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Great tits responding to territorial intrusions sing less but alarm more on colder days

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Abstract

Bird song transmits information required to defend territories and attract mates. These functions contribute to fitness by affecting survival and reproductive success. Singing is also costly due to physiological costs. We used observational data to evaluate support for the hypothesis that lower temperatures result in decreased singing behaviour in wild great tits due to increased energy consumption during cold conditions required for thermoregulation. More than 6,500 simulated territorial intrusions were performed over an 8-year period in twelve nest box populations of great tits *Parus major* south of Munich, Germany. We measured song rate as well as the number of alarm calls and the aggressive response of territorial males to a simulated territorial intrusion. We found a decrease in song rate with decreasing current temperature, but also a concurrent increase in the number of alarm calls. Night temperature did not affect these acoustic traits. We conclude that warmer conditions allow birds to choose more energetically expensive (yet functionally superior) activities during territorial intrusions, thereby facilitating avoidance of physical aggressiveness during territorial intrusions.

KEYWORDS

alarm call, energy consumption, simulated territorial intrusions, song, temperature, trade-off

1 | INTRODUCTION

Acoustic communication is the active transmission of information from sender to receiver (Bright, 1985; Simmons, Popper, & Fay, 2005). Such information can be specific to properties of the sender, such as its age, size or identity, and, ultimately, vocalisations can affect the receiver's behaviour (Aubin, Mathevon, Silva, Vielliard, & Sebe, 2004; Simmons et al., 2005; Vergne, Avril, Martin, & Mathevon, 2007). Acoustic communication has generally been associated with various life-history traits including survival (Zuberbühler, 2001), mate attraction (Klappert & Reinhold, 2003; Suter, Ermacora, Rieille, & Meyer, 2009) and territory defence (e.g. Amrhein & Lerch, 2010). Many birds use song to defend territories, not only against takeovers, but also to discourage extra-pair mating attempts made by other males (Naguib, Altenkamp, & Griessmann, 2001; Slagsvold, Dale, & Sætre, 1994).

There is considerable variation (both among and within-individuals) in singing behaviour. This variation exists, in part, because singing also carries costs (Gil & Gahr, 2002). First, singing increases predation risk because vocalising individuals are more traceable and often sing from a position preferred for sound transmission that is consequently relatively exposed (Bright, 1985; Simmons et al.,

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2005). As a result, birds might reduce song output or choose suboptimal singing locations when perceiving increases in predation levels (Abbey-Lee, Mathot, & Dingemanse, 2016; Campos, Bander, Raksi, & Blumstein, 2009; Møller, Nielsen, & Garamszegi, 2006). Second, singing is energetically demanding as it increases physiological activity (Hasselquist & Bensch, 2008; Oberweger & Goller, 2001; Ward & Slater, 2005). Inspiration, expiration and the contraction of muscles coordinate the production of acoustic signals. Consequently, the amplitude of muscle contractions during singing is significantly higher than during resting (Suthers, Goller, & Pytte, 1999). Ultimately, prolonged singing can lead to exhaustion. Indeed, metabolic rate (i.e. oxygen consumption and heat transfer) is increased during singing compared with resting (Oberweger & Goller, 2001; Ward & Slater, 2005). Third, singing and foraging (as well as other behaviours) are mutually exclusive activities (Strain & Mumme, 1988; Thomas et al., 2003). Consequently, animals have to choose how much of their limited time they invest in each behaviour. Due to these time budgets, physiological costs and limited energy reserves, singing must constantly be traded off with other energetically demanding activities.

Environmental factors can affect the relative balance between the aforementioned costs and benefits of singing. Such factors include weather conditions, altering sound transmission (Bright, 1985) or environmental and anthropogenic noise, masking signals and leading to altered song characteristics such as shifted frequency (Bright, 1985; Pohl, Leadbeater, Slabbekoorn, Klump, & Langemann, 2012). Food availability represents another environmental component that may increase accessible energy, and reduce time required for foraging, thereby positively affecting investments made in singing (Barnett & Briskie, 2007; Reid, 1987; Strain & Mumme, 1988; Thomas, 1999). Importantly, the amount of required and available resources, that is both food and energy reserves, varies as a function of environmental conditions such as temperature. Current temperatures are strongly linked to thermoregulatory costs (Broggi et al., 2007; Dubois, Hallot, & Vézina, 2016; Kendeigh, 1944). Higher energetic demands during periods of lower temperatures can result in a decrease in body weight and fat reserves, and potentially hypothermia (Reinertsen, 1983; Reinertsen & Haftorn, 1986), which consequently increases time required for foraging (Dubois et al., 2016; Reid, 1987). Ultimately, this leads to a trade-off between foraging and singing, especially in colder conditions, when singing activity is consequently decreased (Garson & Hunter, 1979; Godfrey & Bryant, 2000; Reid, 1987; Thomas, 1999). Such temperature effects on singing can either be caused by immediate effects of the current temperature (Gottlander, 1987; Strain & Mumme, 1988) or by carry-over effects of temperatures during preceding nights (Garson & Hunter, 1979; Reid, 1987; Thomas, 1999). Importantly, these two environmental factors are usually strongly correlated (Garson & Hunter, 1979), which may make it difficult to tease apart their respective effects (Naguib, Diehl, van Oers, & Snijders, 2019), particularly in studies with small sample sizes.

