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Asymmetric interspecific aggression in New Guinean songbirds that replace one another along an elevational gradient

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A common pattern in tropical avifaunas is for closely related species to inhabit largely parapatric elevational distributions such that they replace one another along the elevational gradient. A long-standing hypothesis for this pattern is that parapatry is maintained by interspecific interference competition mediated by interspecific aggression. However, empirical tests of this hypothesis remain scarce. We used reciprocal playback experiments to measure interspecific aggression in five species-pairs of New Guinean passerine elevational replacements. We found evidence of interspecific aggression in three species-pairs. In these three cases, interspecific aggression was asymmetric, with the lower elevation species more aggressive towards the upper elevation species than vice versa. Two patterns suggest that this interspecific aggression is a learned response to the presence of a heterospecific competitor rather than misdirected intraspecific aggression or an evolved response to a competitor. First, when present, interspecific aggression was always strongest at the upper elevation range margin of the lower elevation species (i.e. in the elevational zone in which the two species were found in close proximity and thus interacted with each other), and diminished over very short distances away from this zone. Secondly, the two species-pairs that did not exhibit interspecific aggression had narrow 'no man's land' gaps between their elevational distributions such that heterospecifics did not encounter one another, possibly explaining the lack of interspecific aggression in these examples. Our results support the hypothesis that interspecific aggression is one factor influencing elevational limits in species-pairs of New Guinean elevational replacements.

Keywords: distributional limit, elevational distribution, interspecific aggression, interspecific competition, playback experiment, range limit.

INTRODUCTION

Tropical mountains are the most biodiverse terrestrial environments on Earth (Myers *et al.* 2000). Tropical montane hyper-diversity results in large part from the fact that tropical montane species typically inhabit narrow elevational distributions (Patterson *et al.* 1998, McCain 2009), and a common pattern of elevational specialization is for closely related species to inhabit different elevational zones, largely 'replacing' one another along elevational gradients. Elevational replacements are

common in a variety of tropical montane taxa, e.g. bats (Patterson *et al.* 1998), butterflies (Hall 2005), lizards (Bell *et al.* 2010) and dung beetles (Larsen 2012), and have been studied most extensively in songbirds (Terborgh & Weske 1975, Remsen & Graves 1995). However, the abiotic and biotic factors that explain why species-pairs of avian elevational replacements inhabit parapatric elevational distributions remain uncertain (Jankowski *et al.* 2012).

One historically popular hypothesis posits that interspecific interference competition is an important factor limiting the elevational distributions of elevational replacements in tropical montane birds (Diamond 1973, Terborgh & Weske 1975, see

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Bull 1991 for an overview of how interspecific competition can influence parapatric distributions). Initial arguments in support of this hypothesis, as applied to montane birds, relied on distributional patterns, such as examples in which species inhabit broader elevational distributions in regions where their putative competitor does not occur (Diamond 1973, Terborgh & Weske 1975). However, these patterns are consistent with alternative explanations that do not invoke interspecific competition; for example, biotic aspects of environments beyond the absence of the putative competitor may differ between regions, or a species' preferred environment may encompass a broader elevational distribution in one region such that the species inhabits a wider elevational range (Cadena & Loiselle 2007). Thus, experimental studies are necessary to evaluate the hypothesis that interspecific competition influences the elevational distributions of tropical birds that are elevational replacements.

In territorial species, interspecific interference competition is often mediated by behavioural aggression (Peiman & Robinson 2010, Grether *et al.* 2013). The interspecific competition hypothesis therefore predicts that territorial elevational replacements interact aggressively. Interspecific aggression in these cases could result from three non-mutually exclusive mechanisms: (1) an inability to distinguish between conspecifics and heterospecifics due to phenotypic similarity ('mistaken identity'; Murray 1971); (2) an evolved response to the presence of a competitor; or (3) a learned response to the presence of a competitor (e.g. Baker & Lynch 1991, Gil 1997, Sedlacek *et al.* 2006). These mechanisms predict different geographical patterns of interspecific aggression; most notably, the mistaken identity hypothesis predicts that interspecific aggression should occur in both the presence and the absence of heterospecifics, whereas the evolved response and learned response hypotheses predict that interspecific aggression is largely restricted to regions where the heterospecific is present.

We are aware of three recent field experiments that have documented interspecific aggression in elevational replacements of songbird species (five total species-pairs; Jankowski *et al.* 2010, Caro *et al.* 2013, Freeman & Montgomery 2016). Interspecific aggression in these cases was strongest near the zone of overlap where both species

within a species-pair of elevational replacements were found, and markedly diminished at short geographical distances (< 1 km) away from this region (Jankowski *et al.* 2010, Caro *et al.* 2013, Freeman & Montgomery 2016). These results provide some of the first support for the hypothesis that interspecific competition mediated by interspecific aggression is a factor influencing elevational distributions in territorial birds that are elevational replacements, and, because the intensity of aggressive response diminished away from the zone of contact in all cases, suggest that interspecific aggression is a learned response to the presence of a competitor. However, these case studies remain few in number, and further field experiments are needed to assess whether interspecific aggression between elevational replacements is a more widespread phenomenon and, if so, whether interspecific aggression represents misdirected intraspecific aggression, an evolved response to a competitor or a learned response to a competitor.

