



## Nasty neighbours in the Neotropics: seasonal variation in physical and vocal aggression in a montane forest songbird

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Many territorial animals exhibit differences in their responses against intruders based on the level of threat that they pose. The dear enemy effect refers to situations in which territorial aggression is stronger against strangers, and the nasty neighbour effect refers to situations in which territorial aggression is stronger against neighbours. Using playback experiments during prebreeding and postbreeding seasons in a songbird from Neotropical montane forests (grey-browed brushfinch, *Arremon assimilis*), we found that males exhibited the nasty neighbour effect because they responded more aggressively towards neighbours than towards strangers. However, territorial behaviour varied seasonally: (1) aggression towards all intrusions by neighbours were equally strong regardless of the location from which they were perceived prior to reproduction and (2) individuals were more aggressive towards neighbour males when perceived at a different border of their territory to the one they shared during the postbreeding season. We conclude that territorial males respond to neighbours by assessing their threat to paternity and territoriality, and thus modulate their aggressive response based on the season. In contrast, limited responses to strangers suggest that these individuals do not represent a serious threat to males of *A. assimilis* during the seasons we studied them. Territorial aggression against neighbours appears to be a mate-guarding mechanism in this species. Our results differ from those found in temperate zones, where strangers often elicit stronger responses, indicating they may represent a greater threat than neighbours. Additional studies on the behavioural ecology of tropical birds are required to understand the generality of nasty neighbour effects and the drivers of territorial behaviours.

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Many animals hold territories because this guarantees access to resources. However, holding a territory is energetically costly for individuals because of competition with conspecifics or heterospecifics, which may also increase their risk of predation (Rubenstein & Alcock, 2019). Furthermore, food distribution in both space and time determines whether it is feasible to defend a feeding area (Brown, 1964; Duca et al., 2006; Rubenstein & Alcock, 2019). Therefore, individuals must be able to assess when to defend a territory to maximize benefits and reduce costs (Brown, 1964; Carpenter, 1987).

In territorial species, the response of individuals to territorial intrusions may vary depending on whether intruders are known neighbours or strangers (Temeles, 1994). The dear enemy effect (Fisher, 1954) occurs when territorial males exhibit less aggressive

behaviour towards neighbours than towards strangers (Moskát et al., 2017; Temeles, 1994; Weeden & Falls, 1959; Wei et al., 2011). Although both neighbours and strangers might represent a threat to the male's paternity, neighbour individuals with established territories presumably do not pose a threat to a male's own territory to the same degree as strangers, which may potentially usurp it (Temeles, 1994). Thus, identifying which individuals represent a greater immediate threat may reduce the costs of holding a territory (Ydenberg et al., 1988). The dear enemy effect has been reported in a variety of animal taxa including amphibians (Davis, 1987), lizards (Husak & Fox, 2003), primates (Cheney & Seyfarth, 1982), some invertebrates (Fogo et al., 2019), and especially birds (Temeles, 1994; Ydenberg et al., 1988).

Territorial aggression is not always stronger towards stranger individuals, however. The nasty neighbour effect refers to situations in which responses are more intense towards neighbours than towards strangers owing to stronger competition between

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neighbours than between territory holders and strangers (Müller & Manser, 2007; Temeles, 1990). Because neighbours are also territory holders, they have the potential to threaten both the territory and the paternity of another male due to superior physical attributes (Olendorf et al., 2004). Strangers, in contrast, are often lone nonterritorial or wandering individuals (i.e. floaters). If such strangers are of low quality, then it is likely that they would be physically outmatched by the territorial male and its mate, representing only a minor threat to loss of resources (Temeles, 1990). However, not all strangers are of low quality because individuals with a territory may engage in forays seeking to relocate and may thus pose a considerable threat to territory holders (Morton et al., 2000; but see Falls, 1988).

In birds, vocalizations play a major role in territorial defence (Kroodsma & Byers, 1991). Given that neighbours not only share territorial limits but often also vocalizations (Rodríguez-Fuentes et al., 2022; Thomas et al., 2021), birds that display either the dear enemy effect or the nasty neighbour effect are presumably able to distinguish songs of their neighbours from those of strangers (Brooks & Falls, 1975; Stoddard, 1996; but see Botero et al., 2007). However, being able to recognize individual vocalizations may not be sufficient for residents to assess the threat posed by an intruder (Melemis & Falls, 1982; Wiley & Wiley, 1977). Some birds are able to associate a particular song with a particular location in their territory (Amorim et al., 2022; Falls & Brooks, 1975; Stoddard et al., 1991). If a neighbour's song is detected at a different border to the one from where it regularly sings, then territory holders may respond as aggressively to that song as they would to a stranger's song when the dear enemy effect is displayed (Falls & Brooks, 1975). Animals exhibiting the nasty neighbour effect may also discriminate based on location; aggression towards neighbours may be stronger when perceived at the shared territorial border, but neighbours may be treated as strangers when detected at a different border (Müller & Manser, 2007). Individual recognition may also be based on other types of vocalizations (Budka & Osiejuk, 2013; Moskát et al., 2017) or on individual variation within song types (Skierczyński & Osiejuk, 2010).

Studies on the vocal behaviour and territoriality of birds have largely focused on temperate regions. In temperate-zone species, the threat that strangers represent is usually higher than that of neighbours, resulting in the dear enemy effect (Ydenberg et al., 1988). However, a few recent studies have found that aggression towards neighbours can be weaker outside of the breeding season and stronger during the breeding season, while aggression towards strangers remains strong throughout the entire cycle (Jin et al., 2020; Moser-Purdy et al., 2017). Tropical birds differ in many natural history traits from temperate-zone birds, such as holding territories for longer and exhibiting higher adult survivorship and more stable pair bonds (Bard et al., 2002; Busch et al., 2004; Stutchbury & Morton, 2001). Also, breeding seasons in the tropics are longer and more asynchronous than in temperate zones (Fedy & Stutchbury, 2005). Perhaps owing to such differences in natural history, responses to neighbours and strangers in the tropics do not necessarily follow patterns described for temperate-zone species. For example, male spotted antbirds, *Hylophylax naevioides*, respond equally to individuals without showing neighbour–stranger discrimination (Bard et al., 2002), white-bellied antbirds, *Myrmeciza longipes*, respond more aggressively towards any intrusion during the nonbreeding season than during the breeding season (Fedy & Stutchbury, 2005), and rufous-capped warblers, *Basileuterus rufifrons*, respond almost invariably to intrusions throughout the entire year (Demko & Mennill, 2018). Whether the apparent variation in conspecific discrimination existing among tropical birds results from their particular natural history traits or reflects the lack of studies encompassing multiple seasons in which different mechanisms may drive territorial behaviour remains to be assessed.