Most studies of acoustic communication in this context focus solely on singing. However, acoustic signals can come in the forms of either singing *or* alarming (Araya-Ajoy & Dingemanse, 2014; Morton, 1977 and citations therein). While songs are often elaborate and complex signals, alarm calls are in general short and simple, following stereotypic patterns (Marler, 2004). Calls have been observed and studied in various contexts, such as begging (Thielcke, 1976; Wilkinson, 1980), foraging (Bugnyar, Kijne, & Kotrschal, 2001; Williams, 1969) and predator defence (Hope, 1980; Klump & Shalter, 2010). However, even though calls have been reported to be produced during territory defence in some species (Morton, 1977 and citations therein), quantifications of the occurrence and their importance in relation to singing are rare (Araya-Ajoy & Dingemanse, 2014; Araya-Ajoy et al., 2016). In wild great tits, alarms are frequently produced during territorial intrusions, while being negatively correlated with singing (Araya-Ajoy & Dingemanse, 2014). That is, birds that sing much call little and vice versa; within-individual up-regulations in singing are associated with within-individual down-regulations of alarm calling, likely due to time or energy allocation trade-offs (Araya-Ajoy & Dingemanse, 2014). Furthermore, direct comparisons between singing and alarming within species are missing, but cross-species comparison implies that alarming (and other similar calls) is energetically less costly than singing (compare Eberhardt, 1994 and Jurisevic, Sanderson, & Baudinette, 1999). In fact, some studies were unable to report significant energetic costs associated with alarming (Chappell, Zuk, Kwan, & Johnsen, 1995; Horn, Leonard, & Weary, 1995).

A key question is whether environmental conditions that affect energetic trade-offs, such as temperature, influence acoustic behaviours chosen for territory defence. Specifically, we ask how singing, alarming (which has been neglected in the context of territory defence) and the relationship between these two types of acoustic behaviours are altered by temperature. We propose here two scenarios for the effects of temperature, positing a key role for energy demands associated with each behaviour. In both scenarios, two trade-offs are assumed: a temporal trade-off, which means more time spent on one behaviour results in less time for the other and an energetic trade-off, which means that colder temperatures increase thermoregulatory costs leaving less energy reserves for vocalisations. If alarming and singing do not differ in energetic costs, we predict that the number of vocalisations increases with increased temperatures without causing a shift from alarming towards singing or *vice versa* (Scenario 1). If alarming is, by contrast, less costly than singing, we expect birds to vocalise at a similar rate, whereas singing is down-regulated, but alarming up-regulated with lower temperatures (Scenario 2). These predictions are made assuming that any acoustic response to a territorial intrusion is preferable to not responding at all, which seems a reasonable assumption as non-responsive birds may lose their territory and purely behavioural responses without any type of vocalisation are extremely rare (<1%).

Here, we investigated support for these two alternative scenarios by using a longitudinal (8 years) observational data set of simulated territorial intrusions conducted in twelve nest box

populations of great tits. We hypothesised (a) that birds would sing less with lower temperatures due to depleted energy reserves and lower foraging efficiency and (b) that birds would instead alarm more (assuming lower energetic costs of this behaviour compared with singing; see above), thereby supporting Scenario 2. While evaluating the support for our hypotheses, we also investigated whether effects of temperature were attributable to current versus night temperature, which was uniquely possible because of the large sample size of our study. Finally, assuming birds replenish energy reserves during foraging in the morning hours, we predicted (c) that any effect of night temperature on acoustic output would diminish with increasing time between sunrise and a focal behavioural test.

2 | METHODS

2.1 | Study Populations and Territorial Intrusions

We studied twelve nest box populations located in southern Germany, each containing 50 nest boxes distributed in a grid with 50-m distance between adjacent boxes. Nest boxes were checked (bi-)weekly from the beginning of April till August and lay date (back-calculated assuming one egg laid per day), and clutch size was recorded. Seven or ten days after the eggs hatched, the parents were caught, morphologically measured and colour-ringed to allow individual identification (for further details see Nicolaus et al., 2015).

