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Shared territorial defence in the suboscine *Aphrastura spinicauda*

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ABSTRACT

Territorial behaviour is an active and typically aggressive behaviour used to defend resources. Here, we investigated the presence of shared territorial defence behaviour during conspecific intrusions in the Thorn-tailed Rayadito (*Aphrastura spinicauda*), a suboscine species that generally does not maintain long-term pair bonds. We found that, compared to females, males displayed more alarm calling during their response, approached closer and were also more physically aggressive towards conspecific intruders. Despite these differences, the defence behaviour of males and females was highly correlated during territorial responses to simulated intruders. To our knowledge, this is the first report of coordinated or joint territorial defence in a South American suboscine that generally only maintains short-term pair bonds.

Introduction

Territorial behaviour involves the active defence of resources in reproductive or feeding territories against conspecifics or heterospecifics (Brown 1964; Verner 1977). The intensity of territoriality may be affected by several factors including the value of the resource (Brown 1964) and social stability (Wingfield *et al.* 1987; Hau *et al.* 2008).

Classically, territory defence is thought to be a trait more often found in males (Brown 1964; Collins 2004). However, females frequently participate in territory defence, with different levels of intensity and coordination with their mates (Morton and Derrickson 1996; Busch *et al.* 2004). Indeed, in socially monogamous breeding pairs, territory defence should have advantages for both sexes (Hall and Peters 2008). Joint territorial behaviour is the cooperative defence of a territory performed by both members of a pair. This behaviour is commonly associated with long-term pair bonds and territories that are defended over the entire year (Slater and Mann 2004; Fedy and Stutchbury 2005). Additionally, when territorial defence is cooperative, then aggressive responses towards a territorial threat should be coordinated (Hall and Peters 2008; Quinard and Cézilly 2012).

Our current understanding of territory defence in birds may be biased because it is derived mainly from temperate species from the northern hemisphere (Hau *et al.* 2008), where oscine passerines dominate. However, in South America, 59% of passerine species are suboscines and behavioural studies have only recently started to increase, with a relative higher proportion in tropical areas. Therefore, we investigated whether joint territorial defence can occur in a suboscine species without long-term pair bonds, living in the temperate southern region of South America.

Methods

Species and study area

The Thorn-tailed Rayadito (*Aphrastura spinicauda*; Furnariidae) is a non-tropical suboscine species that does not appear to maintain pair bonds throughout the year, nor between subsequent breeding seasons (unpublished data, see below). The species forms simple and mixed flocks during the non-breeding season (Vuilleumier 1967; Ippi and Trejo 2003). They require cavities for nesting, a valuable and relatively scarce breeding resource (Tomasevic and Estades 2006; Cornelius *et al.* 2008). Rayaditos are endemic to the temperate austral forests of Chile and Argentina from Fray Jorge National Park (30° S) in central Chile to the sub-Antarctic forests of Cape Horn (56° S; Remsen

Table 1. Factor loadings of the two PCAs showing the principal components for the nine variables of territorial behaviour. The factor loadings used to name the PCs are in bold.

	PC1	PC2
Eigenvalues	4.92	1.66
% of variance	54.61	18.41
Factor loadings		
Proportion of time out of sight	**−0.897**	−0.067
Average distance	**−0.935**	−0.190
Minimum distance	**−0.809**	−0.086
Proportion of time spent around 2 m	**0.822**	0.291
Pecking rate	0.149	**0.836**
Movement rate	**0.707**	0.499
Proportion of time alarming	**0.881**	−0.011
Proportion of time of repetitive trills	−0.027	0.652
Loud trills rate	0.260	**0.832**

PC1 = alarm/approaching; PC2 = physical aggressiveness.

2003). In order to avoid making general conclusions regarding the territorial behaviour of this species based on a single population, we sampled three populations spanning a large portion of the rayaditos' latitudinal distribution. Field work was conducted during the austral spring and summer (September–January) on Cerro Manquehue (33° S–70° W), Chiloé Island (41° S–73° W), and Navarino Island (55° S–67° W).

We installed 600 nest boxes in these populations (300 in Chiloé, 200 in Navarino and 100 in Manquehue). The proportion of nest boxes used by rayaditos per year per site varied from 6 to 32% (supplementary material, Table 1). For details about the features of the nest boxes see Moreno et al. (2005) and for details of the three study areas see Ippi et al. (2011).

