{\mathrm{residual}} = 51$, Z value = −2.81, $P = 0.005$ for the effect of playback; Table 4; Fig. 2c). We therefore conclude that playback songs positively affected the number of Eurasian Blackcaps captured in the ES, supporting our prediction. Overall, the increase in Eurasian Blackcaps accounted for 48.1% of the total bird increase attributable to playback.

We found no significant effects of age on the increase in the number of Eurasian Blackcaps (likelihood ratio test, $\chi^2_{(\mathrm{df}=-1)} = 0.57$, $P = 0.45$; model 6 in Table 1). Both 2CY and adults were attracted to a similar extent to ES during playback days (2CY increased by 28.3%, from 0.46 ± 0.34 sd during no playback to 0.59 ± 0.28 sd during playback; adults increased by 23.9% from 0.46 ± 0.32 sd during no playback to 0.57 ± 0.35 sd during treatment). Similarly, we found no significant effect of sex on the increase in the number of Eurasian Blackcaps (likelihood ratio test, $\chi^2_{(\mathrm{df}=-1)} = 0.03$, $P = 0.87$; model 7 in Table 1). Both females and males were attracted to the ES during playback days (females increased by 26.5%, from 0.49 ± 0.34 sd during no playback to 0.62 ± 0.31 sd during treatment; males increased by 9.9% from 0.51 ± 0.33 sd during no playback to 0.56 ± 0.26 sd during playback). Finally, the mass to wing-length ratio, our measure of body condition, did not differ significantly between treatments and sites (0.22 ± 0.02 sd at ES on playback days, 0.23 ± 0.02 sd at ES on no

Table 3. Bird abundance for each species category: in this model we explored how the daily proportion of birds captured at the experimental site was affected by played-back sylviid warbler songs, for each of three species categories (played sylviid species; non-played sylviid species; other species).

	χ^2	df	*P*	
(a) Analysis of deviance				
Playback	0.56	1	0.45	*
Species category	24.07	2	< 0.001	
Day	19.7	1	< 0.001	***
Playback: Species category	10.25	2	0.006	**

	Exp (estimate)	Estimate	se	*z* value	*P*	
(b) Generalized linear model						
Intercept	**0.62**	−0.473	0.125	−3.795	< 0.001	***
No playback	1.1	0.097	0.123	0.789	0.43	
Played sylviid species	**1.35**	0.299	0.147	2.039	0.041	*
Non-played sylviid species	**2.01**	0.698	0.144	4.845	< 0.001	***
Day	**1.01**	0.012	0.003	4.367	< 0.001	***
No playback: species category-played sylviid species	**0.54**	−0.609	0.209	−2.918	0.004	**
No playback: species category-non-played sylviid species	**0.62**	−0.479	0.208	−2.307	0.021	*

Playback	Species category	Prob	se	df	Asymp.LCL	Asymp.UCL
(c) Estimated marginal means						
V – on	Played sylviid species	0.55	0.03	Inf	0.47	0.64
X – off	Played sylviid species	0.43	0.03	Inf	0.34	0.52
V – on	Non-played sylviid species	0.65	0.03	Inf	0.57	0.72
X – off	Non-played sylviid species	0.56	0.03	Inf	0.46	0.65
V – on	Non-played other species	0.48	0.02	Inf	0.41	0.55
X – off	Non-played other species	0.50	0.02	Inf	0.44	0.57

Contrast	Estimate	se	df	*z* ratio	*P* value
(d) Contrasts					
V not played other spp. – X not played other spp.	−0.0927	0.123	Inf	−0.751	0.9754
V not played sylviid spp. – X not played sylviid spp.	0.3823	0.168	Inf	2.282	0.2012
V played sylviid spp. – X played sylviid spp.	**0.5115**	**0.168**	**Inf**	**3.04**	**0.0286**