2.2 | Territorial intrusion tests

From 2010 onwards, each male was subjected to four simulated territorial intrusions during its first breeding attempt (defined as attempts initiated within 30 days after the first egg of the year in all plots found; Nicolaus, Both, Ubels, Edelaar, & Tinbergen, 2009). Two tests were performed during egg-laying (1 and 3 days after the first egg was observed) and two during incubation (1 and 3 days after clutch incubation was confirmed). All tests were conducted between 7h00 a.m. and 12h00 p.m.; the specific time was semi-randomly assigned, that is the exact test time was not randomly predefined, but depended on working hours, duration and location of preceding tests. The test consisted of both a visual (in the form of a taxidermic model of a male great tit) and an acoustic stimulus (in form of a playback of a great tit song). The model and speaker (2010–2016: Samsung U5 Digital Audio Player connected to a Radioshack Mini Amplifier; 2017: Foxpro Shockwave speakers) were placed 1 m in front of the subject's nest box. Following previous studies (Derryberry, 2007; Logue & Gammon, 2004; Searcy, Anderson, & Nowicki, 2006), the speaker was placed on the ground, in part because great tits often engage in conflicts on the ground (personal observation; Falls, Krebs, & McGregor, 1982), while the model was placed on a 1.2 m wooden pole for visibility. Model and playback were chosen randomly from an available set of 23 models and 34 playbacks. Song stimuli were

either recordings of great tits of German and Dutch populations from Xeno-Canto (see http://www.xeno-canto.org/) or local great tits recorded outside our study areas before the breeding season 2017. Playbacks were not standardised to contain the same number of songs or to have the same overall length, but rather represented natural singing behaviour and variation within song lengths and rates. Following the onset of a focal test, that is when the male entered a 15-m radius (horizontal) around the nest box, we recorded the focal male's behaviour for a period of 3 min. Considering that the closest neighbours within our plots were usually breeding within 50 m of distance, this radius was used to ensure that any bird scored was in fact the inhabitant of the nest box the test was performed at, which observations of colour-banded birds confirm. Subjects not arriving within 15 min or not entering the radius were scored non-responsive. The observer, positioned at a distance of 15 m from the nest box, counted the number of alarms and songs and estimated the minimum distance to the model ("approach distance"); we have previously shown that the latter behaviour represents an appropriate proxy for willingness to engage in physical attacks (Araya-Ajoy & Dingemanse, 2014). Songs were defined as longer and more complex vocalisations containing repeated sequences of notes. All vocalisations not categorised as songs, were summarised as alarms, defined by short length, simplicity compared with songs, and a monosyllabic structure (Marler & Slabbekoorn, 2004). All observers were thoroughly trained to reliably spot and sex great tits, and categorise and count male vocalisations. For further details on the test procedure, see Araya-Ajoy and Dingemanse (2014, 2017).

2.3 | Temperature measurements

Both night temperature (Garson & Hunter, 1979; Reid, 1987) and ambient temperature (Garson & Hunter, 1979; Thomas, 1999) have been shown to predict song duration and rate; however, these two temperature variables are highly correlated (Garson & Hunter, 1979; Naguib et al., 2019); their respective effects could be teased apart because of the large sample size of this study. Effects of both variables were modelled to assess temperature effects on song rates. We downloaded hourly temperatures for each day from the weather station in Rothenfeld (47°58024″N, 11°13024″E; Agrarmeteorologie Bayern, www.lfl-design3.bayern.de/agm/).

To evaluate whether temperatures within our study area differed substantially between populations and nest boxes, iButton temperature loggers (Thermochron iButton, iButtonLink Technology) were placed on all occupied nest boxes in the breeding season 2017. The loggers were placed on the outside bottom of the nest boxes and measured temperatures during the breeding season in a 30-min interval. All iButtons were tested afterwards in a controlled and common environment to ensure that differences between loggers were not due to measurement errors caused by malfunctions. After correcting for potential deviations, the collected temperature data were analysed using mixed-effect models, to examine the sources of variation in temperatures (see Table S1). Random intercepts were thus

fitted for nest box (n = 201) and plot (n = 12) to account for spatial differences in temperatures, day (n = 65) and time of day (n = 1,440) to account for temporal temperature patterns, cardinal direction of each nest box (alignment of the nest box n = 8) and iButton ID (n = 200) to account for repeated measurements (i.e. pseudo-replication). This analysis showed that in our study area temperatures did not differ substantially among plots or nest boxes (see Table S1) and that temperatures within the plots were highly correlated with the temperatures collected by the weather station (Pearson's product-moment correlation (mean [95% credible interval]: 0.919 [0.919, 0.920]). Minimum and average night temperatures between the day-specific time of sunset and sunrise were collected, but due to the extremely tight correlation between these two proxies for night temperatures (Pearson's product-moment correlation (mean [95% credible intervals]: 0.98 [0.97, 1.00]), we pragmatically performed our analysis using minimum night temperature. Night and current temperature (i.e. temperature measured during the assay) were less tightly correlated (Pearson's product-moment correlation (mean [95% credible intervals]: 0.537 [0.512, 0.560]; we attempted to further lessen the autocorrelation between these two variables in our statistical analyses by expressing minimum night temperature as a deviation from the current temperature during each observation.