Nest boxes were monitored on a weekly basis, from September to mid-January in Chiloé (in 2006) and Manquehue (in 2007), and to December in Navarino (in 2007) and Chiloé (in 2007). We captured rayaditos with mist nets and playback, on the date of first egg laying. Each individual was banded with a unique combination of coloured rings and a numbered metal band. We took a small sample (around 40 μl) of blood by brachial venipuncture in order to genetically determine the sex of the subjects because sexes are indistinguishable in the field (Moreno et al. 2007).

In Chiloé, of the 14 individuals recorded nesting over two or more breeding seasons in our nest boxes, between 2003 and 2007, only one pair bred together in two consecutive seasons (Moreno et al. unpublished data). The remaining 12 individuals switched their partners, including 10 in consecutive seasons, and two with 1 or 2 years of interval. We were not able to identify the causes of mate switching. In all cases, rayaditos breeding over multiple years nested in different, but nearby, nest boxes in each year (Moreno and Ippi unpublished data). Additionally, recent data from other populations also indicate that the majority of pairs do not maintain long-term pair bonds (Vásquez unpublished data).

Territorial trials

We conducted simulated territorial intrusion trials with stuffed decoys of an adult male rayadito, and, as controls, male Rufous-collared Sparrows (*Zonotrichia capensis*). This sparrow is an open-cup nesting, principally granivorous passerine of medium size (20–23 g) (López-Calleja 1995). In order to reduce pseudoreplication (Kroodsma et al. 2001), we used three rayaditos and three sparrows, although we could not completely randomise the order of their presentations, as decoys were used concurrently in multiple populations that are separated by large distances.

We placed the decoys on top of each nest box at Navarino and Manquehue, and on a telescopic pole in Chiloé at approximately 0.2 m from the nest box's entrance. This was because nest boxes at Chiloé had a metal bell-like structure above, to prevent mammalian predators from accessing them. All experiments were recorded using video cameras (Panasonic NV-GS 320) coupled with personal observations of activities recorded with a digital audio recorder (Olympus VN-960PC).

During the egg laying period, rayaditos do not visit the nest frequently, thus playback was used to attract them to the nest boxes by placing speakers on the ground below the nest box. We selected repetitive trills of rayaditos of unknown sex (see supplementary materials, and Ippi et al. 2011) and the typical song of the Rufous-collared Sparrow to conduct territorial trials.

In order to reduce the probability of including human-directed behaviour in the observations we waited 2 min after the installation of the decoy before commencing the playback and behavioural recordings. Therefore, trials consisted of 2 min of silence, followed by 5 min of playback, and 5 min of final silence (10 min of observation). To prevent damage to the decoys, all experiments were stopped when physical aggression by focal animals to the decoy exceeded five pecks. In order to investigate whether this action introduced any biases in our analyses, we reanalysed all data with these observations excluded. The results of these analyses did not differ qualitatively from those presented in the Results, except that, when we excluded these observations, we detected no statistically significant sex differences in behaviour (see more details and results within the supplementary material).

We conducted one rayadito (conspecific male) and one sparrow (control male) trial at each nest box

(alternating the first decoy presented in each nest), over 2 successive days, except in cases of bad weather, and commencing on day 2 of the egg laying period (laying period = 5–11 days). Behavioural observations were conducted by one observer positioned close to the nest (S.I., I.L. or W.v.D. previously trained together), but hidden from view (between 8 and 20 m away). All trials were conducted between 6:50 and 13:00 h.

Data analyses

We used JWatcher 1.0 software (Blumstein et al. 2000) to transcribe the recorded behaviour for subsequent statistical analysis. As some trials were terminated before the full 10-min period, we converted response variables to proportions. The dependent variables measured were: proportion of time out of sight, average distance to the decoy (m), minimum distance to the decoy (m), proportion of time spent within 2 m of the decoy, pecking rate (number of times the decoy was pecked, relative to the duration of the trial), movement rate (number of movements including flights, jumps, and flutters (flights with additional flapping movements) relative to the duration of the trials), proportion of time performing alarm calls and repetitive trills, and loud trills rate (see Ippi et al. 2011). Three trials using the sparrow decoy (6.8%, two trials in Navarino and one in Manquehue, n = 44) were removed from the analyses because one or both parents pecked the decoy more than five times during the initial 2-min non-playback period. We included all the remaining experiments in the analyses. In cases where one or both parents did not respond to the stimulus we fixed the average and minimum distances at 20 m (the maximum distance that allows a good detection of birds), and other variables, such as proportion of time alarming, at zero.

