Prior territorial responses and home range size predict territory defense in radio-tagged great tits

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Abstract

Territorial animals often use signals to advertise territorial occupancy within their larger home ranges. Songbirds are among the best-studied territorial signaling taxa, and when competitors start singing during a territorial intrusion, residents usually show elevated spatial and vocal responses. These responses could be used by intruders and distant eavesdroppers to predict future responses or to compare responses across competitors. Yet, the extent to which responses of a resident to a territorial intrusion predict its future responses and its overall spatial behavior (home range) within a neighborhood is less well understood. We used wild great tits (*Parus major*) as a model species in repeated song playback trials, simulating territorial intrusions combined with radio-tracking before and during playback trials. The time spent close to the loudspeaker in response to an initial simulated intrusion predicted the same response variable during a second simulated intrusion on the next day, whereas singing activity during the first simulated intrusion did not predict singing during the second simulated intrusion. We also show that more explorative males (as determined by a novel environment test) and males with smaller home ranges sang more and spent more time near the loudspeaker in response to both simulated intrusions. Thus, by probing residents, intruders can obtain reliable information about subsequent response probabilities, while eavesdroppers from a distance, who can use auditory information only, would not receive sufficient predictive information. Our findings also suggest that males with larger home ranges are more tolerant toward intruders, which could reflect a trade-off between tendencies to respond strongly and to range widely. The lack of predictability of singing activity with regard to responses to future intrusions might explain why territorial animals continuously exchange vocal signals and regularly foray into neighboring territories, as a way to obtain regular information updates.

Significance Statement

Animals use experience from interactions with conspecifics in their future decision making, such as mate choice and strategies for conflict resolution. The value of such information depends in part on the predictability of the future behavior of that conspecific. In songbirds, territorial individuals respond to intruders by approach and signaling. Here, we tested in radio-tagged great tits (*Parus major*) if territorial responses are predictable and are affected by individual and environmental factors. We show that the time spent near the simulated intruder was more predictable than singing activity and that birds with larger home ranges showed weaker responses. These findings suggest that information based on such spatial responses is more useful for future decision making, as compared to vocal information, and that distant eavesdroppers will thus receive less reliable information. Limited predictability may explain why territorial animals continuously exchange vocal signals and foray into neighboring territories, providing opportunities for regular information updates.

Keywords Animal communication · Bird song · Playback experiments · Predictability · Territorial behavior

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Introduction

Many animals use signals to defend resources, such as mates, feeding sites, or territories. In territorial signaling, acoustic signals are widespread, as they transmit omnidirectionally and quickly over long distances and through dense habitats

(Wiley and Richards 1978; Brumm and Naguib 2009). Territorial signals thus help to define the spatial organization of a population, as they serve to attract or repel conspecifics (Searcy and Nowicki 2005). One complication here is that territory boundaries are not always clearly defined in complex landscapes and may vary over time and with population density. In addition, territorial systems can be highly dynamic with animals moving around also beyond their territorial boundaries. Indeed, competitors frequently trespass into others' territories without necessarily challenging the resident, presumably to explore and assess the territory or resident (Naguib et al. 2008; Snijders and Naguib 2017). Initially, such intrusions may be part of a process in which space gets partitioned, for example, by testing rivals' alertness and responsiveness (Stamps and Krishnan 2001), potentially leading to continuous small changes in initial territory sizes and boundary locations. Yet such intrusions are also known to occur after territories appear to be fully established (Hanski and Haila 1988; Chandler et al. 1994, 1997; Pitcher and Stutchbury 2000; Naguib et al. 2001; Bircher et al. 2020), likely to continually update information about neighboring conspecifics.

For individuals probing a resident's territory, the value of information gained from the resident's response should depend directly on how well this response can predict future responses. Because territory owners often secure advantages by advertising when they win contests (Dugatkin 1997; Rutte et al. 2006; Oliveira et al. 2009; Mouderde et al. 2012), receivers who adjust their future behavior in response to such signals can gain benefit, such as by avoiding conflicts they would be unlikely to win. While prospectors thus would benefit from predictable information, territory owners may also benefit from being predictable, by reducing the probability of repeated challenges and intrusions. Thus, selection may favor predictability of territorial defense responses, through coevolution with intruder responsiveness (Wolf et al. 2011). Prior work indicates that residents might be most alert after an initial intrusion and subsequently adjust future advertisements (Amrhein and Erne 2006; Erne and Amrhein 2008) and territorial responses (Hall et al. 2006; Schmidt et al. 2007). Nevertheless, overall responses are expected to remain predictable when territorial responses result mainly from stable characteristics of the individual or the territory, rather than exclusively from varying short-term motivational factors such as current stress levels or recent experience.

