



Strong asymmetric interspecific aggression between two sympatric New Guinean robins

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Interspecific aggression is predicted to be common in diverse tropical avifaunas but is seldom tested experimentally. I conducted two playback experiments to measure interspecific aggression between two sympatric Australo-Papuan robin species that inhabit the understorey of montane New Guinean forests: Slaty Robin *Peneothello cyanus* and Ashy Robin *Heteromyias albispecularis*. The first experiment, at a location where both species were present, demonstrated strong asymmetric interspecific aggression; the larger Ashy Robin responded as aggressively to Slaty Robin playback as to conspecific playback, but Slaty Robins did not respond to Ashy Robin playback. In contrast, in the second experiment, which took place at a nearby site where Slaty Robins were absent, Ashy Robins did not respond aggressively to Slaty Robin playback. Thus, Ashy Robin interspecific aggression appears to be a learned response to the presence of Slaty Robins, and may reflect resource competition between these two sympatric species.

Keywords: Biotic interaction, competition, elevational gradient, Melanesia, playback experiments, tropical birds.

Interspecific aggression is an important component of direct interspecific competition in animals that can influence species' distributions and abundances (Peiman & Robinson 2010, Grether *et al.* 2013). Interspecific aggression is particularly well documented in territorial birds (Dhondt 2011) and has been predicted to be an important mechanism structuring community assembly of diverse tropical avifaunas (Terborgh & Weske 1975, Diamond 1986, Robinson & Terborgh 1995, Jankowski *et al.* 2010). When present, interspecific aggression can represent either misdirected intraspecific aggression ('mistaken identity'; Murray 1971, Wolfenden *et al.* 2015), an evolved response to interspecific interference competition, or a learned response to the presence of a heterospecific. Typically, interspecific aggression between two species is asymmetric, with the more aggressive species generally behaviourally dominant (Robinson & Terborgh 1995, Martin & Martin 2001, but see McEntee 2014).

In this study, I used reciprocal playback experiments to measure interspecific aggression between

two species of Australo-Papuan robins that are broadly similar in their ecology (i.e. they are both understorey insectivores) and widely sympatric in New Guinean montane forests – Slaty Robin *Peneothello cyanus* and Ashy Robin *Heteromyias albispecularis* (Croxall 1977, Boles 2007). Ecologically similar New Guinean passerines, including robins, seldom occur in sympatry in New Guinea (Pratt & Beehler 2014) and these patterns led Diamond (1973, 1986) to suggest that interspecific competition mediated by interspecific aggression helps structure New Guinean passerine communities. This expectation predicts that confamilial species with overlapping foraging niches display interspecific aggression, but this prediction has yet to be experimentally tested. I therefore conducted two field experiments to measure interspecific aggression between Ashy and Slaty Robins. First, I conducted reciprocal playback experiments at a site where both species were common. Because larger species are typically behaviourally dominant (Freshwater *et al.* 2014, but see Martin & Ghalambor 2014) and Ashy Robins are markedly larger than Slaty Robins, I predicted that aggressive responses by Ashy Robins towards playback of

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Figure 1. Slaty Robin *Peneothello cyanus* (left) and Ashy Robin *Heteromyias albispecularis* (right) are common understorey species found in New Guinean montane forests. Photos: B. G. Freeman.

Slaty Robins should exceed aggressive responses by Slaty Robins in response to Ashy Robin playback. Secondly, I conducted further playback experiments at a second site where Slaty Robins were absent. If interspecific aggression is a learned response to a heterospecific, it should occur only in the presence of the heterospecific. I compared responses of Ashy Robins between the two sites (with and without Slaty Robins) to test this prediction.