The grey-browed brushfinch, *Arremon assimilis* (Passerellidae), is a socially monogamous passerine species that holds year-round territories in montane forests of the Andes from Venezuela to Peru (Rising et al., 2011). Territories seem to be stable between years and are occupied by the same individuals, and territorial borders and sizes do not seem to change when pair members are replaced due to natural mortality (Avendaño & Cadena, 2021; Castaño et al., 2019). Territorial turnover is rare and usually involves territorial individuals that either expand their own territory or switch to a different one. Since 2017, we have recorded three cases of territorial turnover involving novel individuals, one which was previously identified as a likely floater (D. A. Gutiérrez-Carrillo & J. E. Avendaño, personal observations). Behavioural interactions are apparently mediated by the use of different song types among males, with individuals sharing more song types with neighbours than with more distant territory holders (Rodríguez-Fuentes et al., 2022). Because song repertoires vary among males (Rodríguez-Fuentes et al., 2022), differences in song types might be used in individual recognition, as in other sparrows (Brooks & Falls, 1975; Stoddard et al., 1990; but see Skierczyński & Osiejuk, 2010).

We conducted field experiments aiming to assess differences in aggressive responses of territorial males of *A. assimilis* to simulated territorial intrusions by neighbours (i.e. familiar individuals) and strangers (i.e. unfamiliar individuals) to test predictions associated with dear enemy and nasty neighbour effects. One would predict a stronger response towards strangers if individuals exhibit the dear enemy effect, whereas a stronger response towards neighbours would be expected under the nasty neighbour effect. We also tested whether the location where intruders are detected has an effect on the response of territorial males. Assuming that individuals are capable of recognizing the identity of intruders, we expected a stronger response to a neighbour's song when it was sung from the wrong territorial border. Finally, we tested for differences in responses between two seasons of the annual cycle to assess whether the perceived level of threat from a given intruder remains constant or varies over time. We expected to find different behavioural responses between seasons because each type of intruder may represent a different degree of threat to the territorial male at different stages in the reproductive cycle.

## METHODS

### Study Site

Our study site was Condominio Floresta de la Sabana (4°48'34.48"N, 74°0'57.78"W), located in the northeastern mountains of Bogotá, Colombia. This reserve comprises a large area of native high-elevation mountain forest combined with disturbed areas including pastures, residential properties and secondary growth mainly consisting of shrubs and *Chusquea* bamboo. Previous studies of *A. assimilis* in this area have focused on two sectors separated by approximately 2 km covering elevations between 2800 m (sector B) and 3200 m (sector A; see Rodríguez-Fuentes et al., 2022). Our study was conducted in sector B, a 1.5 km transect in which territories are distributed nearly continuously (Castaño et al., 2019; Rodríguez-Fuentes et al., 2022). Territories have an average ( $\pm$  SD) area of  $0.52 \pm 0.31$  ha (see Castaño et al., 2019), and the centre of each is separated from others by an average of  $334 \pm 85$  m (see Rodríguez-Fuentes et al., 2022).

### Neighbour–Stranger and Song Selection

We monitored sector B from December 2020 to March 2021 to determine the current boundaries of territories and their corresponding pairs. Nineteen pairs were located during this period, 17 of

which were used for this study. There has been a slight turnover in pair members of some territories since earlier studies, but 13 of the original owners known to be present since 2017 (Castaño et al., 2019) were alive and 12 remained in the same territories during our study. The remaining four pairs were newly detected; we mapped their territories between December 2020 and March 2021 using the same protocol as in Castaño et al. (2019). Fifteen out of the 17 males and their respective females had been previously banded with a combination of three coloured bands allowing their individual identification and the remaining two individuals were identified by the location of their territories, which was constant throughout the duration of the study. We defined neighbouring birds as those sharing an immediate border between their territories. Territorial pairs had an average of 2.7 neighbours (range 1–6 neighbours,  $N = 17$ ). We considered stranger birds as those living in sector A, which do not share any song types with focal males (Rodríguez-Fuentes et al., 2022).

During territorial interactions, both males and females sing solo songs or engage in duets, in which males participate more actively (Avendaño & Cadena, 2021; Rodríguez-Fuentes et al., 2022). Therefore, we employed male solo songs for our experiments. The repertoire of male grey-browed brushfinches consists of  $9.63 \pm 1.91$  song types; males share solo song types among close neighbours within sectors A and B but do not share any song types with males from the other sector (Rodríguez-Fuentes et al., 2022). Because not a single song type was shared among all neighbours of sector B, we chose three common solo song types from this sector to function as the neighbour treatment (Fig. 1a, b, c). For the stranger treatment, we chose one common song type from sector A (Fig. 1d). Because we used only one song type given by strangers, we cannot ascertain whether the responses of birds are characteristic of how they perceive all unfamiliar songs or of how they perceive the particular song type we used. However, this drawback does not affect our goal of assessing recognition between a familiar and an unfamiliar song type and the information it conveys to focal birds about the threat that intruders would represent. We found no significant effects of the song type on any of the responses to experiments described below (Appendix, Table A1), as previously reported in this species (Avendaño & Cadena, 2021). Each individual was exposed to a combination of one of the three neighbour song types and the stranger song type (Moser-Purdy et al., 2017; Stoddard et al., 1991). Because of the spatial arrangement of territories in sector B, some birds shared neighbours,