Two experimental phases are compared: 'playback' and 'no playback' in the ES site (below). The model also included the day number (1–60) to account for possible temporal variation in the bird assemblage and habitat during the season. ES refers to the experimental site – where song playback was used on alternating days; CS refers to the control site where no song playback was used; se, standard error. The model was structured as follows: Daily bird number at ES/(daily bird number at ES + daily bird number at CS) ~ playback treatment: species category + Day. *Error Distribution*: binomial. *Link function*: logit. The colon indicates statistical interaction. In all tables, variables of special interest are highlighted in grey, variables in bold were found to significantly affect bird abundance, and the asterisks in the right-most column represent the level of significance: *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$. (a) ANOVA table for bird abundance for each species category. (b) Generalized linear model results for each species category. (c) Estimated marginal means for the same model. Two experimental phases are compared: 'playback' (V) and 'No playback' (x) for the three species categories. (d) Contrasts for the comparisons of relevant combinations of the interaction term (for all comparisons see Table S6).

playback days, 0.23 ± 0.02 sd at CS on playback days and 0.23 ± 0.02 sd at CS on no playback days; see independent samples *t* test in Appendix S5; likelihood ratio test, $\chi^2_{(\mathrm{df}=-1)} = 1.27$, $P = 0.26$; model 8 in Table 1; for fat scores see Appendix S4). These results do not support our hypotheses concerning the potential influence of internal state factors on response to playback.

Rüppell's warblers

A single Rüppell's Warbler was captured in the ES during no playback days, whereas 12 were captured during playback treatment days. In the CS,

Table 4. Eurasian Blackcap abundance model: in this model we explored how the proportion of all Blackcaps that were caught at the experimental site (ES) each day was affected by played-back sylviid warbler songs (including Blackcaps).

	χ^2	df	*P*	
(a) Analysis of deviance				
Playback	7.931	1	0.005	**
Day	5.1861	1	0.02	*

	Exp(estimate)	Estimate	se	*z* value	*P*	
(b) Generalized linear model						
Intercept	2.34	0.85	0.28	3.01	0.003	**
No playback	0.62	−0.48	0.17	−2.81	0.005	**
Day	0.99	−0.01	0.01	−2.26	0.02	*

Two experimental phases are compared: 'playback' and 'no playback' days in the ES (below). The model also included the day number (1–60) to account for possible temporal variation in the bird assemblage and habitat through the season. ES refers to the experimental site – where song playback was used on alternating days ('treatment' and 'control' days, respectively); CS refers to the control site where no song playback was used; se, standard error. The model was structured as follows: Daily bird number at ES/(daily bird number at ES + daily bird number at CS) ~ playback treatment + Day. *Error distribution*: binomial. *Link function*: logit. Variables of special interest are highlighted in grey. Variables in bold were found to significantly affect Blackcap abundance and the asterisks at the right-most column represent the level of significance: $*P < 0.05$, $**P < 0.01$. (a) ANOVA table for the Blackcap abundance model. (b) Generalized linear model results for Blackcap abundance.

three were caught during no playback days (without playback at ES), and two when playback was used in the ES. Given the small sample size, we did not perform statistical analyses.

DISCUSSION

Migrating birds may select their stopover site and redistribute between different habitats within the site based on various factors, including structural attributes of the vegetation (e.g. Hutto 1985, Yong *et al.* 1998), food and water availability (Moore & Aborn 2000, Sapir *et al.* 2004a, 2004b and predation risks (e.g. Chernetsov 2012). To date, there is limited research on the response of birds to vocal communication in the context of habitat redistribution at selected stopover sites (but see Panov 2011, Arizaga *et al.* 2015, de la Hera *et al.* 2017, Sebastianelli *et al.* 2020).