We addressed this data gap by conducting reciprocal playback experiments to measure interspecific aggression in five species-pairs of New Guinean songbird elevational replacements. Elevational replacements are particularly prominent in the New Guinean avifauna, where they constitute around 20% of diversity along elevational gradients (Freeman & Class Freeman 2014a). Distributional data suggest interspecific competition may play an important role in limiting elevational limits in this avifauna (Diamond 1973, 1986), but behavioural interactions between species-pairs of elevational replacements have not been previously investigated. We predicted that if interspecific competition is an important factor influencing species' elevational limits, we should detect interspecific aggression between species-pairs in our experiments. The elevational gradient we studied was short and steep, stretching *c.* 3 km in linear distance from lowland (1000 m) to high-elevation forests (2500 m). We therefore predicted that only the learned response hypothesis would generate a pattern whereby individuals show interspecific aggression only at elevations at which they interacted with their putative competitor (e.g. near their shared range edge), as it would be difficult for an evolved response to occur over such small spatial scales (hundreds of metres). Conversely, we predicted that interspecific aggression that results from mistaken identity or an evolved response to a

Table 1. Elevations and number of playback trials conducted for each species in all five species-pairs of elevational replacements.

Species-pair	Species	Playback trials	Elevation of playbacks (m asl)
Slaty/White-winged Robin	White-winged Robin	9	2325–2505
	Slaty Robin	9	1872–2143
White-eyed/Slaty Robin	Slaty Robin	16	1673–1965
	White-eyed Robin	19	1448–1693
White-rumped/White-eyed Robin	White-eyed Robin	19	1240–1411
	White-rumped Robin	23	1042–1282
Chestnut-backed/Spotted Jewel-babbler	Spotted Jewel-babbler	17	1514–2142
	Chestnut-backed Jewel-babbler	15	1242–1455
Black/Dimorphic Fantail	Dimorphic Fantail	13	2050–2520
	Black Fantail	19	1722–2520

For each species-pair of elevational replacements, the higher elevation species is listed above its lower elevation replacement. Within a species-pair, we report the number of playback trials and the elevational zone in which playback experiments occurred for each species. White-eyed and Slaty Robins each appear as the lower elevation species in one species-pair of elevational replacements and the higher elevation species in a second species-pair of elevational replacements.

competitor would lead to individuals showing interspecific aggression across elevations (i.e. not solely near their shared range border).

METHODS

Focal species

We studied five species-pairs of territorial insectivorous bird species (Table 1) that are elevational replacements along forested elevational gradients in New Guinea (Pratt & Beehler 2014). All species are common understorey residents on the northwest ridge of Mt. Karimui, Chimbu Province, Papua New Guinea. This transect, covered in primary humid forest, was originally surveyed by Diamond (1972) in 1965 and resurveyed twice in 2012 (Freeman & Class Freeman 2014a,b). The elevational replacements we studied were a quartet of understorey robins (representing three species-pairs of elevational replacements; lowland White-rumped Robin *Peneothello bimaculatus*, foothill White-eyed Robin *Pachycephalopsis poliosoma*, montane Slaty Robin *Peneothello cyanus* and upper montane White-winged Robin *Peneothello sigillatus*), a species-pair of terrestrial jewel-babblers (foothill Chestnut-backed Jewel-babbler *Ptilorrhoa castanonota* and montane Spotted Jewel-babbler *Ptilorrhoa leucosticta*), and a species-pair of understorey fantails (montane Black Fantail *Rhipidura atra* and upper montane Dimorphic Fantail *Rhipidura brachyrhyncha*).

Playback experiments

We conducted playback experiments in October–December 2012. Breeding seasonality is poorly known in New Guinean forest birds, but these months are likely to constitute the beginning of the breeding season for most forest species (Diamond 1972). We first compiled a collection of locally recorded natural vocalizations ($n = 6$–15 songs per species) using a Marantz PMD661 Field Recorder and a Sennheiser MKH 70 directional microphone. We varied the recordings used in playbacks, and arbitrarily selected the specific recordings used in each playback trial to maximize the independence of trials from each other. Recordings have been archived at the Macaulay Library of Natural Sounds, Cornell Laboratory of Ornithology.