There is a wealth of research on responses to territorial intrusions, specifically in songbirds (McGregor 1992a; Gil and Gahr 2002; Searcy and Nowicki 2005). However, comparatively little information is available on these responses' predictability (Nowicki et al. 2002; Hyman et al. 2004). Classically, experiments examining communication and territorial responses, simulating territory intrusions through

playback, focused on determining the function of different signaling strategies (Gil and Gahr 2002), without repeating playback treatments on the same individuals. Exceptions are, for instance, studies on song sparrows (*Melospiza melodia*), which have shown that territorial responses are repeatable and vary consistently among individuals across repeated trials (Nowicki et al. 2002; Hyman et al. 2004). Moreover, Hall et al. (2017) showed in superb fairy-wrens (*Malurus cynaneus*) that vocal responses to playbacks were repeatable, while spatial responses were not. These findings imply that probing territory owners, and specifically, attending to their vocal responses, could provide intruders predictive information about the territory owner and/or territory. Studies on great tits (*Parus major*) likewise revealed high repeatability of territory holders over several days responding at close range to an exposed taxidermic mount combined with song playback (Araya-Ajoy and Dingemanse 2014, 2017). At a finer scale, Hardman and Dalesman (2018) showed in great tits that multiple response measures were repeatable across playback trials conducted on the same day (Hardman and Dalesman 2018).

When repeatable, behavioral responses to territorial intrusions can be considered as reflecting personality traits, which have been shown to predict behavior within and across contexts (Dingemanse and Réale 2005; Bell et al. 2009; Stamps and Groothuis 2010). Indeed, several studies using great tits as a model organism have shown that exploration behavior, as a repeatable proxy for a personality trait, can predict territorial responses toward intrusions (Amy et al. 2010; Jacobs et al. 2014; Snijders et al. 2015), even though studies on other species have not always revealed such a relation (Hall et al. 2017). Amy et al. (2010), for instance, showed in radio-tagged great tits that slower explorers were more likely to foray into neighboring territories after an intrusion and that neighboring individuals' spatial responses depended on the threatened resident's exploration score. Both Amy et al. (2010) and Snijders et al. (2015) found that more explorative males, as tested under standardized indoor conditions, responded more strongly spatially to simulated intrusions in the wild (e.g., spending more time close to the simulated intruder), while Jacobs et al. (2014) found that less explorative males responded more strongly spatially, yet responded less strongly vocally.

How strongly and predictably individuals respond thus appears to vary with context and might depend on the type of behavioral response in combination with environmental variables. For instance, certain behaviors might be more predictable than others across varying climate conditions, such as temperature (Garson and Hunter 1979; Thomas 2002; Naguib et al. 2019). During colder periods, individuals are perhaps likely to refrain from energetically demanding or risky behaviors, leading to lower consistency. Songbirds in general sing much less when it is colder or when previous

nights were colder (Thomas 1999, 2002). Thus, vocal responses toward territorial threats can likewise be expected to vary with temperature. Responses can also be influenced by differences in activities or states before an intrusion, such that a resting or foraging bird might take longer to respond strongly than a bird already engaged in social interactions.

Territory defense responses could also be modulated by the social and spatial structure of a neighborhood. For example, individuals with relatively small territories, as advertised by singing, or relatively small home ranges, revealed by overall space use, are likely to have more regular encounters on or near their territories, leading to more predictable responses compared to individuals with larger areas. Previous studies on great tits indeed showed that individuals exhibit stronger overall territory responses to taxidermic mounts at higher population densities (Araya-Ajoy and Dingemanse 2017). Yet, home range size can vary independently from population density and the size of defended territories, as individuals frequently leave their territories to foray into the neighborhood at large (Chandler et al. 1997; Pitcher and Stutchbury 2000; Naguib et al. 2001, 2011; Bircher et al. 2020). Male nightingales' (*Luscinia megarhynchos*) home ranges, for instance, are twice the area of the singing territories, and home ranges include singing territories of other males (Naguib et al. 2001). Great tits foray frequently into other males' singing territories (Bircher et al. 2020) and form close range social networks that require leaving their own territories (Snijders et al. 2014), also resulting in home range sizes that well exceed the size of singing territories. Because home range size in great tits might reflect the time an individual is away from its actual defended territory and thus its site attachment, home range size is also expected to impact the strength and predictability of territorial responses.

Here, we tested the predictability of territorial responses to intrusions using great tits as our model system. Few studies to date have integrated data regarding the wider space-use of wild-ranging birds with their singing behavior (Hanski and Haila 1988; Chandler et al. 1994, 1997; Naguib et al. 2001), and even fewer with their territorial responses (Naguib et al. 2004; Amy et al. 2010; Snijders et al. 2017). Because birds often move around silently, such integration requires time-consuming and logistically challenging radio-tracking, especially before automated systems were readily available (Mennill et al. 2012; Snijders et al. 2014; Bircher et al. 2020, 2021). We radio-tagged individuals, after being typed for exploration behavior, several days before playback to determine their home range, the center of their singing activity, and to facilitate locating them during playback even when they were silent. We then exposed these individuals to two territorial intrusions, one day apart, expecting that responses from the first day would predict responses on the second day. We also expected faster-exploring individuals

and individuals with smaller home ranges to show stronger responses and for vocal responses overall to be stronger at higher temperatures.

