Behavioral Ecology

The official journal of the ISBE
International Society for Behavioral Ecology

Behavioral Ecology (2019), XX(XX), 1–7. doi:10.1093/beheco/ary194

Original Article

Interspecific aggression among parapatric and sympatric songbirds on a tropical elevational gradient

Andy J. Boyce[a,b] and Thomas E. Martin[b]
[a]Wildlife Biology Program, W.A. Franke College of Forestry and Conservation, Forestry 108, University of Montana, Missoula, MT 59812, USA and [b]US Geological Survey, Montana Cooperative Wildlife Research Unit, Natural Sciences Room 205, University of Montana, Missoula, MT 59812, USA

Received 24 April 2018; revised 5 November 2018; editorial decision 3 December 2018; accepted 14 December 2018.

Interspecific competition is hypothesized to be a strong force that sets species range limits and drives parapatric distributions of closely related species on tropical mountains. Yet, experimental evidence that competition drives spatial segregation of closely related species on elevational gradients is rare. To test whether competition limits elevational ranges of tropical songbirds, we conducted reciprocal playback experiments on 2 pairs of species with adjacent but nonoverlapping (parapatric) distributions and 1 pair of sympatric species. We found asymmetric interspecific aggression in one parapatric pair *(Pycnonotidae)* and a complete absence of interspecific aggression in the other *(Zosteropidae)*. We also found asymmetric interspecies aggression in a pair of sympatric flycatchers *(Muscicapidae)*. Our results indicate that interspecific aggression may set range limits in some cases, but it is not a prerequisite for parapatry. Furthermore, the presence of interspecific aggression between co-occurring relatives suggests that while competition may play a role in limiting species distributions, interspecific aggression alone is not sufficient evidence to assert that competition is the primary driver of parapatric distributions.

Key words: **competition, mountains, passerine, playback experiments, range limits.**

INTRODUCTION

Species inhabiting tropical mountains often have narrow elevational ranges with closely related species occupying adjacent elevational zones (Terborgh 1971; Stotz et al. 1996; McCain 2009). This pattern leads to rapid species turnover along mountainsides (Huey 1978) and is associated with exceptional biodiversity and endemism on tropical mountains (Cadena et al. 2011; Merckx et al. 2015). Yet, the factors limiting elevational ranges of tropical species remain unclear (Jankowski et al. 2012).

Interspecific competition is hypothesized to be a strong force that can limit species ranges (Connell 1961; Diamond 1973) and explain adjacent but nonoverlapping elevational distributions of closely related species (Heller 1971; Diamond 1973; Terborgh and Weske 1975; Stevens 1992; Jankowski et al. 2010; Freeman 2015). Competitive interactions are generally thought to be most important at the lower "warm" edge of a species range, while abiotic drivers are hypothesized to be more important at upper "cold" boundaries (MacArthur 1972). If this paradigm is accurate, low-elevational species should be competitively dominant over high elevation species and show stronger interspecific aggression toward their high-elevation relative than vice versa (Jankowski et al. 2010). This pattern of asymmetric interspecific aggression means that warming climates may drive range contractions in high elevation species as dominant low elevation competitors expand their range upward. This process is thought to drive "mountaintop extinctions," making montane species particularly vulnerable to extinction or local extirpation as a result of climate change (Colwell et al. 2008; Sekercioglu et al. 2008). Understanding the role of interspecific competition in determining range boundaries is therefore critical to predicting outcomes and prioritizing conservation effort in light of climate change.

Evidence for competition shaping parapatric distributions comes primarily from observations that some species expand their range in areas where a closely-related species is absent, suggesting competitive release in the absence of a competitor (Terborgh and Weske 1975; Remsen and Graves 1995a, 1995b; Martin and Martin 2001a; Gifford and Kozak 2011). However, what appears to be range expansion due to the absence of a presumed competitor can reflect geographic variation in the distribution of suitable

---

Address correspondence to A.J. Boyce. E-mail: andyjboyce@gmail.com, who is now at Conservation Ecology Center, Smithsonian Conservation Biology Institute, 1500 Remount Rd., Front Royal, VA 22630, USA.

habitat rather than competitive release (Cadena and Loiselle 2007). Observations of interspecific aggression between closely related species with abutting ranges are also presented as evidence that competition sets and/or maintains range limits for some species pairs (Heller 1971; Robinson and Terborgh 1995; Jankowski et al. 2010). However, if interference competition sets and/or maintains range boundaries between 2 competitors, we would expect ranges to be perfectly adjacent and nonoverlapping (Terborgh 1971). Yet, in many cases of elevational parapatry, there are significant zones of species overlap or gaps where neither species is present (Terborgh 1971). Overall, the importance of interference competition in limiting distributions of close relatives is unclear.