We conducted playback experiments on active territories of all elevational replacements across a range of elevations (mean = 16 territories per species within each species-pair, see Table 1 for sample sizes of territories tested in experiments). We assumed singing individuals to be actively defending territories, and mapped the locations of singing individuals with a Garmin 62S GPS. To ensure that each playback experiment tested the response on a different territory, we performed experiments on territories separated by at least 100 m (> 200 m in nearly all cases; all tested jewel-babbler territories were > 200 m apart). We initiated playback experiments by placing a Pignose amplifier/speaker (hereafter 'speaker') at the location at

which a GPS location reading was taken. The speaker was attached to an iPod via a 20-m audio cable. We broadcast song stimuli at a volume level that we judged to be the same as that of natural vocalizations, and observed the behavioural response (if any) of the territory owner(s) while we hid behind vegetation *c.* 15 m from the speaker to minimize the influence of our physical presence. We conducted playback experiments between 06:15 and 13:00 h, avoiding periods of moderate or heavy rain.

Each playback experiment consisted of a control, a conspecific and a heterospecific trial (because elevational replacements of understorey robins represent two genera, we term these trials 'heterospecific' instead of 'congeneric'). We began experiments with the control trial of 3 min of playback of a locally common species unlikely to compete with the territory owner (*Pachycephala* whistlers), followed by 5 min of behavioural observation. We next performed conspecific and heterospecific trials (3 min of playback followed by 5 min of behavioural observation for each trial), alternating their relative order (conspecific trial first vs. heterospecific trial first) between experiments. Thus, for each species within each species-pair, there were equal numbers of playback experiments in which the territorial individual(s) heard heterospecific playback before conspecific playback, and where the territorial individual(s) heard conspecific playback before heterospecific playback, allowing us to examine any effects of playback sequence on behavioural response. The conspecific trial tested the focal species' behavioural response to playback of its own species, whereas the heterospecific trial tested the focal species' behavioural response to playback of its elevational replacement. All trials for a given territory were performed sequentially in a single 24-min session, although we used an expanded time period of behavioural observation (8 min in lieu of 5) for jewel-babblers to accommodate their delayed behavioural response to playback.

We quantified four behavioural responses to playback: closest approach to speaker (m) (hereafter 'closest approach'), latency to approach speaker (s), latency of vocal response (s) and number of vocalizations (Jankowski *et al.* 2010, Pegan *et al.* 2015, Freeman 2016). All our study species are relatively shy (Pratt & Beehler 2014), and there were no cases in which we visually observed an individual prior to initiating a playback trial.

We were thus unable to assess whether individuals that did not respond to playback were actively (e.g. flying away in response to playback) or passively (remaining at a distance from the speaker) avoiding the speaker area. Two individuals typically responded to conspecific (and, in some cases, to heterospecific) playback, presumably a mated pair defending their territory. However, most focal species are sexually monomorphic, and we were thus unable to measure the distinct behavioural responses of males and females in most cases. We measured latency to approach as the time elapsed prior to the first observed approach to within 15 m of the speaker, and closest approach as a continuous variable bounded by 0 (if the responding bird perched on the speaker) and 15 m (due to dense understorey vegetation, the maximum distance we could reasonably detect a territory owner approaching the speaker). We estimated closest approach by eye during the course of playback experiments and checked our visual estimates by later pacing off the distance between the speaker and location of the responding bird's closest approach. Finally, we measured latency to vocal response as the first vocalization (call or song) given by the focal individual/pair at any distance from the speaker after initiating a playback trial.

Birds always responded aggressively to conspecific playback, with at least one individual approaching the speaker during each conspecific trial. However, territory owners seldom responded to control playback trials, and response to heterospecific trials varied by species and elevation. We categorized the closest approach of these non-responders as 15 m (see above) and their latency to approach the speaker and vocal response as the summed duration of playback trials and behavioural observation periods (e.g. 480 s for non-jewel-babbler trials).

Elevational limits

We used point counts and *ad hoc* observations to measure species' elevational limits along Mt. Karimui's northwestern ridge in October–November 2012. These elevational limits are similar, but not identical, to those measured using similar methods in June–July 2012 at the same site (Freeman & Class Freeman 2014b); because the playback experiments analysed here took place in October–December 2012, we present species' elevational

limits measured at this same time. One observer familiar with the vocalizations of New Guinean birds (B.G.F.) conducted 5-min point counts at 33 sites located along a single elevational transect stretching from 1150 to 2520 m. Point count sites were located at least 150 m apart, and all sites were visited on each of three mornings (06:00–12:00 h). We used point count data to roughly estimate species' elevational limits, then conducted extensive observational fieldwork at elevations near species' estimated elevational limits to locate territories of focal species for future playback experiments and to determine species' elevational limits at a finer resolution. We found narrow zones of elevational overlap in two species-pairs (White-rumped/White-eyed Robin and White-eyed/Slaty Robin), a larger zone of elevational overlap in one species-pair (Black/Dimorphic Fantail), and narrow 'no man's land' gaps between species' elevational distributions in two species-pairs (Slaty/White-winged Robin and Chestnut-backed/Spotted Jewel-babbler; Table 2). We note that species' abundances were not necessarily uniform within their elevational range. In particular, whereas Black and Dimorphic Fantails co-occurred over a wide swath of upper elevation forests (Table 2), Black Fantails were abundant at middle elevations where Dimorphic Fantails were absent, but were scarce at higher elevations where Dimorphic Fantails were relatively common (B.G.F. pers. obs.).