Methods

Study site and study animals

We conducted playback experiments on 15 radio-tagged male territorial great tits in the spring of 2010 using a nest box population at Westerheide (5°50'E, 52°00'N) near Arnhem, The Netherlands. Westerheide is a mixed pine-deciduous forest with approximately 200 nest boxes distributed within a 1000 m × 1200 m area. Birds in this population are routinely tested for exploration behavior using a novel environment test (Dingemanse et al. 2002), an established operational measure for a personality trait in great tits (van Oers and Naguib 2013). During the breeding season, all nest boxes were checked twice a week to record breeding measures such as the start of egg-laying, clutch size, brood size, and fledging success. On approximately the 10th day after chicks hatched, parents were caught for identification inside their nest boxes using spring traps (radio tags were removed at that time, see 'Radio-tracking'). To minimize observer bias, blinded methods were used as much as possible, i.e., playback data were analyzed only after completion of all trials and home range sizes and exploration scores were calculated without knowledge of the outcome of the playback trials.

General experimental protocol

On the nights of the 15th and 16th of March 2010, 26 males were taken from nest boxes and transported within 2 h to the aviary and bird holding facilities at the nearby Netherlands Institute of Ecology in Heteren, The Netherlands. After weighing and measuring tarsus length, the birds were housed overnight in individual cages (90 cm wide × 40 cm deep × 50 cm high) and provided with food and water ad libitum. The following morning, we quantified their exploration behavior (see [Novel environment test](#), below). After testing, birds were weighed again and equipped with radio tags (see below) before they were released at the nest box of capture. We then performed 30 playback trials, two trials on each of 15 males, between the 29th of March and the 9th of April 2010. We could not use all 26 radio tagged males as playback subjects, as five males had lost their tags before we started the playbacks, one male was found dead prior to playback onset, four males spent most of the time on fenced private property adjacent to our field site (so that we could not track them), and for one male we could not complete the

second playback for logistical reasons. Males were radio-tracked over the days before the playback, to determine their home ranges and centers of activity, as well as during the playback trials, to confirm the presence and identity of the subjects during the trial.

Novel environment test

We quantified birds' exploration behavior individually in a novel environment, a room (4.0 m × 2.4 m × 2.3 m) with five artificial trees. All the individual cages were connected via sliding doors to the experimental room. After darkening the individual cage with a towel, the bird entered the experimental room, and we recorded the total number of flights (movements between trees) and hops (movements within trees) within the first 2 min. These total numbers of movements were subsequently used as an overall exploration score (Dingemanse et al. 2002). To exclude observer bias, exploration scores were unknown to the experimenters at the time of the playback experiment.

Radio-tracking

After the exploration tests and before birds were released back to the field, BD-2 radio-tags (Holohil Systems, Canada, 30 pulses/min, 0.80 g) were attached, using elastic rubber backpack harnesses (Amrhein et al. 2004; Amy et al. 2010). After tagging, birds were monitored for maximally 1 h in their cage and then released back into the field. The 15 subject males had a mean body mass of 18.3 ± 0.8 g (mean $\pm$ SD) when brought in (21:00–21:45) and 16.9 ± 0.7 g (mean $\pm$ SD) before returned to the field (0900–1307 h). We used three-element Yagi antennas and ICOM IC-R20 receivers for radio-tracking, by carefully following the bird movement at a distance without disturbing them. Individuals were tracked in total for 90 to 279 min (mean = 195 min per individual) before playback, spread over 3 to 9 days (mean = 7 days) to estimate their home range. During a tracking session, we tracked an individual for 30-min nonstop by noting its position every minute on a detailed map of the study site, before moving on to the next individual. The analysis of the spatial data was done without knowledge of the outcome of the playback experiments. The outer tracking points then were transferred to ArcView, and exact coordinates were exported. The outer tracking points before playback experiments were used to construct minimum convex polygon sizes (95% MCP) in hectares (ha) as a measure for home range size for each bird, using the 'adehabitatHR' package (Calenge 2006) in R software (R-Core-Team 2017). Home range areas did not correlate significantly with tracking effort (Spearman rank correlation test;

minutes tracked, $r_s = 0.46$, $P = 0.11$; days tracked, $r_s = 0.45$, $P = 0.12$). In addition, home range size did not correlate with breeding density, using the number of breeding pairs (first nests) within a given radius (100 m: $r_s = -0.15$, $P = 0.63$; 150 m: $r_s = 0.27$, $P = 0.36$; 200 m: $r_s = 0.15$, $P = 0.62$) or the distance to the closest breeding pair as proxy (first closest: $r_s = -0.06$, $P = 0.84$; second closest: $r_s = 0.18$, $P = 0.57$; third closest: $r_s = -0.05$, $P = 0.87$).