METHODS

Study site and focal species

Fieldwork took place in the YUS Conservation Area (named after the Yopno, Urawa and Som rivers; coordinates: 6.01°S, 146.83°E), Morobe Province, on the Huon Peninsula in northeastern Papua New Guinea. The first playback experiment took place in June–July 2011 along a ridgeline of primary forest (ridgeline site). Ashy and Slaty Robins were both common at the ridgeline site between 1500 and 2500 m, with an average of >10 individuals captured in mist-net surveys at single elevations within this zone (see Freeman *et al.* 2013 for further details on survey methods). I performed 23 playback experiments on Ashy Robin territories (from 1539 to 2375 m) and 20 on Slaty Robin territories (from 1659 to 2455 m) at this site. Other understorey robin species present in YUS were parapatrically distributed along the elevational gradient and occurred at lower (White-eyed Robin *Pachycephalopsis poliosoma*) or higher (White-winged Robin *Peneothello sigillatus*) elevations (B.G.F. unpubl. data). The second playback experiment took place in May 2012 at a site within YUS located in the middle of a west-facing slope at 2500–2600 m at a distance of 3.5 km

from the ridge site (coordinates: 6.07°S, 146.85°E). Slaty Robins were neither mist-netted nor detected during fieldwork at this site. I performed nine playback experiments on Ashy Robin territories at this 'Ashy-only' site to measure Ashy Robin response to Slaty Robin playback at a site where Ashy Robins were not interacting with Slaty Robins during fieldwork (although Slaty Robins were present near the 'Ashy-only' site at lower elevations, below approximately 2300 m).

While broadly similar in their natural history (Boles 2007), Ashy Robins are larger and approximately 40% heavier than Slaty Robins (35 g compared with 25 g, B.G.F. unpubl. data) and tend to forage on the ground more than Slaty Robins (respectively, 75% and 35% of foraging bouts on the ground; Croxall 1977). Ashy and Slaty Robins are highly divergent in both plumage (Fig. 1) and voice. The typical song of Ashy Robins is a long series of modulated whistles, whereas Slaty Robins have a large repertoire, their typical song being a brief burst of chattering notes (compare representative recordings of Ashy and Slaty Robins at <http://macaulaylibrary.org/audio/166954> and <http://macaulaylibrary.org/audio/167014>).

Playback experiments

I recorded natural vocalizations of singing Ashy ($n = 14$) and Slaty Robins ($n = 11$) not involved in interactions with neighbours using a Marantz PMD661 Recorder and a Sennheiser ME 70 directional microphone (44.1-kHz sampling rate, 16-bit encoding, WAV files). Recordings have been archived at the Macaulay Library of Natural Sounds at the Cornell Laboratory of Ornithology (Ithaca, NY, USA). To minimize pseudoreplication (Kroodsma 1989), I randomly selected recordings

from the bank of previously recorded songs to use in playback experiments.

I found territories of both robin species by searching for singing individuals, and marked the location of singing individuals with an eTrex GPS unit. I considered the approximate location of a singing individual to fall within that individual's territory and later conducted playback experiments by placing a Pignose portable amplifier at the previously marked site. This method is not sufficient to identify territory boundaries rigorously, but is a reasonable protocol for rapidly identifying locations for future playback experiments. The speaker was connected to an iPod by a 20-m audio cable, allowing me to hide behind vegetation approximately 15 m distant from the speaker during playback experiments. I completed playback experiments between 06:15 h and 13:00 h, avoiding periods of moderate or heavy rain.

Playback experiments contained three treatments – control, conspecific and heterospecific. Each treatment consisted of 3 min of playback followed by 5 min of behavioural observation. The control was always performed first and consisted of locally recorded songs of either Sclater's Whistler *Pachycephala soror* ($n = 5$ recordings) or Regent Whistler *Pachycephala schlegelii* ($n = 6$ recordings) depending on the elevation of the robin territory (Regent Whistlers replace Sclater's Whistlers above approximately 1750 m in YUS). Whistlers are common, vocally conspicuous, mid-storey insectivores unlikely to compete with either robin species due to their differences in foraging strata and foraging behaviour (Pratt & Beehler 2014). I then presented conspecific and heterospecific treatments, with their order systematically alternated between experiments.