Statistical analysis

We conducted all statistical analyses in R (R Development Core Team 2014). Because we were interested in behavioural interactions between pairs of species that are elevational replacements, we constructed separate models for each species-pair of elevational replacements. For each species-pair, we used a principal components analysis (PCA) to collapse all four behavioural response variables from playback trials into a single variable that summarized aggressive response (Benites *et al.* 2014, Reif *et al.* 2015). The behavioural response variables were measured in different units (i.e. both metres and seconds), and we therefore scaled variables in R using the scale = TRUE argument in the prcomp function in R. For each species-pair, behavioural responses that indicated greater aggression (closer and faster approaches, faster vocal responses and greater number of vocalizations) loaded positively on PC1, which explained a high percentage (72–79%) of variance in the data for each species-pair (Table 3). We therefore considered PC1 values to be a composite aggression score, and used PC1 values as our response variable in linear mixed models to analyse behavioural responses to playback.

The data from trials of both species within a species-pair were fitted to the same model to allow

Table 2. Elevational distributions of species at the study site measured in October–November 2012.

Species	Elevational distribution (m)
White-rumped Robin	<1000–1282
White-eyed Robin	1240–1693
Slaty Robin	1673–2158
White-winged Robin	2325–2520
Chestnut-backed Jewel-babbler	<1000–1458
Spotted Jewel-babbler	1508–2142
Black Fantail	1330–2520
Dimorphic Fantail	2050–2520

Table 3. PC1 variance and loadings for each species-pair.

Species-pair	PC1	Closest approach	Latency approach	Latency vocalize	Number of vocalizations
White-rumped/White-eyed Robin	73.5%	−0.53	−0.54	−0.46	0.46
White-eyed/Slaty Robin	72.6%	−0.54	−0.53	−0.49	0.43
Slaty/White-winged Robin	74.7%	−0.55	−0.55	−0.49	0.39
Chestnut-backed/Spotted Jewel-babbler	78.1%	−0.53	−0.49	−0.51	0.46
Black/Dimorphic Fantail	78.9%	−0.52	−0.54	−0.49	0.43

For all species, the first principal component explained a large majority of variance in the raw measurements, and all the measured facets of aggression loaded onto the first principal axes such that PC1 scores represent an appropriate measure of aggression in response to playback.

formal comparisons of the responses of two species. We included the following fixed-effect predictor variables in each model: (1) an interaction between trial type and elevation (where trial type has six species-type categories: conspecific, heterospecific and control trials for each species within a species-pair); and (2) playback order (conspecific first vs. heterospecific first). Using the 'trial type' predictor that combines information on focal species and the playback type is statistically equivalent to an alternative formulation that includes species, trial and a species-by-trial interaction instead of 'trial type'. Our formulation allows for more intuitive interpretation of regression parameters. Similarly, using the trial type-by-elevation interaction alone without a main effect of elevation is a formulation of the model that will produce identical results. Again, using the trial type-by-elevation interaction alone without a main effect of elevation is a formulation of the model that will produce an identical result, but with the benefit that the coefficients of this interaction are directly interpretable because each coefficient can be interpreted as a main effect of elevation for a separate trial type. Were a main effect of elevation present, the interaction coefficients would describe deviations in the effect of elevation relative to a reference category of trial type arbitrarily assigned by the software fitting the model. To account for variation among individuals in their response to playback trials, we included territory as a random effect.

The initial step in analysis of data from each species-pair was to examine whether the order of playback trials influenced behavioural responses to playback, and to remove this predictor if not required. We did this by fitting models to the data from each species-pair with and without an order term. Given our small sample sizes, we erred on the side of caution (against model overfitting) by using Bayesian Information Criterion (BIC) model selection (Burnham 2004) to evaluate whether models including the order term outperformed models lacking this predictor variable, and used the best-supported model (the model with the lowest BIC value) for further analysis.

We defined interspecific aggression to have been detected in cases where aggression scores in response to heterospecific trials were significantly higher than aggression scores in response to control trials at the elevations where species interact (Figs 1–3), and used slope estimates of the trial type-by-elevation interaction to determine whether

aggression scores were significantly related to elevation. We evaluated the relative fit of our models by calculating marginal and conditional r^2 for linear mixed models (Nakagawa & Schielzeth 2013) implemented in the MuMIn package in R (Barton 2014). Marginal r^2 is associated with the fixed effects within a linear mixed model, whereas the conditional r^2 is associated with both fixed and random effects. Although our formal statistical tests are based on models with multiple fixed effects and a random effect, graphical presentations of these same results present regression lines from simple linear regressions to illustrate qualitatively identical patterns. We used the output from these simplified linear regressions for figures because there is no generally agreed upon way of calculating confidence intervals around predictions from mixed models, and we wanted our figures to provide illustrations of levels of statistical confidence in patterns.