Principal component analysis (PCA) was performed on nine behavioural variables that were Varimax rotated with Kaiser normalisation (Kaiser 1958). We transformed the principal component (PC) scores to approximate a gamma distribution (by adding one or two, respectively) for analysis using generalised linear mixed models (GLMMs, Bolker et al. 2009). Interpretation and figures presented here are based on the transformed PC scores. GLMMs included population identity and the nest box identity as random effects to control for repeated sampling from the same population, and from the same nest box. Decoy type, sex, and their two-way interactions were included as fixed effects. We estimated degrees of freedom by the Satterthwaite approximation.

In order to explore the relationship between male and female defence, we conducted Spearman correlations between principal component scores for each sex.

Results

We monitored 44 nests, from nest construction to hatching, and conducted trials in 11 nests in Manquehue, 23 in Chiloé, and 10 in Navarino. We conducted 44 and 41 trials using rayadito and sparrow decoys, respectively, and, because we tested both sexes, we obtained 170 total observations.

General territorial defence behaviour

In all three populations, both members of the focal pair typically responded to the conspecific and control male decoys (in 73% of the trials), although females rarely responded without the presence of their mates (in 5% of the trials; supplementary material, Table 2). Males responded to the stimulus first in 30 trials, females responded first in 23 cases and, in 3 trials, both parents responded simultaneously (pooling conspecific ($n = 32$) and control male ($n = 24$) trials with responses of both parents). Stimuli did not elicit any response of the breeding pair in 13.6% of trials with the rayadito ($n = 44$) and in 19.5% of trials with the control ($n = 41$).

Alarm calls were the most frequently used vocalisation during the trials by both members of the pair. Loud trills were emitted in 10.6% of trials with the rayadito decoy and in 11.8% of trials with the sparrow. Rayaditos used repetitive trills in 17.7% of cases in response to the rayadito male, and 16.5% of cases in response to the control.

Two PCs were extracted explaining 73.02% of the variance (Table 1). Higher positive scores in PC1 corresponded to less distant individuals, with more time spent near the model, more time alarming and a higher movement rate. We therefore interpreted PC1 as alarm and approaching behaviour. PC2 was highly correlated with pecking, and loud trills rates. We thus interpreted PC2 as physical aggressive behaviour.

Alarm and approach responses (PC1) were stronger for males than females (PC1: $F_{1, 119} = 13.14$; $p < 0.001$; Figure 1), and stronger in response to the conspecific than heterospecific decoy ($F_{1, 132} = 0.17$; $p = 0.003$). Differences in PC1 responses to the two decoys were not sex-dependent (interaction: $F_{1, 119} = 2.24$; $p = 0.137$).

On the other hand, for physical aggressiveness (PC2), the interaction between decoy and sex was significant, because males and females differed in their aggressive response towards the conspecific decoy but not the heterospecific decoy ($F_{1, 120} = 4.338$; $p = 0.039$;
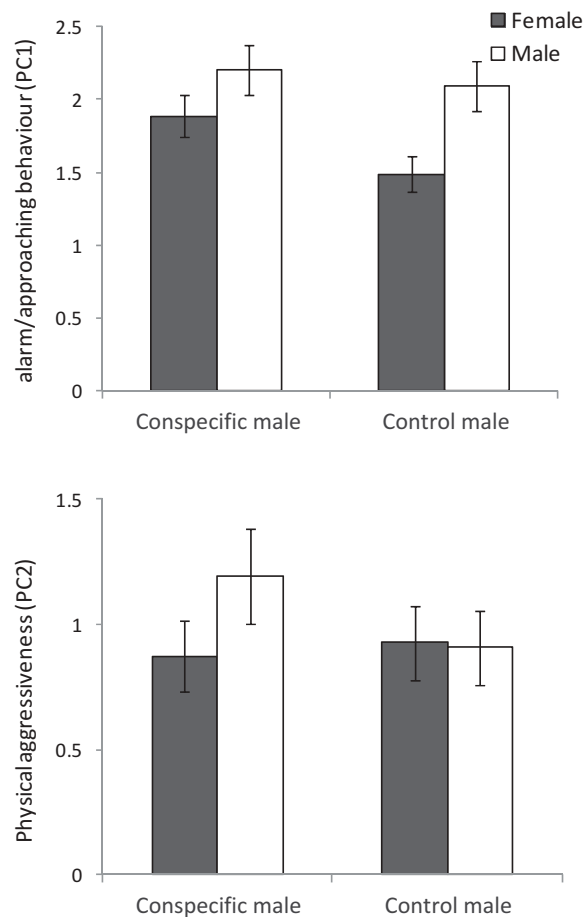
Figure 1. Territorial defence of males and females of the Thorn-tailed Rayadito during the laying period in response to decoy conspecific or controls.. Shown are the alarm/approaching behaviour (PC1) and physical aggressiveness (PC2). Error bars represent standard errors.