I measured three behavioural responses to playback for all treatments: closest approach to speaker (m), latency to approach speaker (s) and latency to vocal response (s) (Class & Moore 2010, Janowski *et al.* 2010). Both robin species, and especially the Ashy Robin, are shy (Boles 2007) and in no cases did I see an individual robin prior to initiating playback in any treatment. Because both robin species are sexually monomorphic, I quantified behavioural response without regard to sex. I measured closest approach as a continuous variable bounded by 0 m (if the responding bird perched on the speaker) and 15 m (given the dense understorey vegetation, the maximum distance from the speaker I could reasonably detect an approaching

territory owner). I estimated the distance between a responding bird and the speaker by eye during playback trials, and later checked my estimates by pacing off the distance between the speaker and the location where the responding bird had perched. I measured latency to approach as the time until a responding individual was first observed within 15 m of the speaker. Finally, I measured latency to vocal response as the time until the first vocalization (call or song) I heard at any distance from the speaker after beginning playback.

Some territory owners did not respond to heterospecific or control treatments. I categorized the closest approach of these non-responders as 15 m and latency to approach speaker and vocal response as the 8 min of combined playback and observation time. I discontinued playback trials on two occasions when non-target individuals approached the speaker (one experiment where multiple Ashy Robins approached the speaker in response to Ashy Robin playback, and one where Ashy and Slaty Robins each approached the speaker in response to Ashy and Slaty Robin playback, respectively), as I could not assess whether the territory owner's behavioural response was directed at the speaker stimulus or the presence of the non-target individual. Playback experiments on Ashy Robin territories at the Ashy-only site followed the methods described above and used the same bank of recordings.

Statistical analysis

For each experiment, I used the 'lme4' package (Bates *et al.* 2014) in R (R Development Core Team 2014) to run a linear mixed effects model that predicted behavioural response using species/treatment (a categorical predictor with multiple levels; Ashy Robin conspecific, heterospecific and control, and Slaty Robin conspecific, heterospecific and control) and order (conspecific first vs. heterospecific first) as fixed effects, and territory (a unique code for each tested territory) as a random effect (see Tables S1 and S2). This model is statistically identical to a different parameterization that includes species, treatment and a species-by-treatment interaction as predictor variables instead of the combined 'species/treatment' variable. Using the combined 'species/treatment' variable facilitates direct testing of whether behavioural

Table 1. Percentage of trials in which a territory owner approached the speaker in response to playback treatments.

	Species	Territories (<i>n</i>)	Conspecific (%)	Heterospecific (%)	Control (%)
Experiment 1 (ridgeline site)	Ashy Robin	23	100	96	0
	Slaty Robin	20	100	5	0
Experiment 2 ('Ashy-only' site)	Ashy Robin	9	100	11	0

Similar patterns occurred when considering other behavioural response variables (e.g. latency to vocalize).

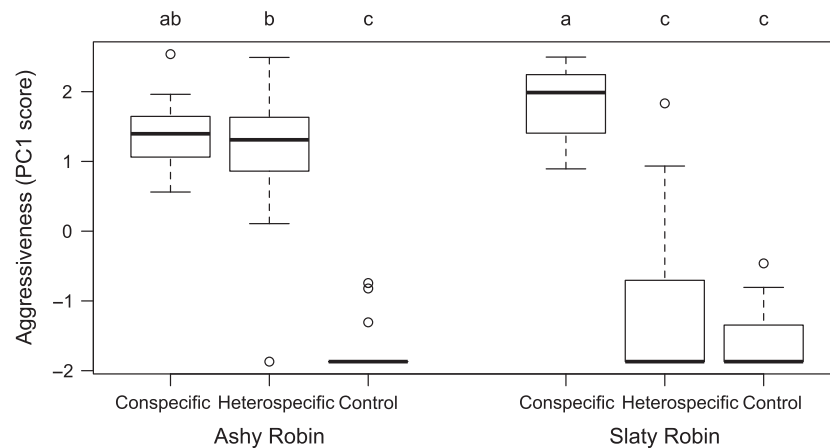


Figure 2. Aggression scores of Ashy and Slaty Robins ($n = 23$ and 20 , respectively) by treatment type at the ridgeline site (Experiment 1). Positive PC1 values represent more aggressive responses (close approaches to speaker and low latencies to vocalize and approach). Letters denote statistical significance of different playback trials based on *post-hoc* Tukey multicomparison tests of linear mixed effects models.