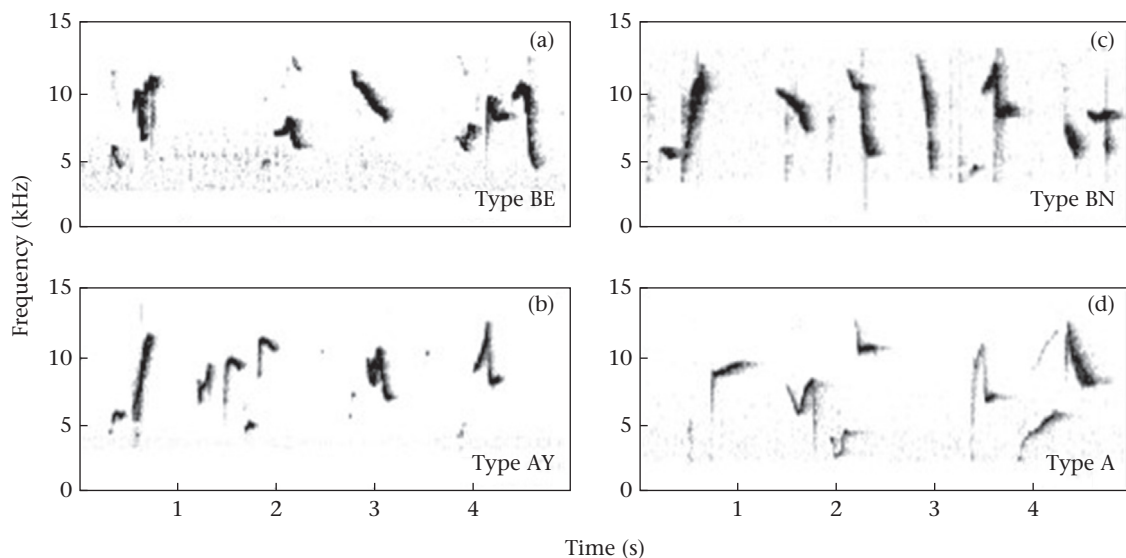
but each combination of neighbour–stranger songs was used for only one individual to avoid pseudoreplication in playback experiments (Courvoisier et al., 2014; Demko & Mennill, 2018).

To build files for playback, we selected recordings of natural solo songs of the three common song types from one current neighbour for each territorial male and selected recordings of the common song type of sector A from four different individuals; recordings were made using a Sennheiser ME 67 shotgun microphone and a TASCAM DR 40 digital recorder, or a LG L70 cellular phone protected inside a water-proof case (WAV format; 44.1 kHz; 16 bits). We used a total of 12 recordings of neighbours and six recordings of strangers given the availability of natural song recordings of the selected song types.

Each playback file consisted of 2 min of silence (preplayback), 2 min of playback and 8 min of postplayback based on response times observed by Avendaño and Cadena (2021). Due to variation in length of the recordings, we chose a 30 s fragment and edited the file to build the 2 min segment of playback. Given that males of *A. assimilis* vocalize by continuously repeating one song type, we decided not to alter the natural pauses between song types to simulate natural singing behaviour as closely as possible. This resulted in files varying in the number of songs delivered. To standardize playback files, we adjusted the pace based on the natural pace measured from natural song (mean  $\pm$  SD =  $0.21 \pm 0.03$  songs/s,  $N = 17$ ). We used Raven Pro 1.6.1 (K. Lisa Yang Center for Conservation Bioacoustics, 2019) to filter background noise below 2000 Hz and edited the files using the software Audacity (Audacity Team, 2021).

#### Experimental Design

In each territory, we set up experimental arenas (2 m radius) in the shared border with the chosen neighbour and in a border in which that particular neighbour would not be expected to be heard given the natural location of territories. Playbacks were reproduced using a MOTOROLA G9 PLUS cellphone connected to a wireless speaker (Bose Soundlink Color II). We set the speaker at a height of ca. 120 cm concealed within the vegetation. All stimuli were played at 80 dB, previously measured with a sound level meter (UNI-T Mini Sound Meter UT353) to simulate the natural amplitude of the species' natural song. To evaluate dear enemy and nasty neighbour effects, as well as individual recognition in this species, each pair



**Figure 1.** Sound spectrograms of the four song types used to build the playback files. (a, b, c) The three common song types from sector B used for the neighbour playback. (d) The common song type from sector A used as the stranger playback. Song type nomenclature is based on Rodríguez-Fuentes et al. (2022).

was exposed to four different treatments: the neighbour's song in the shared border, the stranger's song in the neighbour's shared border, the neighbour's song in the opposite border to the chosen neighbour and the stranger's song in the opposite border to the chosen neighbour. The order in which treatments were presented to each pair was randomized. An observer was concealed at approximately 5 m from the area while recording vocal responses using the same Sennheiser ME 67 shotgun microphone and TASCAM DR 40 digital recorder. Physical responses were dictated to a digital voice recorder (SONY ICD-PX240). Experiments for each pair were separated by at least 48 h. Visibility in our study area was limited by vegetation, so determining the initial position of the focal bird was not possible unless it vocalized. We chose not to use another vocalization (e.g. a call) to attract the bird to the location to avoid altering the response to our treatments. When no response to a particular treatment was detected, either physically or vocally, it was unclear whether this indicated the response of the focal birds or whether the stimulus was not perceived by the focal birds. In such cases, the experiment was repeated immediately. If there was still no response, the experiment was postponed and repeated after the rest of the experiments for the focal pair were concluded. Whenever the corresponding territorial neighbour of the focal pair responded to the treatment, we suspended the experiment and repeated it after the rest of the experiments for the focal pair were completed. All treatments were applied to each pair over a maximum span of 2 weeks (mean  $\pm$  SD = 9.6  $\pm$  2.8 days).

To assess temporal changes in the response of territorial males to simulated intrusions by neighbours and strangers, playback experiments were performed in two different seasons. The first set of experiments was done between 8 March and 15 April 2021, just prior to the breeding season ( $N = 15$  territorial pairs), and the second set between 22 August and 2 October, after the breeding season ( $N = 17$  territorial pairs). In this area, *A. assimilis* exhibits two reproductive peaks during May–August and November–January (Castaño et al., 2023), which coincide with the onset of rains during March–May and September–November (Vargas et al., 2011). However, because of the high asynchrony of breeding among individuals within these peaks and lack of information on the status of individuals, experiments were not performed during breeding seasons. All experiments were performed between 0600 and 1100 hours.