2.4 | Statistical analyses

To investigate how temperature affected acoustic responses to intruders, we focused on three traits recorded during the territorial intrusion tests: (a) the number of songs, (b) the number of alarms and (c) the sum of songs and alarms (i.e. vocalisation count). As approach distance covaries with alarming and singing in our populations (Araya-Ajoy & Dingemanse, 2014), we additionally examined 4) the minimum distance to the taxidermic model as a measure of physical aggression. For all analyses, we used univariate general(ised) mixed-effects models, with the aforementioned traits fitted as response variables. We expected a priori that birds tested later during the day had more time to refill energy storages. All models thus fitted current temperature, the difference between current temperature and minimum night temperature, the time (in hours) between sunrise and the test ("time of day"), as well as the two-way-interactions between the two temperature variables and the time from sunrise (both variables were population-mean centred). We also fitted the time until the focal subject entered the test radius (in seconds from the start of the playback) as a covariate to control for any bias that might result from birds responding later being exposed to the playback for longer. Furthermore, to account for previously observed seasonal changes in responses to artificial intruders (Araya-Ajoy & Dingemanse, 2014, 2017), breeding stage (egg-laying vs. incubating) and test sequence (first vs. second test within breeding stage) were added as categorical fixed effects. Random intercepts were fitted for: individual (n = 813) to account for repeated measurements (i.e. pseudo-replication), nest box (n = 501) and plot (n = 12) to account for spatial variation, date (n = 263) and year identity (n = 8) to account for temporal variation (see Figures S1 and S2), observer (n = 52), and playback

song (n = 34) and taxidermic model (n = 23) to account for different responses induced by features of specific playbacks or models. We also fitted random intercepts for the unique combination of plot and year, called "Plot-year" to account for plot-specific year effects (n = 96; see Abbey-Lee et al., 2018; Araya-Ajoy & Dingemanse, 2017; Araya-Ajoy et al., 2016 for further explanation). Models (1), (2) and (3) were parametrised assuming a Poisson error distribution, while in model (4), the response variable (distance) was square-root transformed and modelled assuming Gaussian errors. Tests scored as "non-responsive" were not considered in our analysis. Furthermore, only males of known identity were included in our analyses.

All statistical analyses were performed using R 3.2.4 (R Core Team, 2018). Generalised linear mixed-effects models were applied using the "glmer" function (package lme4; Bates et al., 2015). All non-Gaussian models were tested for overdispersion; if necessary, we fitted an observation-level random effect ("Observation ID" in our statistical tables) to account for it. Model fit was visually assessed based on the distribution of residuals. We used the "sim" function (package arm) to simulate the posterior distributions of the model parameters based on 2,000 simulations (Gelman & Hill, 2006). The statistical significance of fixed effects was inferred from the 95% credible intervals (CI) associated with the mean parameter estimate (β). We consider an effect to be "significant" in the frequentist's sense when the 95% CI did not overlap zero (Nakagawa & Cuthill, 2007) and we describe such results as showing "strong support" for the predictions. For certain analyses, we further compared parameters among predictor variables estimated within the same model; for such cases, we compared the overlap of their 84% CIs as this avoids over-conservative interpretations caused by compilation of modelling error (Han & Dingemanse, 2017; Julious, 2004).

This study was approved by the Regierung Oberbayern (permit number ROB-55.2-2532.Vet_02-17-215) in accordance with the ASAB/ABS Guidelines for the use of animals in research. Our experiments were designed to minimise subject discomfort.

3 | RESULTS

We performed 6,596 simulated territorial intrusions over the course of 8 years (2010–2017). In 4,476 tests (67.9%), the focal male entered the test radius and its behaviour was scored. In 3,387 (75.7%) of these tests, the identity of the focal male was known. These birds responded acoustically in 96.8% of the simulated territorial intrusions (n = 3,278). Singing was observed in 80.6% and alarming in 41.0% of tests with known birds. Behavioural responses without any vocalisations did occur extremely rarely (<1%).

3.1 | Acoustic traits

Birds did not change their vocalisation count in response to any of the examined predictors but arrival time (Table 1). Specifically, birds responding later produced fewer vocalisations (effect of arrival time male: β = −.109, CI = −0.134, −0.083), an effect caused by it producing

TABLE 1 Estimated effect sizes and 95% credible intervals (CIs) for predictors of vocalisation count (n = 3,278), number of songs (n = 3,334), number of alarms (n = 3,318) and minimum distances (n = 3,340) shown by great tits in response to simulated territorial intrusions