We found that corrected mean bird abundance significantly increased by 14.9% under the playback treatment, without significant changes in species richness. We found no increased abundance of closely related sylviid warblers or other species whose songs were not played, which contradicts previous studies (e.g. Herremans 1990a, Mukhin *et al.* 2008, Panov 2011, de la Hera *et al.* 2017, Sebastianelli *et al.* 2020). This difference is possibly a result of differences in the experimental goals, with past experiments inducing landfall (using playback throughout the night; e.g. Herremans 1990a, 1990b, Mukhin *et al.* 2008, Panov 2011) rather than exploring habitat redistribution during stopover (using playback only from first light; see Appendix S1). Moreover, seasonal differences may affect the rate of attraction to acoustic stimuli (de la Hera *et al.* 2017, Sebastianelli *et al.* 2020), and possibly also differences in species studied or differences in geographical location (in relation to ecological barriers or destination). Our results regarding the response of Eurasian Blackcaps suggest that vocal cues, specifically bird songs, play a role in the redistribution of birds during stopover, by attracting conspecifics.

Sylviid warblers whose songs were included in the playback showed significant attraction. Specifically, we found a significant increase of 15.7% in Eurasian Blackcap corrected mean daily abundance on days with song playback compared with days without it. None of the examined internal state factors (age, sex and body condition index) were associated with this increase. The lack of a statistically significant impact of these factors may be a result of limited sample size, not allowing us to reliably account for all variables in a single model. Still, we find it valuable to provide possible biological explanations for our findings, which contrast with previous studies, which found an effect with similar or smaller samples. Future studies might further explain the discrepancies discussed here. Like Yong *et al.* (1998), we found no differences in response to playbacks between age classes during spring migration. Theoretically, juvenile attraction may be explained by the advantages of obtaining information from other foragers in the habitat, whereas adults may not need to rely on this information (Marchetti & Price 1989, Németh & Moore 2014). We note that Panov (2011) demonstrated a trend of increased adult attraction in Bluethroats *Luscinia svecica* during autumn migration, and thus the opposite trend is also possible. It may be that during spring migration, 2CY songbirds are as experienced foragers as adults, and hence show no behavioural differences. Additionally, we did not find an effect of sex on the response to the playback, in contrast to other playback experiments, which have found higher attraction of either male (Herremans 1989) or female (Weller 1995) Eurasian Blackcaps. Possibly warranting future investigations, we did notice a trend of greater female attraction (26.5% increase) compared with male attraction (9.9%). We also did not find any differences in the physiological condition of the Blackcaps that were captured during playback and no playback days, suggesting the absence of body-condition-related attraction responses to song during habitat redistribution at this stopover site. Considering both that this stopover site is one of the first the birds encounter after crossing the Sahara Desert and that we observed an overall high rate of lean birds (implied by the low mean body condition index; see also Appendix S4 for fat scores), it may be that all birds choosing to stop at this vegetated site surrounded by hostile desert matrix were in search of food (Biebach *et al.* 1986), and so were behaving similarly regardless of song stimuli. Overall, these diverging results suggest a context-dependent response that may vary among species, seasons and stages of the migration journey, calling for further examination.

Why is bird song attractive during spring migration?

In this experiment, we used song playback, a prevailing practice in the field of behavioural ecology of songbirds, in bird ringing and for hunting (e.g. Buxton *et al.* 2020, Sebastianelli *et al.* 2020). However, when interpreting bird attraction to song playback, its biological relevance and function must be borne in mind. Several non-mutually exclusive mechanisms may explain the higher overall abundance of birds observed when songs were played back in our experiment during spring migration. One plausible explanation is an innate behavioural response associated with sexual attraction. Here, this would represent an erroneous response to a non-relevant stimulus (out of breeding range, wrong month). We found no strong sex bias that could support this sexual attraction explanation. Alternatively, birds may be attracted to song to rapidly gather social information about habitat quality or resource distribution (Németh & Moore 2007, Panov 2011) or to convey information regarding predation risks (Krama *et al.* 2008, Hua *et al.* 2013), which could increase survival. Increased response to resource signalling could be at play here, at a prolific stopover site, because previous studies of Eurasian Blackcaps suggest that there is no intraspecific aggression when food availability is high (Chernetsov 2002). If information gathering is the reason for attraction, one may also anticipate the attraction of heterospecific birds, but this was not supported by our results.