### Territorial Responses

We measured 11 vocal and physical variables or behavioural responses of territorial males (Avendaño & Cadena, 2021; Demko & Mennill, 2018; Moser-Purdy et al., 2017; Moser-Purdy & Mennill, 2016) to our four treatments: (1) latency of response (time taken to show either a vocal or physical response to the vocal stimulus); (2) vocal latency (time taken to start vocalizing in response to the stimulus); (3) latency of approach (time taken to be <2 m from the speaker); (4) distance of closest approach to the speaker (measured with a measuring tape from the base of the speaker to the point where the focal bird was closest to the speaker during the experiment); (5) time spent <2 m from the speaker; (6) movements (number of flights/jumps <2 m from the speaker); (7) total time spent singing; (8) time spent singing <2 m from the speaker; (9) number of songs performed; (10) song rate (calculated based on the number of songs performed throughout the total time spent singing); and (11) number of song types used (based on the repertoire description by Rodríguez-Fuentes et al., 2022).

### Statistical Analysis

To reduce correlated variables describing territorial responses, we first calculated pairwise correlations between all variables

(Appendix, Table A2, Fig. A1) and applied the Kaiser–Meyer–Okin test using the function 'KMO' in the R package 'psych' (Revelle, 2021) until an overall measure of sampling adequacy (MSA) >0.7 was achieved. We were left with three physical variables and four vocal variables (Table 1). To summarize these seven behavioural responses, we used principal component analysis (PCA, 'prcomp' command) to produce composite variables representing aggression scores for each individual (Avendaño & Cadena, 2021; Uy et al., 2009). Because independent variables were measured in different scales, we standardized them using the functions 'scale' and 'center' in the R package 'psych' (Revelle, 2021). We considered variables to be correlated to a specific PC if they had a factor loading with an absolute value of at least 0.4 (Budaev, 2010).

We identified two principal components with an eigenvalue >1 that jointly explained 61.2% of the variance (Table 1). To allow for an easier interpretation of the results, PC1 values were multiplied by  $-1$ . After this, PC1 was positively correlated with physical variables like movements (0.52) and negatively correlated with latency of approach ( $-0.54$ ) and distance of closest approach to the speaker ( $-0.43$ ). PC2 was positively correlated with vocal responses like total time spent singing (0.51), time spent singing <2 m from the speaker (0.41) and number of song types used (0.56) and negatively correlated with vocal latency ( $-0.44$ ). In summary, higher values of PC1 and PC2 described behaviours implying stronger physical or vocal aggression, respectively.

To analyse the effect of each of the treatments on the behavioural responses of territorial males, we performed a linear mixed model (LMM) using the function 'lmer' in the R package 'lme4' (Bates et al., 2015). The model included the composite behavioural response obtained through PCA as the response variable and the experimental treatment as a fixed variable. Time, date, order of experiments, male identity (ID) and recording ID were random variables. Results from each season were analysed separately to observe variation in the response levels to each treatment within each season instead of between them (see Moser-Purdy et al., 2017). All analyses were performed using Rstudio (R Core Team, 2021).

### Ethical Note

Our study adheres to the ASAB/ABS Guidelines for the Use of Animals in Research. It also follows Colombian law regarding the use of animals in scientific research. The research protocol was evaluated and approved by the Comité Institucional de Uso y Cuidado de Animales de Laboratorio (Institutional Committee for the Use and Care of Laboratory Animals) at Universidad de los Andes, Bogotá, Colombia (C.FUA\_21-022). Because our study did not involve capturing or manipulating animals, physical stress was minimum to none. We tested birds every other day to avoid

**Table 1**  
Principal component analysis weights for the two PCs with an eigenvalue >1 and component factor loadings for the PC scores

	PC1	PC2
Eigenvalue	2.68	1.60
% Variance explained	38.35	22.88
Cumulative % variance	38.35	61.23
<b>Behavioural variable</b>		
Latency of approach	<b>-0.54</b>	-0.17
Vocal latency	0.27	<b>-0.44</b>
Distance of closest approach to the speaker	<b>-0.43</b>	-0.12
Movements	<b>0.52</b>	0.10
Total time spent singing	-0.26	<b>0.51</b>
Time spent singing <2 m from the speaker	0.31	<b>0.41</b>
Number of song types used	-0.12	<b>0.56</b>

Values in bold denote the PC on which each variable loaded heavily. PC1 and PC2 represent physical and vocal aggression during simulated intrusions, respectively. PCA analysis was run once for both seasons.

habituation. We observed no adverse effect on the focal birds after exposing them to playback. Focal birds resumed normal foraging behaviour after each playback experiment and were observed exhibiting typical behaviour in their territories after our study was concluded.

## RESULTS

Territorial males of *A. assimilis* differed in their behavioural responses and aggression levels towards simulated intrusions against neighbour and stranger individuals in different seasons (Fig. 2). During the prebreeding season, males did not show a differential physical response (PC1) towards any of the treatments ( $F_{3,11} = 0.10$ ,  $P = 0.96$ ; Table 2, Fig. 2a). However, we found a strong effect of the individual on PC1 values, indicating that the intensity of physical responses varied among birds (Appendix, Table A1). Males exhibited stronger vocal responses (PC2) towards neighbours than towards strangers, regardless of the location from which the song was broadcasted ( $F_{3,11} = 6.16$ ,  $P < 0.01$ ; Table 2, Fig. 2b).

In contrast, during the postbreeding season, territorial males showed a stronger physical response (PC1) towards the neighbour's song on the opposite border compared to the other three treatments ( $F_{1,13} = 5.46$ ,  $P = 0.01$ ; Table 2, Fig. 2c). Males did not show a differential vocal response (PC2) towards any of the treatments during the postbreeding season ( $F_{1,13} = 2.03$ ,  $P = 0.14$ ; Table 2, Fig. 2d).

Results from the models we used to assess responses to treatments based on each of the behavioural variables separately confirmed the patterns we found with PC1 and PC2, with some variables showing clearer effects of treatments corresponding to what we observed in the analyses with the overall behavioural responses as a composite (Table A3).