responses differed between different species/treatment ranks. For each experiment, I performed a principal components analysis (PCA) that included closest approach to speaker, latency to approach speaker and latency to vocalize, and used PC1 values ('aggression score') as the response variable in linear mixed models (following, for example, Benites *et al.* 2014, Reif *et al.* 2015). PC1 explained the large majority of variation in behavioural responses in both experiments (Experiment 1: 88.4% of variation, Experiment 2: 89.9% of variation), and all three recorded behavioural responses had similar positive loadings on PC1 (Experiment 1: latency to approach = 0.59, closest approach = 0.59, latency to vocalize = 0.55; Experiment 2: latency to approach = 0.60, closest approach = 0.57, latency to vocalize = 0.56). I compared full models with models lacking the 'order' fixed effect using Akaike information criterion (AIC) values, and then used Tukey multicomparison *post-hoc* tests implemented in the 'multcomp' package (Hothorn *et al.* 2008) to assess differences between species/treatment ranks.

RESULTS

In both experiments, Ashy and Slaty Robins typically responded to conspecific playback by approaching the speaker and vocalizing, but did not approach the speaker and seldom vocalized in response to control playback (see Table 1 for patterns of speaker approaches; patterns are similar for the latency to vocalize and latency to approach response variables). Response to heterospecific treatment varied between species and experiments: Slaty Robins did not respond to heterospecific playback, whereas Ashy Robins responded to heterospecific playback by approaching the speaker and vocalizing in Experiment 1 but not in Experiment 2 (Table 1).

Reduced models without 'Order' fixed effects had lower AIC values than the full model in both experiments, indicating that the relative order of playback (conspecific treatment last vs. heterospecific treatment last) did not influence behavioural response to playback in either experiment. Last, Tukey *post-hoc* tests on the reduced

models confirmed the differences in responses to heterospecific treatments between species and experiments described qualitatively above (letters in Figs 2 and 3 denote statistically significant differences between treatments).

DISCUSSION

I found strong asymmetric interspecific aggression between two sympatric species of montane New Guinean robins. Ashy Robins (the larger species) consistently responded aggressively to playback of Slaty Robins (the smaller species), whereas Slaty Robins did not respond aggressively to Ashy Robin playback (Fig. 2). This asymmetric aggression could represent misdirected intraspecific aggression, an evolved response to competition, a local learned response to the presence of a competitor or a combination of these mechanisms. Further insight into the mechanistic basis of interspecific aggression in this system came from the second experiment; Ashy Robins at a site without Slaty Robins did not respond aggressively to Slaty Robin stimuli (Fig. 3). This geographical variation in Ashy Robin behaviour is most consistent with the hypothesis that interspecific aggression is a local learned response to the presence of a competitor. However, I cannot firmly reject the possibility that

Ashy Robin interspecific aggression at this study site may also represent (in part) an evolved response to competition or misdirected intraspecific aggression (see McEntee 2014 for an example of how behavioural responses to heterospecifics can be geographically variable even in allopatry).

Ashy Robin aggression towards Slaty Robin playback in the first experiment was consistently strong; Ashy Robins responded aggressively to Slaty Robin playback in all but one case (Table 1). Interspecific aggression can result in exclusive territories defended against heterospecifics (reviewed in Grether *et al.* 2013), although even strong interspecific aggression does not always result in exclusive interspecific territoriality (Wiens *et al.* 2014). While both robin species were common at the ridgeline site, there was only one playback trial (of 45 completed experiments) in which both species approached the speaker in response to conspecific playback (i.e. Ashy Robins approached the speaker in response to Ashy Robin playback, and Slaty Robins approached the speaker in response to Slaty Robin playback). This surprising near-absence of playback trials that attracted both species is likely to indicate low territorial overlap and is consistent with the possibility that Ashy and Slaty Robins defend interspecific territories at this site, although telemetry studies are necessary to evaluate this possibility.