Playback protocol

Playback songs were constructed from great tit songs recorded in the study area in the two previous years. Recordings had been made using a Sennheiser ME 66/K6 microphone connected to a Marantz PMD660 solid-state recorder (sample frequency: 44.1 kHz; resolution: 16 bit). All songs were high-pass-filtered at 2,000 Hz to remove low-frequency background noise and adjusted to a standard peak amplitude using Adobe Audition software. Each song was composed of four to seven identical phrases (with two or three elements) at the natural rate typical for the respective song type. Songs ($N = 15$) had a duration of 2.3 ± 0.08 s (mean $\pm$ SE). A playback to each male consisted of 20 repetitions of the same song type, with 3–4 s silence between them. Each male received a different song type as playback to avoid pseudoreplication at this level (Hurlbert 1984; Wiley 2003). The playback broadcasts lasted 118 ± 3 s (mean $\pm$ SD).

The playback trials were conducted between 0850 and 1415 h. Each subject received the same playback on two consecutive days. To simulate the same intruder sampling information, subjects received the same stimulus song twice. No directly neighboring males were tested on the same day. Starting times between the first playback and second playback for a given male differed between -46 min and +65 min. All playbacks were executed before the onset of egg-laying, except for one subject whose mate had started egg-laying before the first playback. The loudspeaker was placed inside the subject's territory, at a location where we had tracked the bird most often and where it was encountered singing during the radio-tracking sessions. Songs were broadcast using a Yamaha NX-U10 loudspeaker and an Archos media player at a sound pressure level of 85 dB SPL at 1 m (Voltcraft® digital sound level meter 322, A-weighting, fast response). The loudspeaker was placed 1.5 to 2 m above ground on a tree branch. Just before playback commenced, the presence of the subject was confirmed using radio-tracking, meaning that the subject had to be within hearing range at the onset of the playback, and all were within approximately 40 m at the onset of playback. Subjects' responses were recorded from the onset of the playback until 2 min after the playback had ended, using a Sennheiser ME 66/K6 microphone connected to one channel of a Marantz PMD660 digital

recorder. Additional observations, such as the estimated horizontal distances from the loudspeaker for each song, were annotated with a handheld microphone (Sennheiser ME 66/K6) connected to the other channel of the recorder. The subjects' vocal responses were analyzed using SASlab Pro (R. Specht, Berlin, Germany) for the entire duration of the playback plus the two minutes that followed.

Statistical analysis

To minimize observer bias, the data were screened and analyzed only after all playback experiments were completed. All statistical analyses were performed using R version 4.0.2 (R-Core-Team 2017) in R Studio version 1.2.5033. Two of the 15 playback subjects were left out of the analyses because they could not be verified as being territorial and breeding and therefore their status as continued territory holders at the time and location of the playback could not be confirmed with certainty. Sample size across all trials was thus $N = 26$ playbacks, i.e., two playback trials with each of the 13 territorial males.

Response variables

We measured six response behaviors following (Snijders et al. 2017): (1) song rate (# songs/sec) during the playback, (2) song rate (songs/sec) during the playback plus the subsequent 2 min observation time, (3) the proportion of time spent singing during the playback plus 2 min observation time, (4) the proportion of songs that overlapped a stimulus song, (5) the proportion of time spent within 5 m of the loudspeaker during the playback plus the following 2 min observation time, and (6) latency to approach within 5 m of the loudspeaker (s). Because six subjects sang fewer than three songs and four birds sang no songs during at least one of the trials, the proportion of overlaps (the fourth response measure) was excluded from the analysis. Individuals that did not approach within 5 m of the loudspeaker were coded with an approach latency value of 240 s (equaling the total duration of a playback trial, consisting of ca 120 s playback and 120 s subsequent observation time).

Principal Component Analysis (PCA)

For dimensionality reduction purposes (McGregor 1992b), a principal component analysis (varimax rotation) was conducted on the five response measures, following Snijders et al. (2015, 2017), using the 'Psych' package (Revelle 2017) in R. Values for the Kaiser–Meyer–Olkin (KMO) measure of sampling adequacy were all above 0.6 for the individual responses and were 0.72 overall. The Bartlett test was significant at $P < 0.001$ (see Figs S1–3 for correlation matrices

of the response measures during both the first and the second intrusions, respectively). Only the first rotated component had an eigenvalue above one (eigenvalue = 3.46), including all the vocal responses but also a spatial response (Table S1). This contrasts with Snijders et al. (2015, 2017) in which both the first and second components had eigenvalues above 1, with the first component primarily representing the vocal measures and the second component the spatial measures. To still be able to separate spatial and vocal responses, we therefore decided to conduct dimensionality reduction by extracting one component only for the three strongly correlated ($r > 0.75$), and therefore redundant, vocal responses and to use the proportion of time spent within 5 m (arcsine transformed) as a representative measure for the spatial response (Spearman rank correlation test for the proportion of time spent within 5 m and latency to arrive within 5 m: $r_s = -0.62$, $P < 0.001$). The resulting principal component for the vocal response measures (PC1) explained 90% of the total variance, and loadings were 0.93, 0.98 and 0.93, respectively, for the song rate during playback, song rate during the total observation time, and the proportion of time spent singing during the total observation time. The overall KMO measure of sampling adequacy was 0.64, and Bartlett's test was significant at $P < 0.001$. The eigenvalue of this principal component was 2.70.