We examine these questions in songbirds (passerines) across an elevational gradient in the tropics. Songbirds are a tractable system in which to examine the drivers of elevational range limits. In the tropics, many clades have parapatric distributions with congeners "stacked" on top of each other in narrow elevational bands (Terborgh 1971; Diamond 1973; Remsen and Graves 1995a, 1995b; Stotz et al. 1996). Birds are easily observed both visually and aurally, and territorial singing behavior allows for straightforward identification to species and facilitates territory location. Yet, evidence for interspecific aggression as a proximate force limiting elevational ranges of songbirds is mixed. Broadly speaking, interspecific aggression in birds is often asymmetric (reviewed in Martin et al. 2017a), where one species either consistently "wins" aggressive interactions, or responds more strongly to the presence of a heterospecific than the other. Along elevational gradients, asymmetric aggression has been reported, with low elevation species dominating high-elevation relatives (Jankowski et al. 2010; Freeman 2016a; Freeman and Montgomery 2016). This pattern has been interpreted as evidence that low-elevation species outcompete high-elevation subordinates who are forced into suboptimal habitat (Martin and Martin 2001b; Jankowski et al. 2010). However, interspecific aggression was absent in some other pairs, calling into question the general importance of competition in setting elevational range limits in birds (Freeman 2016a). Furthermore, strong interspecific aggression has been documented in co-occurring (sympatric) species pairs (Freeman 2016b; Robinson and Terborgh 1995), suggesting that observations of interspecific aggression alone are not sufficient evidence to infer interference competition as a driver of elevational parapatry. Thus, studies assessing strength and directionality of interspecific aggression in both sympatric and parapatric species pairs are needed. To address this gap in knowledge, we performed reciprocal playback experiments to assess the presence and directionality of interspecific aggression in 2 pairs of closely related species that replace each other along an elevational gradient. We also performed reciprocal playback experiments on 2 sympatric species to assess whether patterns of interspecific aggression are equally strong between co-occuring and parapatric species pairs.

METHODS

Study system

All data were collected at Kinabalu Park, Sabah, Malaysia (6°N, 116°E); a large tract of tropical forest spanning 400–4100 m on the island of Borneo. Playback experiments were performed in mid-elevation submontane cloud-forest at Park HQ (1560–1850 m) and high-elevation elfin forest at Laban Rata (3000–3450 m) (Rafiqpoor and Nieder 2006). In general, forest structure becomes simpler, shorter, and with an increasingly dense understory with increasing elevation. The 2 sites are connected by continuous, undisturbed forest bounded below by the park boundary at ~1450 m, and above by a zone of bare granite from ~3800 m to Low's Peak at 4095 m. All fieldwork was conducted from February to June, 2012–2016. This period corresponds with the peak of the breeding season in this region for all focal species (Martin et al. 2015a, 2015b).

Elevational ranges

Pairs of related species were previously documented to replace each other along elevational gradients in Borneo, including 2 of our study species pairs (Smythies 1999; Harris et al. 2012; Sheldon et al. 2015). However, we also conducted repeated point count surveys along a continuous transect from 1450 to 3800 m on Mt. Kinabalu to describe detailed elevational distributions of bird species at our study site. We present these local distributions throughout the rest of the manuscript because elevational ranges for a given species vary across mountains (Cadena and Loiselle 2007) and using global elevational ranges would suggest more elevational overlap between congeners than is present on any individual mountain. Points were placed at least 200 m straight-line distance apart, at a density of 5 points per 200 vertical meters. Counts were 10 min in duration, during which we recorded all individuals detected visually or aurally. Counts were conducted between civil twilight and 08:00 with a maximum of 5 counts per morning. All counts were conducted by AJB. The entire transect was sampled either 2 (2014–2015) or 3 (2012–2013) times per season. The order in which each cluster of points was sampled was reversed after each transect to avoid sampling bias related to time of day. The park boundary limited the low-elevation extent of our point counts at ~1450 m, obscuring variation in lower range boundary for many species. Lower range boundaries for all low-elevation species in this study occur well below 1450 m and are described by Harris et al. (2012).