The statistically significant increase in the daily mean abundance of Eurasian Blackcaps in response to playback constitutes only 48.1% of the overall observed increase in the abundance of individuals from all species. This implies that there may be an effect on other species that we were unable to detect because of small sample sizes or other statistical limitations. All in all, we suggest that the increased abundance observed under playback is more probably due to information collection and habitat suitability assessments, rather than an innate response to breeding cues in bird song.

Possible implications for nature conservation

Globally, increasing noise pollution warrants additional investigation to understand its effects on bird behaviours, particularly those reliant on social interactions and vocal communication. This is especially relevant for behaviours related to migratory stopovers, where an evident research gap exists. As our study demonstrates, acoustic stimuli are used for habitat redistribution on small spatial scales, typically up to several hundred metres. Within such ranges, noise pollution may considerably reduce the listening range of birds (Barber *et al.* 2010, Szymkowiak & Schmidt 2022). Although here we do not provide experimental evidence regarding the direct impact of noise pollution on habitat redistribution, complementary research on noise pollution in other periods of the annual cycle (e.g. Barber *et al.* 2010, Ortega 2018, Szymkowiak & Schmidt 2022) suggests that incorporating precautionary measures into stopover site management practices should be considered. Such measures could include removing noisy infrastructure, noise-conscious planning for future development, and vegetation management, all of which would benefit birds by addressing this and other ecological concerns.

Limitations and future examinations

While the sample size (2262 birds) and period (30 playback and 30 no playback days) were large compared with previous studies, they still limited our ability to explore the response of other species groups by using other playbacks or exploring other aspects of attraction. Additionally, we were able to set only one ES (with alternating playback and no playback days) and one CS within the stopover site while fulfilling experimental requirements for comparable habitat, and ensuring that playback could not be detected at the CS. However, comparing multiple sites is recommended (Kroodsma *et al*. 2001). Furthermore, using playback to imitate social interaction without actual individuals being present is a common method for bird ringing but is subject to limitations, such as the lack of visual stimuli and the inability to adjust song attributes in response to approaching birds as naturally occurs (Ahlering *et al*. 2010, Leedale *et al*. 2015). These limitations suggest that further examination is called for. Future investigations may benefit from comparisons of responses across sites along the migration route (away from or within species breeding ranges), comparing reactions of several taxa and comparing responses in different migration seasons using various vocal cues (e.g. song, contact call or alarm calls).

Concluding remarks

Despite a good understanding of the function of bird song (e.g. mate attraction and territory defence; Catchpole & Slater 2003), there remains a lack of comprehensive knowledge concerning the reasons for attraction to bird song throughout the annual cycle, and particularly during migration. This gap is especially surprising given the widespread use of song playback to attract birds *en route* by bird-ringers, hunters and increasingly also nature photographers. Bridging this knowledge gap may facilitate a better understanding of the function of bird song and could promote safer use of bird song playback to minimize negative impacts. In this respect, our study represents a unique investigation into this subject.

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AUTHOR CONTRIBUTIONS

Yael Lehnardt: Conceptualization; investigation; writing – original draft; software; formal analysis; methodology; funding acquisition; validation; visualization; project administration; data curation; writing – review and editing. **Nir Sapir:** Conceptualization; writing – review and editing; project administration; supervision; methodology; funding acquisition; validation; data curation.

ETHICAL NOTE

None.

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None.

CONFLICT OF INTEREST STATEMENT

All authors declare no conflict of interest.

Data Availability Statement

Data used in this study are available in the Appendices (Data S1; Appendices S1–S6). For further details please contact the authors.