Model selection

We conducted a model selection procedure to identify the variables that significantly predicted the singing activity response (PC1) and a spatial response (Proportion of time within 5 m). Six predictor variables (i.e., fixed effects) were included in both the initial model for the vocal response and the model for the spatial response. These predictor variables included the two variables of interest (exploration score and size of home range area as polygon size in ha), one structural variable that was inherent to our experimental design (first or second playback intrusion), and three control variables (temperature in degrees Celsius, body condition as residual of the linear relationship between tarsus length and weight when the subject was brought in, and the number of days until the subject's partner started egg-laying). Females are fertile up to presumably at least 7 days before egg-laying until the day of the penultimate egg (Birkhead and Møller 1992), and this might influence the subject male's response to the intrusion. Temperature values during the time of the intrusions were retrieved from the KNMI weather station (Deelen, < 10 km of the field site) and ranged from 3.3 to 18 degrees Celsius. Because we had reliable age values (one year or older) for only ten of the subjects, this variable was not included in the analysis. Adding age to the final models did not reveal a significant effect of age. Subject identity was included as a random effect.

For the model selection procedure, we used linear mixed models (LMM), with the function *lmer* in the ‘lme4’ package (Bates et al. 2015). All continuous predictor variables were scaled and centered using the *scale* function of the ‘base’ package. Subject and playback treatment (first or second intrusion) were always kept in the model to account for repeated measures inherent to the experimental design of our study. In addition, exploration and home range size were kept in the model as these were our predictor variables of interest. The predictor variables that served as control variables and were unrelated to experimental design (i.e., temperature, body condition, and days until egg-laying) were excluded from the model when not significant ($P \leq 0.05$), starting with the least significant variable. Significance was determined by comparing the model still including the respective predictor variable to the same model excluding it, using type II Wald Chi-square tests of the *Anova* function in the ‘car’ package (Fox et al. 2019). Models for evaluating the significance of the predictor variables were constructed using the ‘ML’ method; otherwise, ‘REML’ was used. Estimates were derived from the last model still including the variable using ‘REML’. The significance of the predictor variables of interest (i.e., exploration score and home range size) did not differ between the initial and final models. For

time spent within 5 m of the loudspeaker, we also examined the use of a model with a beta family error distribution and logit link, using the ‘glmmTMB’ package (Brooks et al. 2017), as suggested by Douma and Weedon (2019). This procedure led to the same qualitative conclusions for the effects of our predictor variables of interest (i.e., exploration score and home range size), but due to incompatibility with other model diagnostic and analysis tools we opted for our original LMM with arcsine transformation (in which the variances were equal and the residuals normally distributed).

We derived repeatability (R) values and their 95% confidence intervals using the ‘rptR’ package (Stoffel et al. 2017). Repeatability was calculated as the variance among subject male means over subject-level and data-level (residual) variance combined. The ‘rptR’ package allows estimation of the uncertainty around the repeatability estimate by parametric bootstrapping and thus offers the possibility to control for fixed effects (i.e., adjusted repeatability). Adjusted repeatability was calculated based on the model including playback treatment (first or second intrusion), to account for potential effects of the repeated trials (e.g., habituation), and any significant control variables (e.g., temperature, body condition and days until egg-laying; Table 1). In case of significant repeatability, we also ran the model including the

Table 1 Model statistics for vocal responses (PC1) and spatial response (proportion of time spent within 5 m). Statistics are retrieved from the last model still including the indicated variable (SE=standard error, SD=standard deviation, DF=degrees of freedom, 95% CI=95% confidence interval). Significance values

based on model comparison including and excluding the respective variable (type II Wald Chi-square tests). $N=26$, i.e., two simulated intrusions with each of the thirteen territorial males. Explanatory variables in bold were included in the final model. Significant P-values (≤ 0.05) are indicated in bold

	Explanatory	Estimate (SE)	DF	t	χ^2	P
PC1-Vocal	<i>Intercept</i>	0.30 (0.24)	21.00	1.23		
	Playback treatment	-0.60 (0.34)	21.00	-1.73	3.70	0.054
	Exploration score	0.39 (0.18)	21.00	2.19	5.96	0.01
	Home range	-0.60 (0.22)	21.00	-2.68	8.90	0.003
	Condition	-0.22 (0.19)	19.00	-1.18	1.90	0.18
	Temperature	0.54 (0.22)	21.00	2.45	7.45	0.01
	Days to first egg	0.28 (0.18)	20.00	1.57	3.20	0.08
Variance (SD)	Subject identity	0.00 (0.00)*				
	Residual	0.75 (0.86)*				
Marginal R^2 (95% CI)		0.33 (0.15–0.63)*				
Proportion of time spent within 5 m (arcsine transformed)	<i>Intercept</i>	0.47 (0.08)	18.65	6.27		
	Playback treatment	-0.02 (0.09)	11.86	-0.26	0.06	0.80
	Exploration score	0.20 (0.06)	9.40	3.16	13.72	<0.001
	Home range	-0.31 (0.07)	12.94	-4.18	22.71	<0.001
	Condition	0.02 (0.07)	8.61	0.256	0.12	0.72
	Temperature	0.16 (0.07)	20.87	2.41	6.66	0.01
	Days to first egg	0.005 (0.07)	8.01	0.07	0.0002	0.99
Variance (SD)	Subject identity	0.02 (0.14)*				
	Residual	0.05 (0.23)*				
Marginal R^2 (95% CI)		0.52(0.31–0.74)*				