Fixed effects	Vocalisation count[a] β (95% CI)	Song rate β (95% CI)	Alarm rate β (95% CI)	Minimum distance[b] β (95% CI)
Intercept[c]	2.919 (2.839, 2.997)	2.055 (1.928, 2.176)	−1.383 (−1.554, −1.209)	0.047 (−0.11, 0.197)
Current temperature (CT)	−0.007 (−0.015, 0.001)	0.023 (0.009, 0.036)	−0.081 (−0.12, −0.041)	0.005 (−0.008, 0.018)
Night temperature (NT)[d]	0.003 (−0.005, 0.01)	0.005 (−0.009, 0.019)	−0.017 (−0.058, 0.023)	0.013 (−0.001, 0.026)
Time of day	−0.01 (−0.037, 0.016)	0.009 (−0.038, 0.053)	−0.205 (−0.358, −0.058)	0.026 (−0.018, 0.071)
Interaction (CT * Time)	−0.001 (−0.008, 0.005)	−0.007 (−0.018, 0.005)	−0.026 (−0.063, 0.01)	0.003 (−0.008, 0.013)
Interaction (NT * Time)	0.004 (−0.003, 0.01)	−0.004 (−0.017, 0.009)	−0.008 (−0.048, 0.034)	0.003 (−0.008, 0.015)
Arrival time male	−0.109 (−0.134, −0.083)	−0.071 (−0.114, −0.026)	−0.164 (−0.306, −0.022)	0.047 (0.005, 0.087)
Breeding context	−0.022 (−0.049, 0.005)	0.198 (0.153, 0.243)	−0.914 (−1.049, −0.776)	0.285 (0.244, 0.329)
Test sequence	−0.012 (−0.039, 0.013)	0.072 (0.029, 0.116)	−0.273 (−0.407, −0.136)	0.062 (0.022, 0.102)
Random effects	σ^2 (95% CI)	σ^2 (95% CI)	σ^2 (95% CI)	σ^2 (95% CI)
Individual	0.042 (0.038, 0.047)	0.179 (0.161, 0.198)	1.344 (1.21, 1.488)	0.248 (0.225, 0.272)
Nest box	0.007 (0.006, 0.008)	0.019 (0.016, 0.023)	0 (0, 0)	0.119 (0.105, 0.135)
Date	0.005 (0.004, 0.006)	0 (0, 0)	0 (0, 0)	0.015 (0.012, 0.017)
Plot-year	0.003 (0.002, 0.004)	0.01 (0.008, 0.013)	0 (0, 0)	0.018 (0.013, 0.024)
Observer	0.031 (0.023, 0.04)	0.058 (0.04, 0.08)	0 (0, 0)	0.074 (0.055, 0.095)
Playback	0 (0, 0.001)	0 (0, 0)	0 (0, 0)	0 (0, 0)
Model	0 (0, 0)	0 (0, 0)	0 (0, 0)	0 (0, 0.001)
Population	0.006 (0.002, 0.012)	0.01 (0.003, 0.019)	0 (0, 0)	0.023 (0.008, 0.043)
Year	0 (0, 0.001)	0.007 (0.002, 0.015)	0 (0, 0)	0.024 (0.006, 0.052)
Residual	0.053 (0.049, 0.057)	0.121 (0.108, 0.136)	1.607 (1.47, 1.746)	1.155 (1.103, 1.211)
Observation ID[e]	0.476 (0.456, 0.495)	1.443 (1.382, 1.502)	10.098 (9.613, 10.593)	–

[a]Sum of the number of songs and calls during a territorial intrusion test.

[b]Minimum approach distance of the focal bird to the dummy during a territorial intrusion test.

[c]Reference category; estimate for average current temperature, average night temperature, average time of day, average arrival time male and for tests during sequence 1 in the egg-laying phase.

[d]Night temperature was expressed as deviation of minimum night temperature from current temperature.

[e]Observation-level random effect to account for overdispersion.

both fewer songs (β = −.071, CI = −0.114, −0.026) and fewer alarm calls (β = −.164, CI = −0.306, −0.022). Birds sang more in warmer conditions (main effect of current temperature β = .023, CI = 0.009, 0.036; Figure 1a), increased song rate over the season (effect of breeding context: β = .198, CI = 0.153, 0.243) and with repeated testing (effect of test sequence: β = .072, CI = 0.029, 0.116), whereas night temperature did not affect singing (main effect of night temperature: β = .005 CI = −0.009, 0.019). The 84% credible intervals did not overlap between the main effects of night versus current temperature (for a rational of comparing 84% CIs between parameters from the same model; see Han & Dingemanse, 2017), implying that their effects were distinct (non-overlapping; effect of current temperature: β = .023, 84% CI = 0.016, 0.030; effect of night temperature: β = .005, 84% CI = −0.002, 0.012). Time of day did not affect how much birds sang (main effect of time

of day: β = .009, CI = −0.038, 0.053; Figure S3a). Opposite to expectations, the effects of current and night temperature were both not a function of time of day: the increase in song rates in warmer conditions was not lessened for tests conducted earlier in the morning (effect of the interaction term current temperature × time: β = −.007, CI = −0.018, 0.005), neither did birds sing more later the day following comparably colder nights (effect of the interaction term night temperature × time: β = −.004, CI = −0.017, 0.009; Table 1).