REFERENCES

Ahlering, M.A., Arlt, D., Betts, M.G., Fletcher, R.J. Jr., Nocera, J.J. & Ward, M.P. 2010. Research needs and recommendations for the use of conspecific-attraction methods in the conservation of migratory songbirds. *Condor* **112**: 252–264.

Alday, P.M. 2016. *Interactions in mixed effects models with lme4*. RPubs. Available at: https://rpubs.com/palday/mixed-interactions (accessed 24 February 2024).

Alessi, M.G., Benson, T.J. & Ward, M.P. 2010. Nocturnal social cues attract migrating yellow-breasted chats. *Wilson J. Ornithol.* **122**: 780–783.

Arizaga, J., Musseau, R., Laso, M., Esparza, X., Unamuno, E., Azkona, A. & Fontanilles, P. 2015. Biases associated with the use of a playback in stopover ecology studies of Bluethroats *Luscinia svecica*. *Bird Study* **62**: 280–284.

Bairlein, F. 1983. Habitat selection and associations of species in European passerine birds during southward, post-breeding migrations. *Ornis Scand.* **14**: 239.

Barber, J.R., Crooks, K.R. & Fristrup, K.M. 2010. The costs of chronic noise exposure for terrestrial organisms. *Trends Ecol. Evol.* **25**: 180–189.

Bates, D., Mächler, M., Bolker, B. & Walker, S. 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**: 1–48.

Benson, A.-M. & Winker, K. 2005. Fat-deposition strategies among high-latitude passerine migrants. *Auk* **122**: 544–557.

Biebach, H., Friedrich, W. & Heine, G. 1986. Interaction of bodymass, fat, foraging and stopover period in trans-Sahara migrating passerine birds. *Oecologia* **69**: 370–379.

Borras, A. & Senar, J. 1986. Sex, age and condition bias of decoy trapped Citril finches (*Serinus citrinella*). *Misc. Zool.* **10**: 403–406.

Both, C. & Visser, M.E. 2001. Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature* **411**: 296–298.

Brotons, L. 2000. Attracting and capturing coal tits *Parus ater*: biases associated with the use of tape lures. *Ring. Migr.* **20**: 129–133.

Buxton, V.L., Enos, J.K., Sperry, J.H. & Ward, M.P. 2020. A review of conspecific attraction for habitat selection across taxa. *Ecol. Evol.* **10**: 12690–12699.

Caspi, T., Johnson, J.R., Lambert, M.R., Schell, C.J. & Sih, A. 2022. Behavioral plasticity can facilitate evolution in urban environments. *Trends Ecol. Evol.* **37**: 1092–1103.

Catchpole, C.K. & Slater, P. 2003. *Bird Song: Biological Themes and Variations*. New York, NY: Cambridge University Press.

Chernetsov, N. 2002. Spatial behaviour of first-year blackcaps (*Sylvia atricapilla*) during the pre-migratory period and during autumn migratory stopovers. *J. Ornithol.* **143**: 424–429.

Chernetsov, N. 2006. Habitat selection by nocturnal passerine migrants en route: mechanisms and results. *J. Ornithol.* **147**: 185–191.

Chernetsov, N. 2012. Habitat selection and use by passerine migrants. In Chernetsov, N. (ed) *Passerine Migration: Stopovers and Flight*: 75–103. Berlin: Springer.

DeJong, L.N., Cowell, S.D., Nguyen, T.N.N. & Proppe, D.S. 2015. Attracting songbirds with conspecific playback: a community approach. *Behav. Ecol.* **26**: 1379–1388.

Deppe, J.L. & Rotenberry, J.T. 2008. Scale-dependent habitat use by fall migratory birds: vegetation structure, floristics, and geography. *Ecol. Monogr.* **78**: 461–487.

Dixon, P. 2003. VEGAN, a package of R functions for community ecology. *J. Veg. Sci.* **14**: 927–930.

Domer, A., Vinepinsky, E., Bouskila, A., Shochat, E. & Ovadia, O. 2021. Optimal stopover model: a state-dependent habitat selection model for staging passerines. *J. Anim. Ecol.* **90**: 2793–2805.