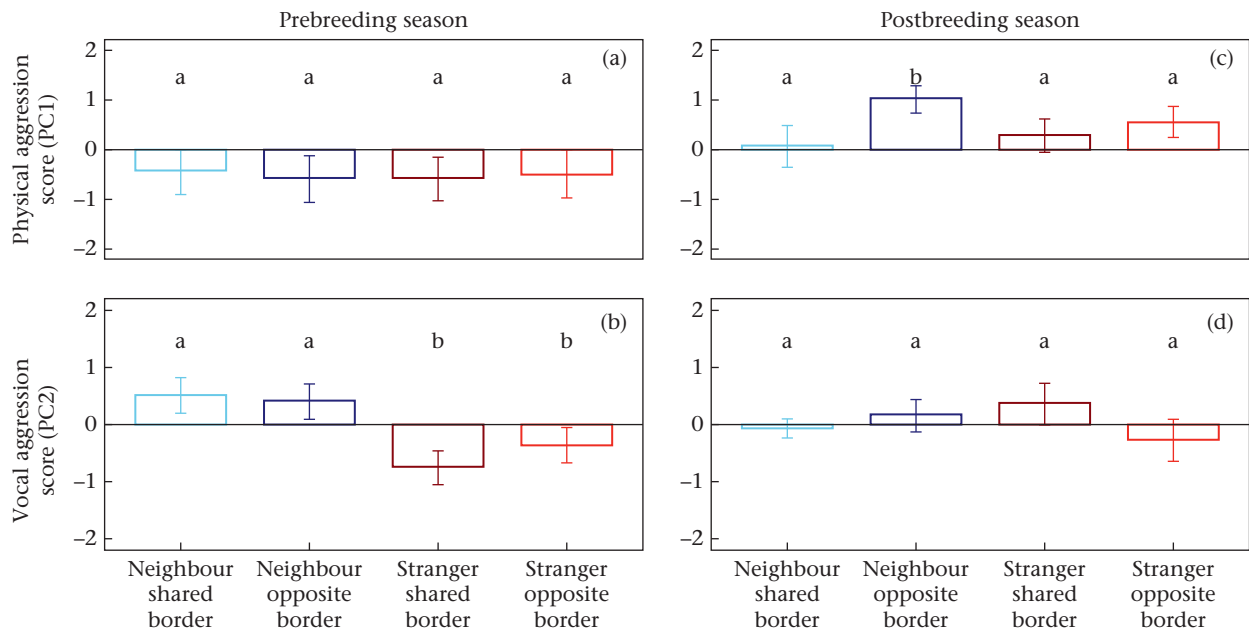
## DISCUSSION

Territorial birds in temperate zones consistently show the dear enemy effect by exhibiting stronger aggressive responses to strangers than to neighbours (Ydenberg et al., 1988). In contrast, the few studies dealing with territorial defence and conspecific

discrimination in tropical species have found varied results (Bard et al., 2002; Demko & Mennill, 2018; Fedy & Stutchbury, 2005). Given that defending a year-round territory (as many tropical birds do) may have different energetic costs than defending it over a limited time frame (as in seasonal temperate zones) and considering that tropical and temperate-zone species differ in multiple life-history attributes (Stutchbury & Morton, 2001), an increased understanding of how tropical species respond to territorial intrusions is important to uncover the social and ecological interactions that influence the demography and spatial ecology of populations (e.g. Mikami & Kawata, 2004). We found that males of *A. assimilis* showed stronger behavioural responses towards neighbours than towards strangers during the prebreeding and postbreeding seasons, but responses during the latter depended on the location from which the neighbour was perceived, being stronger when the neighbour was perceived at a different border to the shared one. These patterns suggest that interactions with neighbours and strangers may pose different threats during different seasons, and that territorial males adjust their responses accordingly.

Our work revealed that individuals of *A. assimilis* likely have the ability to distinguish a neighbour's song from a stranger's song. What is the mechanism allowing individuals to assess the nature of a particular intruder's song? Males of *A. assimilis* share a large portion of their repertoire with their close neighbours but do not share any song types with individuals separated by 2 km (Rodríguez-Fuentes et al., 2022); therefore, the degree and pattern of song sharing may enable individuals to distinguish neighbour songs from stranger songs as documented in other species (Moser-Purdy & Mennill, 2016; Stoddard, 1996; Wei et al., 2011). Furthermore, the behaviour of intruders during territorial contests may allow for individual assessment. Males of *A. assimilis* usually respond to their neighbours' vocalizations by vocalizing themselves and, in some cases, performing song type matching (D. A. Gutiérrez-Carrillo, personal observation), which could reinforce familiarity with them.

Most studies on territorial responses to neighbours and strangers have reported the dear enemy effect, and most have



**Figure 2.** Aggression scores (PC1 and PC2; mean  $\pm$  SE) for territorial males of *A. assimilis* for each of the treatments. Prebreeding season results are shown in the left column and postbreeding season results are shown in the right column. Positive values indicate higher levels of aggression, whereas negative values indicate lower levels of aggression. Different letters above each bar represent significant differences.

**Table 2**  
Results from the linear mixed models for PC1 (physical variables) and PC2 (vocal variables) during the prebreeding season ( $N = 15$ ) and the postbreeding season ( $N = 17$ )

	Value	df	<i>f</i>	<i>P</i>
<b>Prebreeding season (PC1)</b>				
<i>Fixed effect</i>				
Treatment	0.22	3.00	0.10	0.96
<b>Prebreeding season (PC2)</b>				
<i>Fixed effect</i>				
Treatment	5.60	3.00	6.16	<b>&lt;0.01</b>
<i>Post hoc contrasts</i>				
Neighbour/Shared border – Neighbour/Opposite border	<b>Estimate ± SE</b>		<b>t</b>	<b>P</b>
Neighbour/Shared border – Stranger/Shared border	–0.12 ± 0.35		–0.33	0.74
Neighbour/Shared border – Stranger/Opposite border	–1.27 ± 0.35		–3.65	<b>&lt;0.01</b>
Neighbour/Opposite border – Stranger/Shared border	–0.88 ± 0.35		–2.51	<b>0.02</b>
Neighbour/Opposite border – Stranger/Opposite border	–1.16 ± 0.35		–3.32	<b>&lt;0.01</b>
Stranger/Shared border – Stranger/Opposite border	–0.76 ± 0.35		–2.19	<b>0.03</b>
Stranger/Shared border – Stranger/Opposite border	0.39 ± 0.35		1.12	0.27
<b>Postbreeding season (PC1)</b>				
<i>Fixed effect</i>				
Treatment	0.01	3.00	5.46	<b>0.01</b>
<i>Post hoc contrasts</i>				
Neighbour/Shared border – Neighbour/Opposite border	<b>Estimate ± SE</b>		<b>t</b>	<b>P</b>
Neighbour/Shared border – Stranger/Shared border	0.96 ± 0.27		3.60	<b>&lt;0.01</b>
Neighbour/Shared border – Stranger/Opposite border	–0.10 ± 0.33		–0.31	0.76
Neighbour/Opposite border – Stranger/Shared border	0.07 ± 0.32		0.21	0.84
Neighbour/Opposite border – Stranger/Opposite border	–1.06 ± 0.34		–3.11	<b>0.01</b>
Stranger/Shared border – Stranger/Opposite border	–0.90 ± 0.31		–2.93	<b>0.01</b>
Stranger/Shared border – Stranger/Opposite border	0.164 ± 0.28		0.58	0.57
<b>Postbreeding season (PC2)</b>				
<i>Fixed effect</i>				
Treatment	1.12	3.00	2.03	0.14