Though birds sang more (see above), they alarmed less in warmer conditions (main effect of current temperature: β = −.081, CI = −0.12, −0.041; Figure 1b). By contrast, colder nights did not cause a similar pattern (main effect of night temperature: β = −.017 CI = −0.058, 0.023). The 84% CIs of the effects of the two temperature variables did not overlap, implying again that their effects were distinct (main
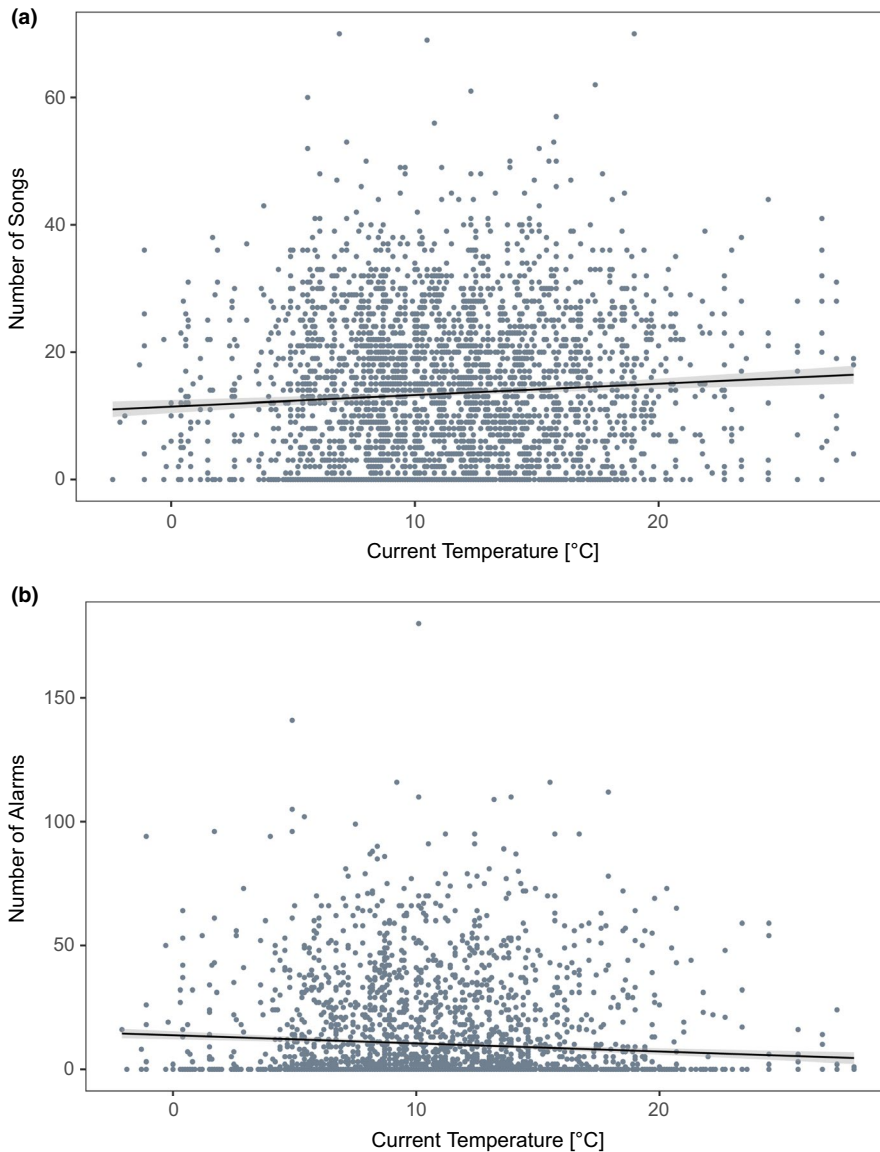
(a)

(b)

FIGURE 1 The effect of current temperature on (a) song (*n* = 3,334) and (b) alarm rate (*n* = 3,318) expressed by territorial great tits during simulated territorial intrusions. Black lines represent regression lines and grey areas 95% confidence intervals. Graph based on raw data [Colour figure can be viewed at wileyonlinelibrary.com]

effect of current temperature: β = −.081, 84% CI = −0.101, −0.062; main effect of night temperature: β = −.017, 84% CI = −0.037, 0.005). Birds alarmed less later in the morning (main effect of time of day: β = −.205, CI = −0.358, −0.058; Figure S3b). Furthermore, alarming decreased from egg-laying to incubation (effect of breeding context: β = −.914, CI = −1.049, −0.776) and between consecutive tests (effect of test sequence: β = −.273, CI = −0.407, −0.136). Time of day did not alter the effects of the two temperature variables on alarming (effect of the interaction current temperature × time: β = −.026, CI = −0.063, 0.01; effect of the interaction night temperature × time: β = −.008, CI = −0.048, 0.034; Table 1).