RESULTS

The two potential sources of noise that we modelled in our analyses proved to have had minor impacts. With playback order, in all cases BIC values were lower for the simpler model lacking the order term (Table S1). Thus, playback sequence (the relative order of conspecific and heterospecific trials within experiments) explained minimal variation in behavioural response to playback. Therefore, we only present results from the simpler, better-supported models (full model details are given in Tables S2–S6). Similarly, we did not detect strong variation among individual birds' responses to the playback experiments, as evidenced by similar marginal and conditional r^2 values for models for each species-pair (Table S2), indicating that the random effect of territory explained little variation in our data in each model.

We identified cases of interspecific aggression when responses to heterospecific trials were more aggressive than responses to control trials at the elevations where both species within a species-pair are found. Regression coefficients from the final models are given in Tables S3–S7, and graphical representations of the patterns are shown in Figures 1–3. In these figures, the 95% confidence intervals for heterospecific and control trials are non-overlapping at the upper elevation limit of the lower elevation species in three species-pairs of elevational replacements (White-rumped/White-eyed Robin,
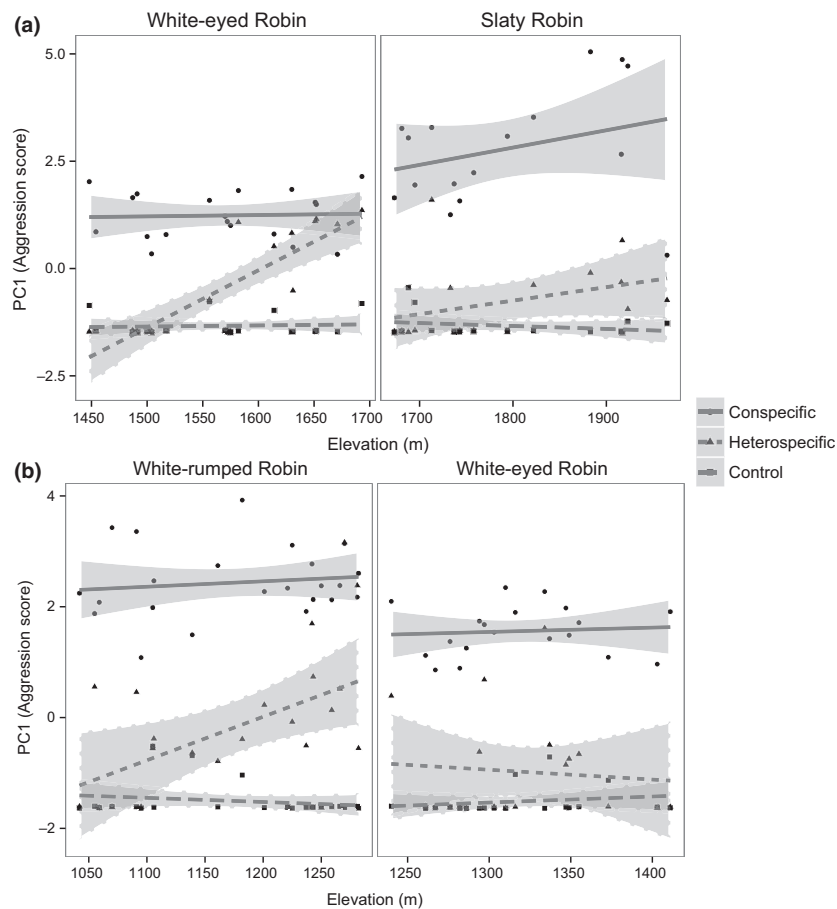
Figure 1. Aggression scores in response to playback trials in two species-pairs of understorey robin elevational replacements that exhibited interspecific aggression: (a) White-eyed/Slaty Robin and (b) White-rumped/White-eyed Robin. Higher aggression scores indicate more aggressive responses to playback. For each species-pair, the lower elevation species is shown in the left column, and the higher elevation species in the right column; note that scales of the *x*-axes differ between columns (and species-pairs) to minimize the amount of uninformative white space. Dots depict raw data of territorial birds' response to playback trials. Trend lines with 95% confidence intervals are shown for each trial type. Trend lines and confidence intervals represent separate least squares regressions for each line, and are qualitatively similar to results from mixed models. The random effect of territory explained little variation in our data in each model, and support our use of linear regressions in figures to depict trends.

White-eyed/Slaty Robin and Black/Dimorphic Fantail), indicating significant interspecific aggression (although we note that statistical significance in such cases does not require non-overlapping 95% confidence intervals). In contrast, we did not find interspecific aggression in two species-pairs of elevational replacements (Slaty/White-winged Robin and Chestnut-backed/Spotted Jewel-babbler; Fig. 3), the two species-pairs with 'no man's land' gaps between their elevational distributions (Table 2).