Playback experiments

We selected 2 pairs of elevationally parapatric relatives and 1 pair of sympatric relatives for playback experiments. All species are common year-round residents and males of all species sing territorial songs and defend breeding territories (AJB, personal observation). Parapatric species pairs included bulbuls (*Pycnonotidae*); ochraceus bulbul (*Alophoixus ochraceus*) and pale-faced bulbul (*Pycnonotus leucops*), and white-eyes (*Zosteropidae*); black-capped white-eye (*Zosterops atricapilla*) and mountain black-eye (*Chlorocharis emeliae*). For bulbuls, *A. ochraceus* occupies submontane and montane forest, and *P. leucops* is restricted to montane and elfin forest surrounding high mountain summits (Harris et al. 2012; Sheldon 2015). The low elevation *A. ochraceus* (~50 g) is larger than the high elevation *P. leucops* (~30 g). Both bulbul species are primarily frugivorous, forage in the subcanopy and understory and build nests in small saplings and shrubs (Smythies 1999; AJB, personal observation). For white-eyes, *Z. atricapilla* inhabits submontane and montane forest and scrub, while *C. emeliae* is restricted to montane forest and high-elevation elfin forest (Harris et al. 2012; Sheldon et al. 2015). The high elevation *C. emeliae* (~15 g) is larger than the lower elevation *Z. atricapilla* (~9 g). White-eyes feed primarily on fruit and nectar throughout forest strata and along habitat edges and build nests in a variety of substrate in the subcanopy (Smythies 1999; AJB, personal observation). Although not congeners by current taxonomy, both pairs are each other's closest relative at the site. Furthermore, recent phylogenetic studies show *Chlorocharis* nested within the *Zosterops* clade (Moyle et al. 2009).

We chose 2 understory flycatchers (*Muscicapidae*) as our sympatric species pair; snowy-browed flycatcher (*Ficedula hyperythra*) and eyebrowed jungle-flycatcher (*Vauriella gularis*). Both species are common residents in submontane and montane forest and, feed primarily on insects and small invertebrates taken on the ground and understory, and construct nests of live moss in trees/shrubs from 1 to 6 m above ground (Smythies 1999; AJB, personal observation). *Vauriella gularis* (~25 g) is larger than *F. hyperythra* (~8 g).

All 3 species pairs have easily recognizable songs that differ qualitatively within each pair in both sound and pattern of delivery (Supplementary Figures S1–S6). Playback experiments for mid-elevation species and sympatric flycatchers were conducted in the vicinity of Park Headquarters (1450–1850 m). Experiments for high elevation species were conducted in the vicinity of Laban Rata substation (3000–3450 m). Logistical difficulties prevented intensive sampling at intervening elevations.

Territories of focal species for both recordings and playback trials were located opportunistically throughout the study area during point counts and other concurrent fieldwork. Locations of singing birds were recorded using a Garmin GPSMap 60CSx portable GPS unit (Garmin International, Olathe, KS). Song recordings were made using a Sennheiser ME67 shotgun microphone (Sennheiser, Old Lyme, CT) and a Marantz PMD661 digital recorder (Marantz, Chatsworth, CA). All recordings were postprocessed in Raven Pro (Bioacoustics Research Program 2014) to filter out low-frequency background noise (<750 Hz), to amplify recordings to normalize amplitude across all recordings, and to clip recordings to identical length. Each recording was only used once, and was chosen at random to avoid pseudo-replication (Kroodsma et al. 2001).

Each playback trial was structured to include 3 auditory stimuli; conspecific song, putative competitor song, and control species song. We chose Golden-naped Barbet (*Psilopogon pulcherrimus*) as a control because it occupies a divergent niche from all focal species as a canopy frugivore and cavity-nester and is common and vocal at both mid and high elevation sites. Observations of the focal bird were made during 1 min of playback and 1 subsequent min of silence. We then waited a further 2 min before continuing the trial with the next stimulus. Conspecific playback was always played last to avoid elevating the focal bird to a heightened state of territoriality before control or heterospecific playback. Heterospecific and control stimuli were shuffled randomly.