*Based on the final model (i.e., only including the bold formatted variables)

subject-level variables of interest (i.e., exploration score and home range size) and any significant subject-level control variables (there were none, see [Results](#), Table 1) to evaluate if these subject-level variables may partly account for the revealed repeatability (i.e., subject identity explaining a significant proportion of the variance in response).

The initial and final models were validated by evaluating heterogeneity of variances, normality, collinearity, and outliers. No variance heterogeneity was detected (residual versus fitted plot, Levene's test $P > 0.05$). The model residuals did not deviate significantly from a normal distribution (Shapiro–Wilk test $P > 0.05$). Variance inflation factors (VIF), assessed with the *vif* function of the 'car' package, were all below 2.5. Potentially influential subjects in the analysis were evaluated using the *influence* and *cooks.distance* function from the 'influence.ME' package (Nieuwenhuis et al. 2012). Using the same package, the influence of subjects with a Cook's distance of $4/N-k-1$ (k =the number of variables in the model) was excluded using the *exclude.influence* function. The significance of the variables of interest did not change following such exclusions, and results are therefore reported for models without exclusions. Potentially influential observations were evaluated with the *outlierTest* function of the 'car' package; no outliers were detected (Bonferroni $P > 0.05$). As a measure of goodness-of-fit, the proportion of variance explained by the (fixed) predictor variables in the final models was calculated following Nakagawa and Schielzeth (2013), by using the *r2beta* function (method='nsj') of the 'r2glmm' function (Jaeger 2017). Figures were created using the 'ggplot2' package (Wickham 2016).

Results

Home range (polygons in ha) and exploration scores varied substantially among the 13 males (exploration score, mean $\pm$ SD: 17.08 ± 5.38 , range: 8.71–24.96; home range, mean $\pm$ SD: 2.24 ± 1.94 , range: 0.36–7.47). Faster explorers showed a nonsignificant trend to have larger home ranges ($r_s = 0.50$, $P = 0.08$). Males with higher exploration scores had higher PC1 scores, indicating that faster explorers sang more in response to a simulated intrusion. They also spent more time within 5 m of the loudspeaker (Table 1, Fig. 1a,c). In addition, males with larger home ranges showed lower PC1 scores, reflecting less singing, and these males spent less time within 5 m of the loudspeaker (Table 1, Fig. 1b,d). The temperature during the intrusion positively predicted both the vocal and spatial responses (Table 1). Playback treatment (first or second playback trial), body condition, and days until the first egg of the mate did not significantly affect the PC1 scores or the time spent within 5 m of the loudspeaker, but there was a nonsignificant trend for males

to sing less (lower PC1 score) during the second simulated intrusion (Table 1).

Male identity did not significantly explain variation in PC1 score (singing activity) to the two simulated intrusions (adjusted repeatability $R_{adj} \pm$ SD = 0.11 ± 0.21 , 95% confidence interval (95% CI) = $0 - 0.68$), $P = 0.38$; Fig. 2a), indicating that the singing activity of a male to the first playback did not predict its singing activity to the second playback. In contrast, male identity explained variation in the time they spent within 5 m of the loudspeaker ($R_{adj} = 0.59 \pm 0.19$, 95% CI = $0.16 - 0.88$, $P = 0.03$; Fig. 2b), indicating that the time spent close to the loudspeaker during the first playback predicted the time spent close during the second playback. This was no longer the case when exploration score and home range size were accounted for ($R_{adj} = 0.26 \pm 0.24$, 95% CI = $0.00 - 0.79$, $P = 0.33$; Table 1). Specifically, variance explained by male identity decreased from 0.09 to 0.02 when exploration score and home range size were included in the model. In contrast, the unexplained (residual) variance remained relatively constant, going from 0.06 to 0.05. These statistics suggest that individual differences in male spatial responses were explained mainly by subjects' exploration scores and size of home range areas.