Dooling, R.J., Lohr, B. & Dent, M.L. 2000. Hearing in birds and reptiles. In Dooling R.J., Fay R.R. & Popper A.N. (eds) *Comparative Hearing: Birds and Reptiles*: 308–359. New York: Springer.

Dooling, R.J. & Popper, A.N. 2007. Some lessons from the effects of highway noise on birds. *Proc. Meet. Acoust.* **27**: 10004.

Figuerola, J. & Gustamante, L. 1995. Does use of a tape lure bias samples of curlew sandpipers captured with mist nets? (¿Afecta el Uso de Grabaciones Sonoras la Composición de las Muestras de Calidris ferruginea Capturadas con Redes Verticales?). *J. Field Ornithol.* **66**: 497–500.

Fisher, R.A., Corbet, A.S. & Williams, C.B. 1943. The relation between the number of species and the number of individuals in a random sample of an animal population. *J. Anim. Ecol.* **12**: 42–58.

Fransson, T., Barboutis, C., Mellroth, R. & Akriotis, T. 2008. When and where to fuel before crossing the Sahara desert – Extended stopover and migratory fuelling in first-year garden warblers *Sylvia borin*. *J. Avian Biol.* **39**: 133–138.

Ginat, H., Shlomi, Y., Batarseh, S. & Vogel, J. 2011. Reduction in precipitation levels in the Arava Valley (southern Israel and Jordan), 1949-2009. *J. Dead-Sea Arava. Res.* **1**: 1–7.

Harper, D.G. 1994. Ethics of artificially inducing landfall by migrants. *Trends Ecol. Evol.* **9**: 263.

de la Hera, I., Fontanilles, P., Delalande, L., Glad, A. & Sarraude, T. 2017. Attraction of other species by Bluethroat *Luscinia svecica* song playback during autumn migration: an experimental test using bird-ringing data. *Ardeola* **64**: 5–13.

Herremans, M. 1989. Habitat and sampling related bias in sex-ratio of trapped blackcaps *Sylvia atricapilla*. *Ring. Migr.* **10**: 31–34.

Herremans, M. 1990a. Can night migrants use interspecific song recognition to assess habitat? *Le Gerfaut* **80**: 141–148.

Herremans, M. 1990b. Body-moult and migration overlap in reed warblers (*Acrocephalus scirpaceus*) trapped during nocturnal migration. *Le Gerfaut* **80**: 149–158.

Hoi-Leitner, M., Nechtelberger, H. & Hoi, H. 1995. Song rate as a signal for nest site quality in blackcaps (*Sylvia atricapilla*). *Behav. Ecol. Sociobiol.* **37**: 399–405.

Hua, F., Fletcher, R.J., Sieving, K.E. & Dorazio, R.M. 2013. Too risky to settle: avian community structure changes in response to perceived predation risk on adults and offspring. *Proc. R. Soc. Lond. B Biol. Sci.* **280**: 20130762.

Hutto, R.L. 1985. Habitat selection by nonbreeding, migratory land birds. In Cody, M.L. (ed) *Habitat Selection in Birds*: 455–476. London: Academic Press.

Hutto, R.L. 1998. On the importance of stopover sites to migrating birds. *Auk* **115**: 823–825.

Kaiser, A. 1993. A new multi-category classification of subcutaneous fat deposits of songbirds (Una Nueva

Clasificación, con Multi-categorías, para los Depósitos de Grasa en Aves Canoras). *J. Field Ornithol.* **64**: 246–255.

Krama, T., Krams, I. & Igaune, K. 2008. Effects of cover on loud trill-call and soft seet-call use in the crested tit *Parus cristatus*. *Ethology* **114**: 656–661.

Kroodsma, D.E., Byers, B.E., Goodale, E., Johnson, S. & Liu, W. 2001. Pseudoreplication in playback experiments, revisited a decade later. *Anim. Behav.* **61**: 1029–1033.