Ashy Robin aggression toward Slaty Robin playback appears to be learned rather than misdirected intraspecific aggression or an evolved response. Misdirected intraspecific aggression is *a priori* unlikely between these two species, which last shared a common ancestor approximately 12 million years ago (Loynes *et al.* 2009) and are widely divergent in plumage (Fig. 1) and voice. Learned interspecific aggression by Ashy Robins may be related to foraging niche overlap, as both species forage for insects in the low understorey (Croxall 1977, Boles 2007). Alternatively, other ecological interactions, such as competition for nesting or roosting sites, could underpin learned interspecific aggression. A noteworthy pattern is that the four other species of understorey insectivorous robins found in YUS (and more broadly in New Guinea) inhabit parapatric elevational distributions and do not co-occur with Ashy and Slaty Robins in montane forests (Diamond 1986, Freeman & Class Freeman 2014). This limited co-occurrence of understorey insectivorous patterns is consistent with the possibility that foraging niche overlap is

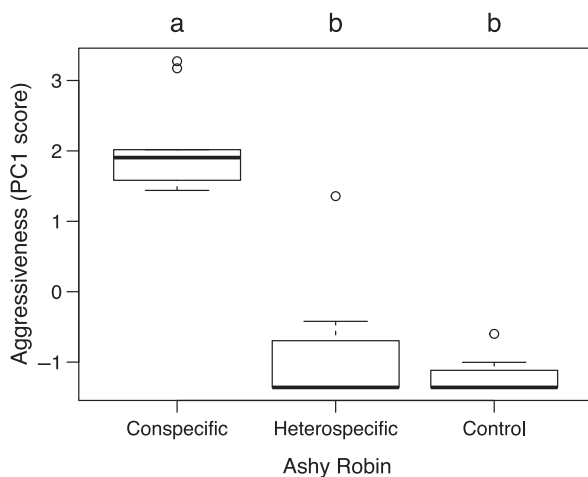


Figure 3. Aggression scores of Ashy Robins ($n = 9$) by treatment type at the 'Ashy-only' site (Experiment 2). Positive PC1 values represent more aggressive responses (close approaches to speaker and low latencies to vocalize and approach). Letters denote statistical significance of different playback trials based on *post-hoc* Tukey multicomparison tests of linear mixed effects models.

important, but could also reflect other mechanisms of competition.

In conclusion, I documented strong asymmetric aggression between two sympatric species of understory New Guinean robins. These results suggest that Ashy and Slaty Robins compete with one another for food resources, nest-sites, roost sites or some other ecological factor. Future studies should address whether strong asymmetric aggression by the putative dominant species (Ashy Robin) influences the distribution and abundance of the putative subordinate species (Slaty Robin), as has been found in other avian study systems (Martin & Martin 2001, Jankowski *et al.* 2010, MacNally *et al.* 2012), and whether interspecific aggression is prevalent in ecologically similar New Guinean passerines, as originally hypothesized by Diamond (1973, 1986).