When present, interspecific aggression was asymmetric: the lower elevation species exhibited stronger interspecific aggression towards the upper elevation species than vice versa (Figs 1 and 2). Interspecific aggression also declined away from the upper elevation limit of the range of the lower elevation species, indicated by heterospecific trial-by-elevation interaction terms that were significantly positive for all the three lower elevation species that exhibited significant interspecific aggression (Figs 1 and 2). These declines in levels of aggression occurred over very short distances (hundreds of metres) from the upper elevation limit of the lower elevation species. The level of interspecific aggression at the upper range margin of the lower elevation species varied among
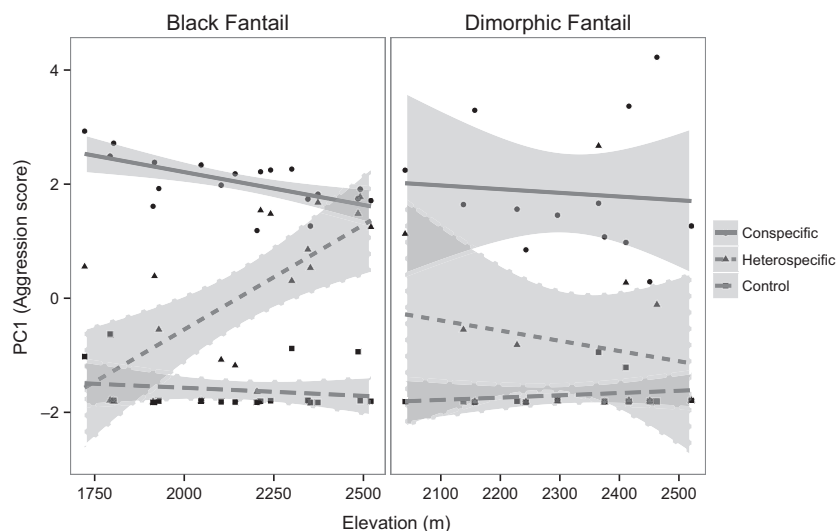
Figure 2. Aggression scores in response to playback trials for a pair of elevationally replacing species of fantails that exhibits interspecific aggression: the lower elevation Black Fantail and higher elevation Dimorphic Fantail (in the left and right panels, respectively). Dots represent raw data of territorial birds' response to playback trials. Higher aggression scores indicate more aggressive responses to playback. Dots depict raw data of territorial birds' response to playback trials. Trend lines with 95% confidence intervals are shown for each trial type. Trend lines and confidence intervals represent separate least squares regressions for each line, and are qualitatively similar to results from mixed models. The random effect of territory explained little variation in our data in each model, and support our use of linear regressions in figures to depict trends.

species-pairs that showed interspecific aggression (Figs 1 and 2). Models predicted that White-rumped Robin aggression scores in response to heterospecific (White-eyed Robin) trials were 54% that of conspecific trials (a significant difference between intra- and interspecific aggression; Table S3), whereas the corresponding values for White-eyed Robins (to Slaty Robin playback) and Black Fantails (to Dimorphic Fantail playback) were 97 and 92%, respectively (Tables S4 and S6). Thus, for White-eyed Robins and Black Fantails, at their upper range margins, there was no significant difference between intra- and interspecific aggression.

DISCUSSION

We document interspecific aggression in three species-pairs of New Guinean songbird elevational replacements. In each case, interspecific aggression was strongly asymmetric; the lower elevation species responded more aggressively to playback of upper elevation species than the reverse (Figs 1 and 2). Our results provide the first support for the hypothesis that interspecific interference competition mediated by interspecific aggression is a factor influencing the elevational distributions of

species-pairs of elevational replacements in the New Guinean montane avifauna. More broadly, our findings add to a growing list of field experiments that demonstrate interspecific aggression (typically asymmetric) in species-pairs of territorial elevational replacement in Neotropical birds (Jankowski *et al.* 2010, Caro *et al.* 2013), Neotropical rodents (Pasch *et al.* 2013) and Nearctic birds (Freeman & Montgomery 2016).