Post hoc contrasts are shown when the fixed effect was significant ( $P < 0.05$ ). *P* values in bold indicate significant results.

focused in temperate-zone birds (Temeles, 1994). In such cases, neighbours likely represent a lower threat than strangers because the former only represent a threat to the male's paternity, whereas strangers are potentially threatening to paternity as well as territory tenure (Olendorf et al., 2004; Temeles, 1994). Our results suggest that males of *A. assimilis* exhibited the nasty neighbour effect by showing stronger vocal responses towards neighbours than towards strangers. However, this pattern was only clear during experiments conducted during the prebreeding season. The nasty neighbour effect is thought to arise when neighbours pose a stronger threat than strangers due to a high abundance of neighbours that causes strong social competition among them for resources such as territories or mates (Müller & Manser, 2007). This can lead to neighbours not respecting territorial boundaries (Courvoisier et al., 2014; Temeles, 1990).

Our finding of a nasty neighbour effect in *A. assimilis* relates to temporal dynamics in territorial ownership in this species. We have observed very little territorial replacement among males of *A. assimilis* (e.g. some have held their territories for at least 6 years), which could imply strong intraspecific competition to maintain territories for long periods. We have also observed new territory owners alone for some time before a mate appears. In many species, holding a territory is important for a male to find a mate (Courvoisier et al., 2014), and this seems to be the case in *A. assimilis*. The few events of territorial replacement that we have observed mostly involved territorial males that either switched to a new territory or expanded their current one once a territorial male died or disappeared; establishment by nonterritorial birds was rare. This is consistent with findings in other tropical systems in which nonterritorial individuals are either rare or incapable of taking vacant territories (Morton et al., 2000; but see Smith, 1978). Therefore, a conspecific song that is heard from an adjacent territory would most likely come from a territorial, mated male (i.e. a potentially nasty neighbour). The physical threat that a territorial pair could represent during a territorial dispute might explain the stronger aggression towards neighbours (Müller & Manser, 2007; Odom & Omland, 2017).

Another explanation for the stronger responses towards neighbours could be mate guarding. Socially monogamous birds,

such as *A. assimilis*, often exhibit some degree of extrapair paternity (Hill et al., 2011). Males of several species respond strongly towards intruders as a way to avoid extrapair copulations during the breeding season (Akçay et al., 2009; Botero et al., 2007; Moser-Purdy et al., 2017). For example, male red-winged blackbirds, *Agelaius phoeniceus*, assess the physical condition of rivals and respond more aggressively to males that are more likely to get extrapair copulations (Olendorf et al., 2004). Given the proximity to the breeding season during our experiments, males of *A. assimilis* might have been guarding their mates against potential rivals once reproduction began. Neighbours are more likely to be involved in extrapair matings when competition among neighbours is higher than it is among strangers (Schrading et al., 2010) as our results suggest. Therefore, although the frequency of extrapair copulations remains to be studied in this system, we hypothesize that aggressive interactions with neighbours in *A. assimilis* might also function as a mate-guarding strategy during the prebreeding season.

During the prebreeding season, vocalizations were the response that evidenced neighbour–stranger discrimination in *A. assimilis*. All individuals vocalized in response to all treatments, but their responses were stronger towards their neighbours, potentially due to strong competition with them. Prior to building the nest and laying the clutch, competition for territories and resources is expected to be at its highest (Fedy & Stutchbury, 2005). Males of *A. assimilis* vocalize to defend their territory (Avendaño & Cadena, 2021), and song is likely to be an honest predictor of aggressive behaviour as in other songbird species (Searcy et al., 2014). Because vocalizations may also induce the reproductive state in females as in other bird species (Amrhein et al., 2008), males of *A. assimilis* might sing to guard their mates against potential rivals as well as to stimulate them to reproduce.

In contrast to vocal responses, physical responses did not vary based on the treatment during the prebreeding season but depended mostly on the identity of the territorial male. In addition to responding with song, some individuals displayed a physical response to our intrusion experiments; these individuals responded equally towards neighbours and strangers. Physical condition could determine whether an individual is physically aggressive

towards a rival, but because condition and territory size are unrelated in *A. assimilis* (Castaño et al., 2019), condition is likely not a factor influencing territory holding and defence. A more plausible explanation of our finding that only some individuals responded physically is that some birds are naturally more aggressive than others, as found in previously simulated territorial intrusions (Avendaño & Cadena, 2021). Thus, personality traits may affect aggressive signalling strategies as reported in other sparrow systems (Akçay et al., 2013).

The type of stimulus (neighbour or stranger) that elicited stronger aggression and the response that evidenced neighbour–stranger discrimination differed between seasons. Specifically, during the postbreeding season, males of *A. assimilis* showed a greater number of movements and other physical reactions towards neighbours when these were detected on a territorial border that did not match the shared one. Responses to neighbours on a different border were significantly stronger than responses to both treatments involving strangers. Responses towards the neighbour in the shared border and towards both treatments involving strangers were weak and not significantly different from each other. Such behavioural responses do not match a strict nasty neighbour effect, in which aggression is stronger against neighbours when detected at the shared border (Müller & Manser, 2007). Once *A. assimilis* breeds, neighbours are no longer a threat to a male's paternity, and the only threat that remains would be that of territory loss. Hearing the neighbour's song from a border different from the shared one might therefore be interpreted as a territorial challenge (Falls & Brooks, 1975; Godard, 1993). In some cases, birds are able to discriminate the neighbour's song coming from different points by associating a specific vocalization with a specific location; when animals exhibit the dear enemy effect, neighbours are treated as aggressively as strangers when their vocalizations come from a different location than the shared border (Davis, 1987; Falls & Brooks, 1975; Husak & Fox, 2003; Stoddard et al., 1991). Males of *A. assimilis* seem to be capable of making this type of recognition with their neighbours, which could further explain the variation in aggression depending on where they vocalize as revealed by our experiments. Given that many *A. assimilis* pairs shared territorial borders with more than one territorial pair, our results suggest that males from *A. assimilis* could potentially recognize the identity of their neighbours, but further studies are required to understand the mechanism that underlies neighbour recognition.