Figure 1). Overall, however, physical aggressiveness did not vary with decoy identity ($F_{1, 135} = 1.709$; $p = 0.193$) and sex of focal bird (PC2: $F_{1, 120} = 3.30$; $p = 0.072$). The percentage of individuals that pecked the decoys was moderately low: 9.8% of females and 19.5% of males pecked the control while the 15.9% of females and 29.6% of the males pecked the rayadito.

Territorial behaviour of males and females was correlated for alarm and approach response (PC1; rayadito: Spearman's rho = 0.627; $P < 0.001$; $n = 44$; control: rho = 0.526; $P < 0.001$; $n = 41$) and for physical aggressiveness (PC2; rayadito: rho = 0.327; $P = 0.030$; control: rho = 0.755; $P < 0.001$).

Discussion

Thorn-tailed Rayaditos displayed more non-physical aggression (alarm and approaching) towards the conspecific male than towards the control. The intensity of physical aggression towards the two different intruders depended on the rayadito's sex: females maintained the same level of physical aggressiveness towards the conspecific and control male, while males were more aggressive towards the conspecific intruder. Greater male aggression has been described in many passerine species (e.g. Duckworth 2006), especially in response to male intruders (e.g. Fedy and Stutchbury 2005). Rayadito males also displayed more intense defence than females in response to other threatening stimuli such as predators during breeding (Ippi et al. 2013). These differences between sexes could be partially explained by the larger body size of males (Moreno et al. 2007), or by stronger sexual selection on males (Fedy and Stutchbury 2005). This is despite males and females sharing nest construction, incubation and feeding of nestling (Moreno et al. 2007).

Intrasexual aggressiveness during territorial encounters is common amongst males (Morton and Derrickson 1996). However, female birds often play a role in territory defence (Langmore 1998; Fedy and Stutchbury 2005), sometimes in tight coordination with their mates. Although we cannot be entirely certain that the trills were of male origin, rayadito females displayed physical aggression towards male

intruders and, in addition, male and female defence behaviour was positively correlated, suggesting joint territorial defence. Joint territorial defence may result from cooperation in the defence of a valuable shared resource (Bossema and Benus 1985; Hall and Peters 2008), or to reinforce pair bonds (Hall 2000). This cooperative behaviour has been described in birds with long-term pair bonds (Bossema and Benus 1985; van den Heuvel *et al.* 2014), which in turn also appears to be more common in tropical birds (e.g. Quinard and Cézilly 2012; Koloff and Mennill 2013), where environmental stability is greater. To our knowledge, rayaditos normally do not form long-term pair bonds. However, rayaditos form flocks during the non-breeding season, and no information exists about whether breeding pairs maintain some bonds during this period. Our results suggest that joint territorial defence could be advantageous even when mates and territories are not maintained during the entire year, or between consecutive years. These benefits could be associated with the presence of a valuable breeding resource, such as natural cavities, which could be particularly valuable in the logged and fragmented forests that the species regularly inhabits (Quilodrán *et al.* 2012).

This study found that territorial defence in rayaditos was highly coordinated between the sexes during the laying period, despite the virtual lack of long-term pair bonds. To our knowledge, there is no previous information suggesting that cooperative territoriality can be advantageous in birds with short-term pair bonds.

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