In contrast, we did not detect interspecific aggression in two species-pairs. We are not aware of previous publications that have documented an absence of interspecific aggression between elevational replacements, which may be because interspecific aggression in such cases is generally common, or may simply reflect publication bias. These negative results occurred in the two species-pairs that had 'no man's land' gaps between their elevational distributions and therefore probably did not directly interact with one another during our field study (Fig. 3). This lack of apparent direct interaction at our study site (at least at the time of our study) may explain the qualitatively different response to heterospecific playback, and is consistent with a need for direct interaction between species for the occurrence of interspecific aggression. Supporting this hypothesis, interspecific
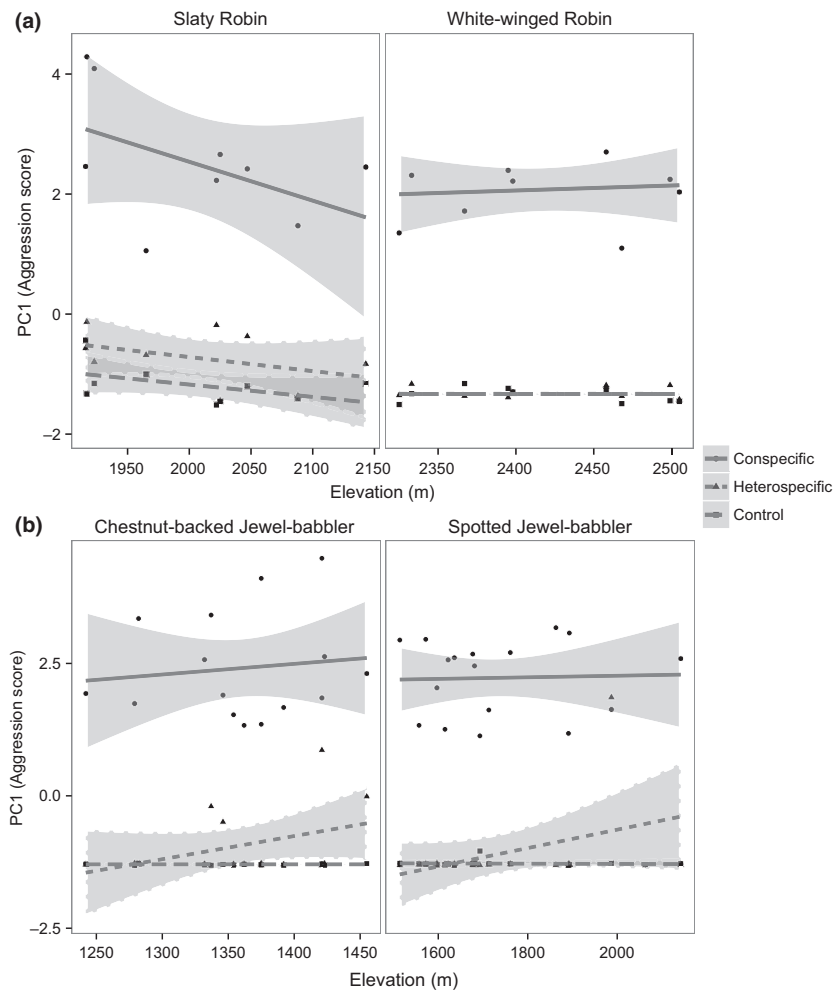
Figure 3. Aggression scores in response to playback trials in two species-pairs of understorey elevational replacements that did not exhibit interspecific aggression: (a) Slaty Robin and White-winged Robin and (b) Chestnut-backed Jewel-babbler and Spotted Jewel-babbler. Higher aggression scores indicate more aggressive responses to playback. For each species-pair, the lower elevation species is shown in the left column, and the higher elevation species in the right column – note that scales of the *x*-axes differ between columns (and species-pairs) to minimize the amount of uninformative white space. Dots depict raw data of territorial birds' response to playback trials. Trend lines with 95% confidence intervals are shown for each trial type. Trend lines and confidence intervals represent separate least squares regressions for each line, and are qualitatively similar to results from mixed models. The random effect of territory explained little variation in our data in each model, and supports our use of linear regressions in figures to depict trends.

aggression by lower elevation species in this study in the three species-pairs with elevational overlap was always strongest at the lower elevation species' upper range margin (where it interacted with its elevational replacement; Figs 1 and 2). In each case, interspecific aggression declined downslope from this contact zone over very short distances (< 0.5 km), most consistent with the hypothesis that interspecific aggression is a learned response to the presence of a heterospecific competitor. This echoes the results of previous studies of

songbird elevational replacements (Jankowski *et al.* 2010, Caro *et al.* 2013, Freeman & Montgomery 2016) that suggest direct encounters between closely related heterospecifics are often necessary for individuals to express interspecific aggression, although we cannot conclusively rule out the possibility that interspecific aggression in our study could represent, at least in small part, misdirected intraspecific aggression (Murray 1971, Wolfenden *et al.* 2015) or an evolved response to interspecific competition.

Interspecific competition upon secondary contact appears to drive the evolution of elevational divergence between closely related species in the New Guinean avifauna (Freeman 2015). This study suggests that current interspecific competition also influences the present-day elevational distributions of elevational replacements, at least in some species. According to this view, interspecific competition may have complementary evolutionary and ecological consequences on species' elevational distributions in the New Guinean avifauna. Given that elevational replacements make up roughly 20% of the total avifauna along New Guinean elevational gradients (Freeman & Class Freeman 2014a), interspecific competition mediated by interspecific aggression could be an important mechanism influencing current elevational patterns in this avifauna. Our results are based on a small sample of elevational replacements whose ecological traits (e.g. high relative abundance, known territorial behaviour) made experimental song playback tests of interspecific aggression along a single elevational gradient feasible, and we expect that future examinations of the same hypotheses within a limited geographical area will typically be limited to small samples of elevational replacements.