Discussion

Using a combination of radio-tracking and playback trials that simulated territorial intrusions, we show that territory owners' time spent close to a simulated intruder was predicted by this same measure during a prior intrusion. We also show that this predictability was partly explained by exploratory behavior and home range area. In contrast, singing activity in response to simulated intrusions was not predicted by males' singing activity in response to a prior intrusion. Moreover, we show that faster explorers sang more (higher PC1 scores) and spent more time close to the simulated intruder than did slower explorers, which is in line with previous studies in this population (Amy et al. 2010; Snijders et al. 2015). We further reveal that males with smaller home ranges responded more strongly, both with respect to singing activity (PC1 scores) and time spent near the simulated intruder, than did those with larger home ranges. Home range did not correlate with population density. Both these measured vocal and spatial responses were significantly affected by temperature, with males responding more strongly on warmer days. Thus, by combining playback experiments with radio-tracking, we were able to gain new insights into the predictability of territorial responses to repeated intrusions, and how territorial responses vary with spatial behavior within a neighborhood. It also allowed us to standardize the playback procedure by initiating a simulated territory intrusion only when territory holders were indeed nearby.

Fig. 1 Vocal and spatial responses to simulated territory intrusions as a function of individual exploration score and home range size. Vocal activity of 13 territorial male great tits during the first intrusion (filled circles) and second intrusion (open circles), represented by the principal component of song rate during the intrusion and song rate, was positively predicted by the male's exploration score (a) and negatively predicted by the male's home range size, measured as the 95% minimum convex polygon (b). Spatial responses to the simulated territory intrusions, measured as the proportion of

time spent within 5 m of the loudspeaker, was likewise positively predicted by the male's exploration score (c) and negatively predicted by the male's home range size (d). Regression lines show the predicted final model values for significant predictors. Shaded areas around the lines reflect the 95% confidence interval. A minor jitter was added to reduce the overlap of datapoints (jitter height and width for panels a and c were 0.02 and 0.2, respectively, and for panels b and d 0.02 and 0.02, respectively)

By simulating a context as it would occur when neighbors or prospectors repeatedly probe a resident, we thus show predictability in the resident's time spent near the simulated intruder but not in its singing activity (PC1 score) in response to the simulated intrusion. Thus, predictable information in this case would be available to the intruder, but not to more distant eavesdroppers who would have only auditory information available (McGregor 2005; Snijders and Naguib 2017). Previous studies on song sparrows and superb fairy wrens, likewise focusing on the predictability of territorial responses, showed that territory holders are predictable in both their singing and spatial response across repeated simulated intrusions (Hyman et al. 2004; Hall et al. 2006), but studies also that birds may adjust their responses

to integrate previous experiences (Amrhein and Erne 2006; Hall et al. 2006; Schmidt et al. 2007). Likewise, in great tits vocal response in reaction to a taxidermic mount as a visual stimulus combined with playback was repeatable (Araya-Ajoy and Dingemanse 2017). Differences among studies in the repeatability of vocal responses may be explained in part by species and context-specific factors. Specifically, the study of Araya-Ajoy and Dingemanse (2017) used a taxidermic mount, thus a stationary visual cue, focusing on those subjects that approached closely. Vocal responses among individuals with a strong spatial response toward a clearly localizable strong visual stimulus indeed may be more repeatable compared to individuals who only have auditory information available for decision making without

Fig. 2 Vocal and spatial responses to the second intrusion as a function of responses to the first intrusion. (a) Vocal activity of 13 territorial male great tits during the second intrusion was not predicted by vocal activity during the first intrusion. Vocal activity is represented by the first principal component of song rate during playback, song rate during total observation time, and the proportion of time spent singing during the total observation time. (b) Spatial response to the second intrusion was significantly predicted by the

spatial response during the first intrusion. Spatial response is represented as the proportion of time spent within 5 m of the loudspeaker. Regression lines show the predicted simple linear model values calculated by the 'geom_smooth()' function in the 'ggplot2' package for cases in which repeatability was significant. Shaded areas around the lines reflect the 95% confidence interval. A minor jitter was added to reduce the overlap of datapoints (jitter height and width for both panels were 0.01 and 0.01, respectively)

any localized visual stimulus. Variation in predictability of territorial responses across studies and response traits may reflect a trade-off between the advantage of being predictable while at the same time modifying responses based on context and previous experiences.

We had here performed repeated simulated intrusions for each male on two consecutive days, while keeping the playback stimulus to each male constant. With this design, we simulated the same individual returning as intruder, yet with the risk of generating order effects such as habituation or sensitization. In our study, birds did not appear to significantly modify their spatial response following the first intrusion, although there was a nonsignificant trend for a reduction in vocal activity during the second intrusion. We controlled for potential general effects of habituation or sensitization in our analyses. Nevertheless, if habituation occurred in some birds but not others, this could be a proximate explanation for the lack of overall predictability in singing activity from the first to the second simulated intrusion. In light of these findings, it would be interesting to determine if some birds intruding repeatedly will choose to sing consistently across events, so as to induce habituation to reduce the probability of retaliating responses (Godard 1993; Hyman 2002). In addition, to evaluate the generalizability of our findings for larger biologically relevant time intervals, next steps would be to test predictability of spatially tracked individuals throughout periods of territory establishment or within the first weeks of the breeding season when owning a territory is key to raising a brood (Nowicki et al. 2002).