Ktitorov, P., Tsvey, A. & Mukhin, A. 2010. The good and the bad stopover: behaviours of migrant reed warblers at two contrasting sites. *Behav. Ecol. Sociobiol.* **64**: 1135–1143.

Kuznetsova, A., Brockhoff, P.B. & Christensen, R.H.B. 2017. lmerTest package: tests in linear mixed effects models. *J. Stat. Softw.* **82**: 1–26.

Lecoq, M. & Catry, P. 2003. Diurnal tape-luring of wintering chiffchaffs results in samples with biased sex ratios (Uso de grabaciones para atraer individuos de Phylloscopus collybita resulta en sesgo en la proporción de sexos). *J. Field Ornithol.* **74**: 230–232.

Leedale, A.E., Collins, S.A. & de Kort, S.R. 2015. Blackcaps (*Sylvia atricapilla*) increase the whistle part of their song in response to simulated territorial intrusion. *Ethology* **121**: 403–409.

Lenth, R.V., Buerkner, P., Giné-Vázquez, I., Herve, M., Jung, M., Love, J., Miguez, F., Riebl, H. & Singmann, H. 2022. Emmeans: Estimated marginal means, aka least-squares means. Available at: https://rdrr.io/cran/emmeans/ (accessed 1 March 2023).

Lindström, A. & Alerstam, T. 1992. Optimal fat loads in migrating birds: a test of the time-minimization hypothesis. *Am. Nat.* **140**: 477–491.

Marchetti, K. & Price, T. 1989. Differences in the foraging of juvenile and adult birds: the importance of developmental constraints. *Biol. Rev.* **64**: 51–70.

Moore, F.R. & Aborn, D.A. 2000. Mechanisms of en route habitat selection: how do migrants make habitat decisions during stopover? *Stud. Avian Biol.* **20**: 34–42.

Moore, F., Gauthreaux, K. & Simons, T.R. 1995. Habitat requirements during migration: important link in conservation. In Martin, T.E. & Finch, D.M. (eds) *Ecology and Management of Neotropical Migratory Birds. A Synthesis and Review of Critical Issues*: 121–144. New-York, NY: Oxford University Press.

Mukhin, A., Chernetsov, N. & Kishkinev, D. 2008. Acoustic information as a distant cue for habitat recognition by nocturnally migrating passerines during landfall. *Behav. Ecol.* **19**: 716–723.

Németh, Z.Á. & Moore, F.R. 2007. Unfamiliar stopover sites and the value of social information during migration. *J. Ornithol.* **148**: 369–376.

Németh, Z. & Moore, F.R. 2014. Information acquisition during migration: a social perspective. *Auk* **131**: 186–194.

Nocera, J.J. & Betts, M.G. 2010. The role of social information in avian habitat selection. *Condor* **112**: 222–224.

Norris, D.R. & Taylor, C.M. 2006. Predicting the consequences of carry-over effects for migratory populations. *Biol. Lett.* **2**: 148–151.

Ortega, C.P. 2018. Effects of noise pollution on birds: a brief review of our knowledge. *Ornithol. Monogr.* **74**: 6–22.

Panov, I.N. 2011. Song-luring and net trapping of turdidae species in the northern taiga during period of autumn migration. *Zool. Zhurnal* **90**: 987–997.

Panov, I.N. & Chernetsov, N.S. 2010. Migratory strategy of Bluethroats, *Luscinia svecica*, in eastern Fennoscandia. Part 2: response to acoustic markers and habitat selection at stopover. *Proc. Zool. Inst. Russ. Acad. Sci.* **314**: 173–183.

Preiszner, B. & Csörgő, T. 2008. Habitat preference of sylviidae warblers in a fragmented wetland. *Acta Zool. Acad. Sci.* **54**: 111–122.