3.2 | Minimum distance

Neither current nor night temperature nor time of day affected approach distance (Table 1). By contrast, birds increased the distance to which they approached the intruder when responding later (effect

of arrival time male: β = .047, CI = 0.005, 0.087) as well as later in the season (effect of breeding context: β = .285, CI = 0.244, 0.329) and with later test sequences (β = .062, CI = 0.022, 0.102), echoing our earlier analyses (Araya-Ajoy & Dingemanse, 2014, 2017) (Table 1).

4 | DISCUSSION

This study examined the links between temperature and the acoustic response behaviours of territorial great tit males to a male intruder using long-term observational data. We evaluated support for the hypothesis that birds would either shift from singing to alarming in colder conditions, assuming higher energetic costs for singing, or would decrease their overall acoustic output, indicating no difference in energy demands between the two types of vocalisation. Great tits indeed sang less and alarmed more in colder current temperature conditions, but the vocalisation count was not affected. Interestingly, night temperature did not affect acoustic

responsiveness in any trait examined. Follow-up analyses demonstrated that these temperature-related changes in behaviour resulted from both among- and within-year within-individual plasticity in response to macro-temporal (among-year) and micro-temporal (within-year) variation in current temperature (Texts S1 and S2 and Table S2). Contrary to expectations, increasing the time between sunrise and the measurement of their acoustic responsiveness to a simulated intrusion did not affect the impact of current and night temperature for either singing or alarming. Instead, birds generally alarmed less later in the morning. Finally, the level of physical aggression (measured as minimum approach distance to the taxidermic model; Araya-Ajoy & Dingemanse, 2014) was not affected by either current or night temperature. In conclusion, our study shows that great tits prefer to respond to intruders by singing, but that they shift from singing to alarming in colder conditions. This finding supports the idea of alarms being less costly, therefore supporting our Scenario 2.

4.1 | Temperature effects on the acoustic responsiveness to intruders

Consistent with previous studies positing a trade-off between singing and other activities (e.g. foraging), we found a positive effect of current temperature on song rate (Gillooly & Ophir, 2010; Gottlander, 1987; Ophir, Schrader, & Gillooly, 2010; Reid, 1987; Strain & Mumme, 1988). Colder conditions require more energy for thermoregulation (Broggi et al., 2007; Dubois et al., 2016) leading to reduced body mass and fat reserves (Dubois et al., 2016; Moiron, Mathot, & Dingemanse, 2018; Reid, 1987). At the same time, singing is energetically demanding (Eberhardt, 1994; Oberweger & Goller, 2001; Ward & Slater, 2005). Consequently, in colder conditions, when energy reserves are depleted and foraging is difficult, birds might be unable to sustain high song rates. High temperatures could lead to a similar effect, when physiologically demanding behaviours lead to hyperthermia and therefore need to be reduced or stopped (Guillemette et al., 2016). Temperature might thus have a non-linear effect on singing, where the number of songs is reduced under both, cold and warm conditions. However, the lack of a quadratic pattern in our data implied that his mechanism was not supported, perhaps because temperatures during the behavioural tests never exceeded 20°C (see Text S3, Table S3 and Figure S1).

Interestingly, great tits have been shown to respond to an intruder not only by singing but also by alarming (Araya-Ajoy & Dingemanse, 2014). Alarms might offer an alternative to songs, especially when costs of singing increase, because they are by definition shorter and simpler than songs (Marler, 2004), therefore, potentially imposing lower production costs; an assumption that is in line with previous findings based on species comparisons implying that alarming (vs. singing) is associated with relatively smaller energetic costs (Chappell et al., 1995; Horn et al., 1995; Jurisevic et al., 1999). In fact, we found that, contrary to singing, alarm rates decreased with increasing temperatures. Because the vocalisation count was not affected by temperature, this finding indicates a shift from singing to alarming when the environment is colder. Follow-up analyses demonstrated that the observed temperature-related shifts were attributable to within-individual behavioural plasticity (see Texts S1 and S1 and Table S2). Overall, our study thus indicates that, in response to temperature, birds shift their acoustic response behaviour to the shorter and simpler alarms, away from songs, the most frequent and supposedly more efficient signal. We assume such a difference in efficiency, because the majority of birds responded to an intruder with singing highlighting the importance of this behaviour in the context of territory defence (Amrhein & Lerch, 2010). Furthermore, our previous work showed that relatively aggressive birds using alarming as a response to intrusions also gain relatively little extra-pair paternity (Araya-Ajoy et al., 2016), implying that alarming has a different signal value, potentially signalling a lack of reserves required for using song as a response. Furthermore, especially if alarming is associated with lower costs, shifting from singing to alarming might enable birds to save energy reserves for later. Despite the imminent necessity to spend energy to defend one's territory, this extra energy might be needed later, given that colder conditions are likely to persist. Nevertheless, responding with alarming should be preferable to not responding acoustically at all, considering that no response could lead to a territory loss. Indeed, in extremely few cases (3.2%; n = 3,278 observations), the response to an intruder was totally non-acoustic (i.e. birds entering the 15-min radius without vocalising). Thus, when environmental conditions reduce energy available for acoustic communication, individuals seem to shift to cheaper means of acoustic communication, despite thereby signalling reduced competitive ability.