Another finding here was that temperature had a strong positive effect on the strength of our subjects' territorial responses. The strong temperature differences across playback days, with some very cold mornings, may have masked any individual characteristics in vocal response by making singing more costly for some males but not others (Thomas 2002). Because birds that explore a neighborhood and probe different territory holders might do so over several days (and thus across different environmental gradients), such earlier experiences may be relatively poor predictors for future territorial responses, unless responding and eavesdropping birds can adjust their expectations according to temperature. This could be one reason why birds continue to foray around the neighborhood throughout the breeding season (Bircher et al. 2020), as a way to update and refine the information they have gathered earlier. Such repeated sampling would reduce the probability of errors and increase the reliability of the information (Wiley 1994, 2015; Waas 2006).

Spatial response to intrusions appears to have been, at least partly, driven by the overall spatial embedding of an individual in its environment. Our finding that birds with smaller home ranges sang more and spent more time near the simulated intruder is in line with our predictions. Home range is not completely independent of territory size as birds with large (singing) territories cannot have small home ranges, yet it is not restricted by singing territory size or population density. Home ranges include forays outside the defended area (Naguib et al. 2001) and thus, to some extent, can be expected to be independent of population density, which previously

was shown to affect territorial responses (Araya-Ajoy and Dingemanse 2017). Indeed, we found no evidence for a correlation between home range size and local breeding density. Hyman et al. (2002) showed that neighboring birds expressed similar patterns of response, leading to clusters of high or low aggression. These studies together support the idea that the territorial responses are not just linked to the individual or territory but also to the wider social embedding in the neighborhood (Snijders and Naguib 2017). Indeed, home ranges of territorial birds can be a magnitude larger than singing territories, and forays cover distances that do not always permit auditory contact with the foraging individual's territory. Our finding that males with larger home ranges responded less strongly and thus were more tolerant toward intruders could reflect a trade-off between the benefits of staying on the territory and the benefits of ranging more widely (and thus be more frequently away from their defended area) to collect information from the broader neighborhood and landscape. It may also be that birds with smaller home ranges generally encounter more intrusions and thus need to defend their territory more vigorously in order to maintain it.

Finally, the higher singing activity of faster-exploring males, and the more time they spent near the simulated intruder, is in line with earlier studies on this population, which also revealed stronger vocal and spatial responses by faster explorers (Amy et al. 2010; Snijders et al. 2015). Interestingly, faster exploring great tits are also more likely to be physically aggressive (Verbeek et al. 1996), and observing territorial defense responses may thus provide a conspecific with some indication of a bird's personality traits and therefore the physical risk an intrusion may bring. Yet, Jacobs et al. (2012) found the opposite for great tits, i.e., stronger spatial response, measured as approach distance, by slower explorers, suggesting that there is no simple relationship between territorial responses and personality traits across all contexts in the wild. Even though faster explorers are considered to be bolder individuals engaging in more risk-taking (van Oers et al. 2004), the way personality traits drive the decision on how to respond to a territorial threat is, apparently, not as straightforward. Under which conditions such personality effects on territorial responses emerge, and in which way, therefore largely remains unknown. Similarly, we found not a clear relationship but rather a nonsignificant positive trend for faster explorers to have larger home ranges. Given the relatively small sample size of our study, further investigations with larger sample sizes will be necessary to draw stronger conclusions about these associations.

In conclusion, our finding that individuals challenged with simulated intrusions are more consistent in their time spent near the simulated intruder than in their singing activity suggests that prospectors and neighbors would obtain more reliable information from close-range direct spatial experience. By contrast, information on the predictability

of territory defense would not be available to those eavesdropping on interactions from a distance (McGregor 2005). Challenging a territory holder to the point that it responds spatially as opposed to vocally, however, can carry higher costs as it increases the risk of a physical encounter. Therefore, birds would benefit from integrating a range of information, including unchallenged singing behavior, which has also been shown to predict territorial responses (Snijders et al. 2015). Individuals might intrude on others' territories repeatedly only when they can afford to or when they might reap significant benefits. In turn, territory holders may adapt their responses based on previous experience and the threat perceived, weighed against the advantage of responding predictably, a trade-off that could be influenced by their personality and home range size.

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Authors' contributions MN designed the study and conducted the playback experiments. PS, JRW, MT, KvO, and MN conducted the radio-tracking and were involved in the exploration tests. LS and MT analyzed the data with feedback from all authors. MN and LS drafted the manuscript and all authors contributed to revising it.

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Data availability The datasets generated during and/or analyzed during the current study are available in the Dryad repository, https://datadryad.org/stash/share/1hkOvMi0D1sudVaM0kxkx5GZUAPNMwQR5gfjBa_yI

Code availability R code of the analysis can be made available if needed.

Declarations

Ethics approval All applicable international, national, and institutional guidelines for the use of animals were followed. The research was conducted with the permission of the Animal Experimentation Committee of the Royal Netherlands Academy of Sciences (DEC KNAW), protocol CTE 09.02 to MN.

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