Contrary to the prebreeding season, the responses that evidenced neighbour–stranger discrimination after the breeding season were physical instead of vocal. Physical responses are indicators of aggression in birds such as song sparrows, *Melospiza melodia* (Moser-Purdy et al., 2017), but in the case of *A. assimilis*, they might also be interpreted as search behaviour, as we did not employ taxidermic mounts to create a visual stimulus as well (see Avendaño & Cadena, 2021). We have not observed neighbours occupying a different territorial border to the shared one; therefore, neighbours are not expected to be heard from any other location. Given that the breeding season has already finished and extrapair paternity should no longer be a threat, detecting a neighbour's song coming from a different territorial border might incite the territorial male to search for the source of the vocalization, leading to the higher number of physical responses that we observed. The strong vocal responses to neighbours during the prebreeding season and not the postbreeding season support the idea that vocalizations do serve as a mate-guarding strategy during the prebreeding season.

Our results from both seasons indicating limited responses to strangers suggest that strangers do not play a significant role in territorial disputes with resident males, a pattern observed in other tropical birds (Busch et al., 2004; Morton et al., 2000). Stranger individuals in other systems that display the nasty neighbour effect tend to be floaters that do not represent a threat to territorial

individuals due to being outnumbered (Müller & Manser, 2007). Floaters are present in our study site but these tend to exhibit inconspicuous behaviour and to not vocalize or respond to vocalizations of territorial individuals. Therefore, we believe floaters and strangers are not equivalent in this system. An alternative explanation for lower aggression towards strangers could relate to the dispersal behaviour of our study species. We hypothesize that individuals do not settle far away from their sector of origin and, therefore, do not sing differently from their neighbours. If this is the case, then territorial individuals may not encounter strangers often enough to be able to recognize them as threats. Future studies should focus on dispersal in the grey-browed brushfinch to better understand how often might individuals partake in vocal exchanges with strangers.

## Conclusions

We found that territorial males of *A. assimilis* changed their behavioural responses against intruders based on the season. During the prebreeding season, males displayed a nasty neighbour effect by responding more aggressively towards intruding neighbours regardless of where they sang. During the postbreeding season, males responded more aggressively to neighbours when heard at a territorial border different to the one they shared, suggesting that individuals are able to associate a specific song to a specific location. Strangers do not seem to pose a high threat at any time because responses towards them were low during both seasons. Our results suggest that neighbours pose different types of threats depending on the season, leading resident males to adjust their territorial responses. More broadly, our work provides evidence that behavioural patterns associated with territorial defence against different intruders may differ between tropical and temperate-zone birds: males of *A. assimilis* were more aggressive towards neighbours whereas males of species of birds from the temperate-zone tend to be more aggressive towards strangers. Our research highlights the importance of studying the effect of natural history traits of tropical birds to uncover the generality and variations in behavioural patterns and phenomena (e.g. dear enemy and nasty neighbour effects), which have mostly been studied in temperate regions.

## Author Contributions

**Daniel Alejandro Gutiérrez-Carrillo:** Conceptualization, Methodology, Formal analysis, Investigation, Writing – Original draft. **Carlos Daniel Cadena:** Conceptualization, Writing – Review & Editing. **Juliana Rodríguez-Fuentes:** Methodology, Writing: Review & Editing. **Jorge Enrique Avendaño:** Conceptualization, Methodology, Formal analysis, Writing: Review & Editing.

## Data Availability

The raw data for this study is available from the Dryad repository: <https://datadryad.org/stash/share/w3DEjHpDfgluajqHBRen0-xszkKg-vIMThBVFIYcMHI>.

## Declaration of Interest

None.

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**Appendix**

**Table A1**

Fixed and random effects from the linear mixed models for PC1 (physical variables) and PC2 (vocal variables) during the prebreeding season ( $N = 15$ ) and the postbreeding season ( $N = 17$ )

	Value	df	f	P
<b>Prebreeding season (PC1)</b>				
<i>Fixed effect</i>				
Stimulus	0.22	3.00	0.10	0.96
<i>Random effect</i>				
	<b>Variance</b>	<b>SD</b>		
Time	0.00	0.00		
Date	0.00	0.00		
Playback	0.00	0.00		
Individual ID	<b>2.16</b>	<b>1.47</b>		
Song type	0.00	0.00		
Experiment order	0.00	0.06		
Residual	0.73	0.86		
<b>Prebreeding season (PC2)</b>				
<i>Fixed effect</i>				
Stimulus	16.81	3.00	6.16	<b>&lt;0.01</b>
<i>Random effect</i>				
	<b>Variance</b>	<b>SD</b>		
Time	0.00	0.00		
Date	0.00	0.00		
Playback	0.00	0.00		
Individual ID	0.45	0.67		
Song type	0.00	0.00		
Experiment order	0.03	0.16		
Residual	0.91	0.95		
<b>Postbreeding season (PC1)</b>				
<i>Fixed effect</i>				
Stimulus	0.01	3.00	5.46	<b>0.01</b>
<i>Random effect</i>				
	<b>Variance</b>	<b>SD</b>		
Time	0.53	0.73		
Date	0.52	0.72		
Playback	0.09	0.30		
Individual ID	0.66	0.81		
Song type	0.00	0.00		
Experiment order	0.09	0.30		
Residual	0.00	0.02		
<b>Postbreeding season (PC2)</b>				
<i>Fixed effect</i>				
Stimulus	3.36	3.00	2.03	0.14
<i>Random effect</i>				
	<b>Variance</b>	<b>SD</b>		
Time	0.17	0.41		
Date	0.00	0.00		
Playback	0.07	0.26		
Individual ID	0.65	0.80		
Song type	0.00	0.00		
Experiment order	0.07	0.26		
Residual	0.55	0.74		

Significant fixed or random effects are highlighted in bold.