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REFERENCES

- Bates, D., Maechler, M., Bolker, B. & Walker, S. 2014. lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1–7 <http://CRAN.R-project>.
- Benites, P., Campagna, L. & Tubaro, P.L. 2014. Song-based species discrimination in a rapid Neotropical radiation of grassland seedeaters. *J. Avian Biol.* **46**: 55–62.
- Boles, W.E. 2007. Family Petroicidae (Australasian robins). In del Hoyo, J. (ed.) *Handbook of the Birds of the World. Vol 12. Picathartes to Tits and Chickadees*: 438–489. Barcelona: Lynx Edicions.
- Class, A.M. & Moore, I.T. 2010. Is there a trade-off between caring for offspring and territorial aggression in tropical male Rufous-collared Sparrows (*Zonotrichia capensis*)? *Behaviour* **13**: 1819–1839.
- Croxall, J.P. 1977. Feeding behaviour and ecology of New Guinea rainforest insectivorous passerines. *Ibis* **119**: 113–146.
- Dhondt, A.A. 2011. *Interspecific Competition in Birds*. Oxford: Oxford University Press.
- Diamond, J. 1986. Evolution of ecological segregation in the New Guinea montane avifauna. In: Diamond, J. & Case, T.J. (eds) *Community Ecology*: 98–125. New York: Harper & Row.
- Freeman, B.G. & Class Freeman, A.M. 2014. The avifauna of Mt. Karimui, Chimbu Province, Papua New Guinea, including evidence for long-term population dynamics in undisturbed tropical forest. *Bull. Br. Ornithol. Club* **134**: 30–51.
- Freeman, B.G., Class, A.M., Mandeville, J., Tomassi, S. & Beehler, B.M. 2013. Ornithological survey of the mountains of the Huon Peninsula, Papua New Guinea. *Bull. Br. Ornithol. Club* **133**: 4–18.
- Freshwater, C., Ghalambor, C.K. & Martin, P.R. 2014. Repeated patterns of trait divergence between closely related dominant and subordinate bird species. *Ecology* **95**: 2334–2345.
- Grether, G.F., Anderson, C.N., Drury, J.P., Kirschel, A.N.G., Losin, N., Okamoto, K. & Peiman, K.S. 2013. The evolutionary consequences of interspecific aggression. *Ann. N. Y. Acad. Sci.* **1289**: 48–68.
- Hothorn, T., Bretz, F. & Westfall, P. 2008. Simultaneous inference in general parametric models. *Biometrical J.* **50**: 346–363.
- Jankowski, J.E., Robinson, S.K. & Levey, D.J. 2010. Squeezed at the top: interspecific aggression may constrain elevational ranges in tropical birds. *Ecology* **91**: 1877–1884.
- Kroodsmas, D.E. 1989. Suggested experimental designs for song playbacks. *Anim. Behav.* **37**: 600–609.
- Loynes, K., Joseph, L. & Keogh, J.S. 2009. Multi-locus phylogeny clarifies the systematics of the Australo-Papuan robins (Family Petroicidae, Passeriformes). *Mol. Phylogenet. Evol.* **53**: 212–219.
- MacNally, R., Bowen, M.E., Howes, A.L., McAlpine, C.A. & Maron, M. 2012. Despotic, high-impact species and the sub-continental scale control of avian assemblage structure. *Ecology* **93**: 668–678.
- Martin, P.R. & Ghalambor, C.K. 2014. When David beats Goliath: the advantage of large size in interspecific aggressive contests declines over evolutionary time. *PLoS ONE* **9**: e108741.
- Martin, P.R. & Martin, T.E. 2001. Behavioral interactions between coexisting species: song playback experiments with Wood Warblers. *Ecology* **82**: 207–218.
- McEntee, J.P. 2014. Reciprocal territorial responses of parapatric African sunbirds: species-level asymmetry and intraspecific geographic variation. *Behav. Ecol.* **25**: 1380–1395.
- Murray, B.G. 1971. The ecological consequences of interspecific territorial behavior in birds. *Ecology* **52**: 414–423.
- Peiman, K.S. & Robinson, B.W. 2010. Ecology and evolution of resource-related heterospecific aggression. *Q. Rev. Biol.* **85**: 133–158.
- Pratt, T.K. & Beehler, B.M. 2014. *Birds of New Guinea*, Vol. 2nd. Princeton: Princeton University Press.
- R Development Core Team. 2014. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.
- Reif, J., Jiran, M., Reifová, R., Vokurková, J., Dolata, P.T., Petrusek, A. & Petrusková, T. 2015. Interspecific territoriality in two songbird species: potential role of song convergence in male aggressive interactions. *Anim. Behav.* **104**: 131–136.
- Robinson, S.K. & Terborgh, J. 1995. Interspecific aggression and habitat selection by Amazonian birds. *J. Anim. Ecol.* **64**: 1–11.
- Terborgh, J. & Weske, J.S. 1975. Role of competition in distribution of Andean birds. *Ecology* **56**: 562–576.
- Wiens, J.D., Anthony, R.G. & Forsman, E.D. 2014. Competitive interactions and resource partitioning between

northern spotted owls and barred owls in western Oregon. *Wildl. Monogr.* **185**: 1–50.

Wolfenden, A., Jones, C.G., Tatayah, V., Züel, N. & de Kort, S.R. 2015. Endangered Pink Pigeons treat calls of the ubiquitous Madagascan Turtle Dove as conspecific. *Anim. Behav.* **99**: 83–88.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. Fixed effects for linear mixed model of Experiment 1 (ridgeline site).

Table S2. Fixed effects for linear mixed model of Experiment 2 (Ashy-only site).