Contrary to previous findings, night temperature did not affect the number of songs or calls (Garson & Hunter, 1979; Thomas, 1999). Furthermore, we also expected birds to replenish energetic shortages after colder nights by increasing early-morning foraging, as we have recently demonstrated for this population during winter (Moiron et al., 2018). This should help mitigate the expected detrimental effects of cold nights on song rate, particularly later during the day. The lack of an interactive effect of night temperature and time of day was therefore unexpected. However, these two findings make sense if night temperature only affects singing around sunrise, that is during the dawn chorus (Reid, 1987; Thomas, 1999). Importantly, all tests in this study were performed later during the day, perhaps providing the birds enough time to replenish their energy reserves. This would also explain why the correlation between night and day temperature in our study was much lower than reported in other studies (Garson & Hunter, 1979; Naguib et al., 2019).

We did not detect a significant interaction between time and current temperature, which, on first sight, contradicts the idea that more time before an intrusion would allow birds to replenish their energy reserves and sing at higher rates (Thomas, 1999). We offer the following explanations. First, given that temperatures in subsequent periods are usually strongly correlated, colder conditions normally persist throughout the day. Therefore, birds may save (re-)filled energy reserves for later to compensate for fast depletion

due to increased metabolic costs and decreased foraging efficiency (Avery & Krebs, 2008). Second, other costly song characteristics (such as song complexity or amplitude) that we did not measure may have increased over the day (Franz & Goller, 2003; but see Ward, Speakman, & Slater, 2003) rather than song rate. Indeed, our finding that birds can plastically alternate between singing and alarming already implies that such changes in "acoustic structure" occur in our populations. This explanation also seems plausible because alarm rates did show time of day effects, potentially because this acoustic signal is relatively fixed in length and structure (Marler, 2004) and thus has little scope for exhibiting plasticity in its structure.

An individual's level of physical aggressiveness, measured as its minimum approach distance, was not affected by temperature. While previous studies have shown positive links between temperature and aggression (González-Gómez, Ricote-Martinez, Razeto-Barry, Cotorás, & Bozinovic, 2011), others showed the opposite (Fisher, Poulin, Todd, & Brigham, 2004); therefore, a null result is not unexpected. Apparently, ecological conditions that remain unquantified moderate the association between aggressiveness and temperature. Nevertheless, given our finding that alarm rates increased after colder nights, we would have expected increased aggressiveness (i.e. shorter minimum distances) as an attempt to compensate for the less efficient transmission of alarm calls (Ryan, 1988). Furthermore, we also expected an effect on approach distance because alarming and minimum distance are negatively correlated both within- and among-individuals in our population (Araya-Ajoy & Dingemanse, 2014). Previously, we hypothesised that these negative within-individual correlations resulted from all three traits responding to variation in the same environmental factor(s) (Araya-Ajoy & Dingemanse, 2014). Our study demonstrates that this is clearly not (fully) the case: variation in temperature only underpins the negative correlation between the two acoustic traits. Thus, the negative covariance with physical aggressiveness (minimum approach distance), indicative of animals approaching closer singing less and alarming more, must be caused by another environmental effect uncorrelated with current temperature. Ultimately, these findings might imply, in contrast to previous suggestions (Araya-Ajoy & Dingemanse, 2014), that singing, alarming and minimum distance may ultimately represent a quasi-independent (rather than a single overarching) functional unit as the acoustic traits are proximately underpinned by more of the same environmental factors. Similarly, our finding that songs are plastically adjusted to within-year changes in temperature, while alarms are not, implies that the two acoustic traits do not vary as a function of the same environmental factors.

5 | CONCLUSION

We analysed effects of temperature on acoustic communication traits using data from more than 6,500 standard territorial intrusion tests conducted over an 8-year period. We demonstrate that birds show phenotypic plasticity in response to within- and among-year changes in temperature, plastically down-regulating singing versus up-regulating alarm rating with decreasing current temperature. Though we did not measure energetic costs of singing and alarming directly, overall, our findings are in line with proposed differences in energetic production costs and signal efficiency between singing and alarming. Furthermore, they are consistent with the notion that great tits switch to assumed energetically cheaper acoustic responses (alarming as opposed to singing) when faced with energetic shortfalls. Consequently, current temperature affects territory-defence strategies. Future research should address whether singing (rather than alarming) is more effective in avoiding territory takeovers following territorial intrusions, whether energetic costs of singing are indeed larger than those for alarming in this species and whether acoustic (vs. non-acoustic) responses are indeed favoured by natural selection.

CONFLICT OF INTEREST
None.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.