**Table A2**  
Correlation matrix for the 11 variables initially measured for this study

	Latency of response	Latency of approach	Vocal latency	Distance of closest approach to speaker	Time spent <2 m from the speaker	Movements	Total time spent singing	Time spent singing <2 m from the speaker	Number of songs performed	Song rate	Number of song types used
Latency of response	1.00										
Latency of approach	0.10	1.00									
Vocal latency	0.47	-0.28	1.00								
Distance of closest approach to speaker	0.08	0.58	-0.12	1.00							
Time spent <2 m from the speaker	-0.09	-0.72	0.25	-0.44	1.00						
Movements	-0.14	-0.75	0.87	-0.48	0.68	1.00					
Total time spent singing	-0.11	-0.35	1.00	-0.26	0.38	0.93	1.00				
Time spent singing <2 m from the speaker	-0.04	-0.46	0.38	-0.25	1.00	0.13	0.06	1.00			
Number of songs performed	-0.15	-0.35	0.08	-0.07	0.13	1.00	0.93	0.24	1.00		
Song rate	-0.15	-0.20	0.23	-0.27	0.15	0.24	-0.06	1.00	0.19	1.00	
Number of song types used	-0.13	-0.28	0.04	-0.04	0.09	0.41	0.37	0.19	1.00	0.19	1.00

Values indicate the correlation coefficient between the corresponding variables.

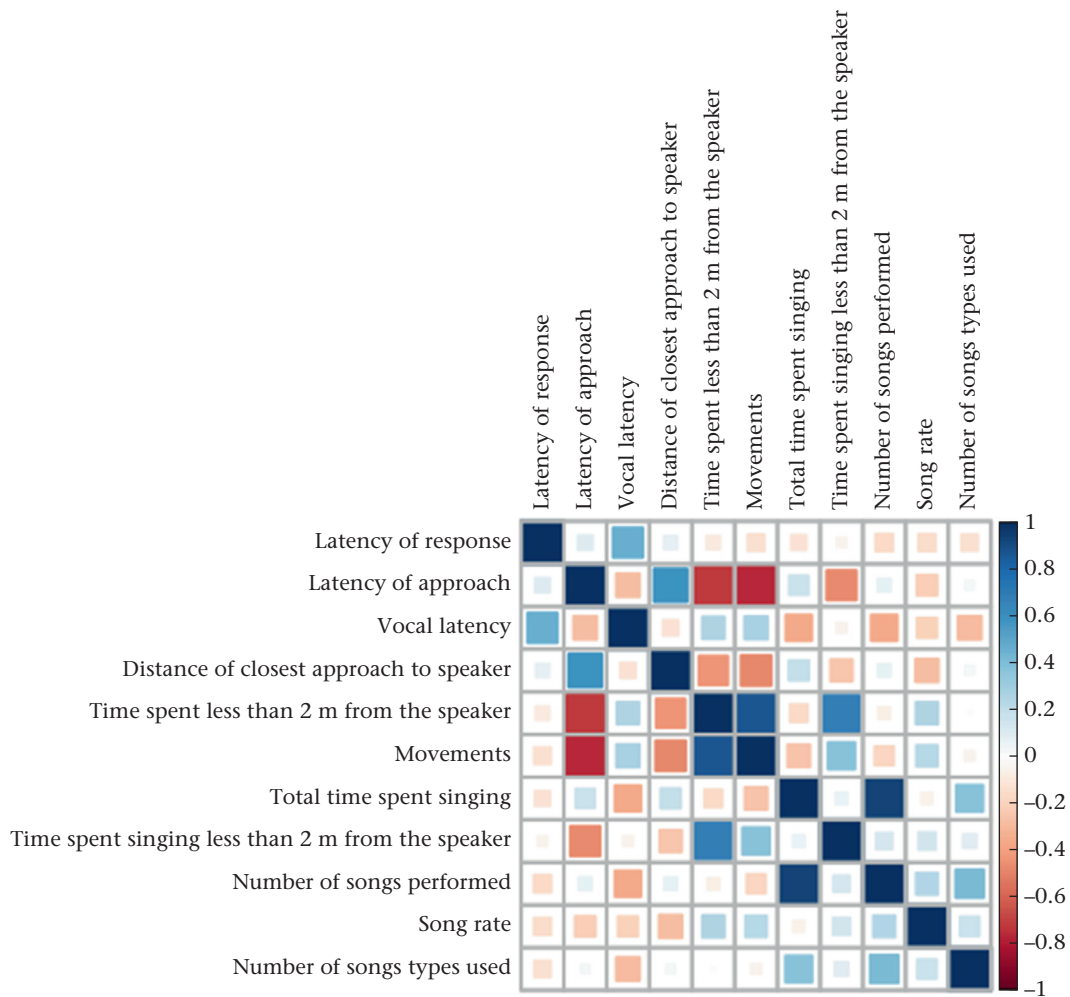
**Table A3**

Results of the linear mixed models for the effect of the treatments as a fixed factor to the seven individual response variables utilized for PCA

Response variable	Value	df	f	P
<b>Prebreeding season</b>				
Latency of approach	5505	3	0.10	0.96
Vocal latency <sup>1</sup>	25 855	3	1.54	0.25
Distance of closest approach to the speaker	2638.9	3	0.09	0.96
Movements	53.16	3	0.49	0.69
Total time spent singing	12 808	3	1.75	0.17
Time spent singing <2 m from the speaker	577.85	3	1.53	0.23
Number of song types used	1.84	3	5.36	<b>&lt;0.01</b>
<b>Postbreeding season</b>				
Latency of approach	66.23	3	2.84	<b>&lt;0.05</b>
Vocal latency	1.11	3	1.31	0.3
Distance of closest approach to the speaker	301 346	3	1.48	0.25
Movements	0.08	3	4.11	<b>0.01</b>
Total time spent singing	19283	3	2.1	0.11
Time spent singing <2 m from the speaker	0.08	3	2.86	0.09
Number of song types used	1.85	3	6.81	<b>&lt;0.01</b>

Results are shown for the prebreeding and postbreeding season separately. Significant effects on the response variables are shown in bold.

<sup>1</sup> Time was removed for vocal latency during the prebreeding season to improve the model's convergence. However, results remained nonsignificant when improving convergence by removing other random factors and by performing the analysis with all the factors included.



**Figure A1.** Correlation plot depicting the strength and directionality of the correlations between the 11 variables initially measured for this study. Blue indicates positive correlations and red indicates negative correlations, with darker colours indicating stronger correlations.