Evidence for interspecific aggression alone is not sufficient to demonstrate that interspecific aggression limits species' distributions (Martin & Martin 2001). Thus, further experiments (ideally removal experiments) are required to assess rigorously the hypothesis that interspecific aggression influences species' elevational distributions in this system, although such efforts would be logistically difficult. We also do not suggest that interspecific aggression is the dominant factor limiting our study species' present-day elevational distributions. Most obviously, we did not detect interspecific aggression in two of the species-pairs we investigated (Fig. 3). If interspecific aggression plays a role in limiting species distributions, as we suggest for the three species-pairs in which we documented significant interspecific aggression, additional factors (e.g. physiological adaptation, apparent competition mediated by predators or parasites) must be operating that prevent the more aggressive species from continually expanding its distribution upslope (Bull 1991).

We found that lower elevation species showed asymmetric interspecific aggression towards their upper elevation relatives (see also *Catharus* thrushes in Jankowski *et al.* 2010 and Freeman &

Montgomery 2016). Most interspecific aggression in birds is asymmetric and asymmetric aggression is typically (but not always) associated with behavioural dominance (Robinson & Terborgh 1995, Dhondt 2011). Behaviourally dominant species in North America tend to have more proximate breeding and wintering distributions than subordinate species, suggesting species' relative dominance can influence their occupied distributions (Freshwater *et al.* 2014), and behavioural dominance is thought to have facilitated recent range expansions in several North American species (Duckworth & Badyaev 2007, Wiens *et al.* 2014). In tropical mountains, populations of birds (and other taxa) are shifting upslope associated with recent global warming (Chen *et al.* 2011, Freeman & Class Freeman 2014b), and it has been suggested that interspecific aggression may influence warming-driven distributional shifts in species-pairs of elevational replacements. Specifically, behaviourally dominant lower elevation species could 'push' a subordinate montane species' population upslope at a faster rate than if the lower elevation species was absent, or, if upper elevation species are behaviourally dominant, upper elevation species could maintain their position as 'kings of the mountain' (Jankowski *et al.* 2010).

Because most species at our study site on Mt. Karimui have shifted upslope in the past half-century, a change linked to regional temperature increases (Freeman & Class Freeman 2014b), we have some preliminary data with which to assess the hypothesis that behavioural dominance plays a role in warming-associated distributional shifts. Although our sample size of species-pairs is very small, it is intriging to note that the three species that show interspecific aggression towards their upper elevation replacement (White-rumped Robin, White-eyed Robin and Black Fantail) have all expanded their upper elevational limits upslope (169, 123 and 197 m, respectively), whereas the two species that do not show interspecific aggression to their upper elevation replacement (Chestnut-backed Jewel-babbler and Slaty Robin) have barely shifted upslope (10 and 24 m, respectively; comparisons of upper elevation limits measured in October–December 2012 and those measured in 1965 by J. Diamond). Assuming that asymmetric interspecific aggression is correlated with behavioural dominance, this observation is consistent with the possibility that interspecific aggression may facilitate species' upslope shifts and thus be

one biotic factor influencing species' warming-associated upslope shifts at this site.

In conclusion, our study nearly doubles the number of avian species-pairs that have been examined for evidence of interspecific aggression along elevational gradients. We found evidence consistent with the hypothesis that a biotic interaction – interspecific aggression, most likely a learned response to the presence of a heterospecific competitor – influences the elevational distributions of New Guinean passerine elevational replacements. This adds support to the argument that biotic interactions may be important determinants of species' distributions, and should, when possible, be considered when predicting species' future geographical distributions (HilleRisLambers *et al.* 2013, Wisz *et al.* 2013). We conclude with a call to conserve entire elevational gradients on tropical mountains, the most diverse terrestrial habitats on Earth (Laurance *et al.* 2011). These gradients not only serve as irreplaceable working laboratories to investigate abiotic and biotic drivers of distributional limits and community assembly, but also provide the necessary space to accommodate warming-associated upslope shifts for most species into the foreseeable future.

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SUPPORTING INFORMATION

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

Table S1. BIC model comparison of linear regression models for each species-pair.

Table S2. Marginal and conditional r^2 for linear mixed models.

Table S3. Parameter estimates with standard errors for fixed effects in the White-rumped/White-eyed Robin mixed model.

Table S4. Parameter estimates with standard errors for fixed effects in the White-eyed/Slaty Robin mixed model.

Table S5. Parameter estimates with standard errors for fixed effects in the Slaty/White-winged Robin mixed model.

Table S6. Parameter estimates with standard errors for fixed effects in the Black/Dimorphic Fantail mixed model.

Table S7. Parameter estimates with standard errors for fixed effects in the Chestnut-backed/Spotted Jewel-babbler mixed model.