R Core Team 2022. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. Available at: https://www.r-project.org/

Rosenzweig, M.L. 1995. *Species Diversity in Space and Time*. Cambridge: Cambridge University Press.

RStudio Team 2022. *RStudio: Integrated Development for R*. Boston, MA: Posit, PBC. Available at: http://www.rstudio.com/

Sapir, N., Abramsky, Z., Shochat, E. & Izhaki, I. 2004a. Scale-dependent habitat selection in migratory frugivorous passerines. *Naturwissenschaften* **91**: 544–547.

Sapir, N., Tsurim, I., Gal, B. & Abramsky, Z. 2004b. The effect of water availability on fuel deposition of two staging *Sylvia* warblers. *J. Avian Biol.* **35**: 25–32.

Schaub, M. & Jenni, L. 1999. Does tape-luring of migrating Eurasian reed-warblers increase number of recruits or capture probability? *Auk* **116**: 1047–1053.

Schulze, A. & Dingler, K.H. 2007. *The Bird Songs of Europe, North Africa and the Middle East*, Musikverlag edn. Germering: AMPLE.

Sebastianelli, M., Savva, G., Moysi, M. & Kirschel, A.N.G. 2020. Tape lures swell bycatch on a Mediterranean Island harbouring illegal bird trapping. *Biol. Lett.* **16**: 20200458.

Seewagen, C.L. 2008. An evaluation of condition indices and predictive models for noninvasive estimates of lipid mass of migrating common yellowthroats, ovenbirds, and Swainson's thrushes. *J. Field Ornithol.* **79**: 80–86.

Shirihai, H., Dovrat, E., Christie, D.A. & Harris, A. 1996. *The Birds of Israel*. London: Academic Press.

Shirihai, H., Gargallo, G. & Helbig, A.J. 2001. *Sylvia Warblers: Identification, Taxonomy and Phylogeny of the Genus Sylvia*. London: A&C Black.

Stamps, J.A. 1988. Conspecific attraction and aggregation in territorial species. *Am. Nat.* **131**: 329–347.

Stamps, J.A. 1991. The effect of conspecifics on habitat selection in territorial species. *Behav. Ecol. Sociobiol.* **28**: 29–36.

Szymkowiak, J. & Schmidt, K.A. 2022. Deterioration of nature's information webs in the Anthropocene. *Oikos*. Available at: https://doi.org/10.1111/OIK.08504

Szymkowiak, J., Thomson, R.L. & Kuczyński, L. 2017. Interspecific social information use in habitat selection decisions among migrant songbirds. *Behav. Ecol.* **28**: 767–775.

Valente, J.J., LeGrande-Rolls, C.L., Rivers, J.W., Tucker, A.M., Fischer, R.A. & Betts, M.G. 2021. Conspecific attraction for conservation and management of terrestrial breeding birds: current knowledge and future research directions. *Ornithol. Appl.* **123**: duab007.

Ward, M.P. & Schlossberg, S. 2004. Conspecific attraction and the conservation of territorial songbirds. *Conserv. Biol.* **18**: 519–525.

Weller, A.A. 1995. Attraction of migrating blackcaps to conspecific song in spring. *Le Gerfaut* **85**: 95–98.

Yong, W., Finch, D.M., Moore, F.R. & Kelly, J.F. 1998. Stopover ecology and habitat use of migratory Wilson's warblers. *Auk* **115**: 829–842.

Zuur, A., Ieno, E.N., Walker, N., Saveliev, A.A. & Smith, G.M. 2009. *Mixed Effects Models and Extensions in Ecology with R*. New York: R. Springer Science & Business Media.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Data S1. Bird ringing data.

Appendix S1. Landfall analysis.

Appendix S2. Summary of bird ringing.

Appendix S3. Statistical model structure and likelihood ratio test results.

Appendix S4. Eurasian Blackcap fat analysis.

Appendix S5. T-test for non-integer variables.

Appendix S6. Supplementing Table 3 in the main text.