To broadcast playback stimuli, we used a waterproof speaker (Grace Digital, Inc., San Diego, CA) and an Apple iPod Nano (Apple, Inc., Cupertino, CA). During playback trials we noted distance from the focal individual to the speaker following all movements of more than 1 m and noted all vocalizations of the focal individual. Distances were estimated visually and aurally during trials and calibrated afterwards using a digital rangefinder. In some cases, the focal individual left the immediate area during or in between stimuli or became silent and obscured such that observation was impossible. In other cases, conspecific (nontarget) individuals responded to stimuli making it difficult to keep track of the target individual and potentially altering the behavior of the target individual. If data had been successfully collected for at least 1 stimulus, the trial was resumed within 48 h. If not, the trial was abandoned and re-attempted at a later date.

Statistical analyses

Behavioral observations were transformed into 3 indices of aggression; closest approach to speaker, latency to approach speaker, and number of vocalizations. If the focal individual did not approach the speaker, we recorded the maximum value of 120 s. Closest approach to speaker was square-root transformed due to a right-skewed distribution. We performed principle components analysis to reduce these 3 behavioral variables into a single index of aggressiveness (Freeman 2016b). Because species may respond aggressively in different ways (i.e., vocalizations vs. physical approach) we performed separate PCAs for each species. All 3 behavioral variables were scaled before PCA. We generated PCA scores for each stimulus for each individual based on the first principle component as our index of overall aggression. We then fit linear mixed-effects models for each species with aggression (PC1) as the dependent variable, stimuli type as a fixed effect and individual as a random effect. We performed post hoc Tukey multicomparison tests in package "multcomp" to compare the intensity of aggression between control, conspecific, and heterospecific stimuli. Identical analyses were performed on each behavioral variable independently to characterize species-specific aggressive responses. While the same data were used in both sets of analyses, only the PCA-based metrics of aggression were used to determine levels of interspecific aggression. All statistical analyses were performed in R (R Core Team 2015).

RESULTS

Elevational ranges

Bulbul species on Mt. Kinabalu showed no elevational overlap and a significant elevational gap was present between high and low elevation species. Ochraceus Bulbul (*A. ochraceus*) occupied forest from the park boundary at 1450 to 1810 m. Pale-faced Bulbul (*P. leucops*) occupied forest from 1890 to 3332 m. White-eyes showed a broadly parapatric distribution, but overlapped at their mutual boundary. Black-capped White-eye (*Z. atricapilla*) occupied forest from the nearest park boundary at 1450–2131 m. Mountain Blackeye (*C. emeliae*) was present from 1845 to 3681 m. The 2 species both occupied an approximately 300 m zone of overlap and were sometimes detected on the same point counts within this zone. Of 27 point counts during which a *Zosteropidae* species was detected in the zone of overlap, both species were present 18.5% (5 of 27) of the time. However, this low percentage was mainly driven by the lower overall abundance of *Z. atricapilla* at these elevations. On counts where *Z. atricapilla* was detected, both species were present 50% (5 of 10) of the time. The 2 focal flycatcher species were sympatric throughout our mid elevation study site. Eyebrowed Jungle-Flycatcher (*V. gularis)* was present from the park boundary at 1450–1850 m. Snowy-browed Flycatcher (*F. hyperythra*) occurred from the park boundary at 1450–2924 m. Both species were encountered on the same point count on 16% (4 of 25) of counts with at least 1 species of flycatcher. This estimate likely understates their degree of overlap due to difficulty in detecting *V. gularis*. On counts where *V. gularis* was detected, both species were present on 80% (4 of 5) of counts. Based on mark recapture studies, both species are widespread and abundant between 1450 and 1850 m (Martin et al. 2015a; Martin et al. 2017b).

Playback experiments

We conducted a total of 47 playback experiments on 6 species ($\bar{x}$ = 7.83, range: 6–11 individuals). All species showed an aggressive response to conspecific playback compared with a control, but responses to parapatric or sympatric relatives varied among species (Figures 1 and 2). The first principal component from our PCA had parallel loadings for all 3 behavioral variables across all species. That is, positive scores indicate closer approach to the speaker, shorter latency to approach and increased vocalization rate.

Among parapatric bulbuls, interspecific aggression was strongly asymmetric (Figures 1A and 2A). The first principle component

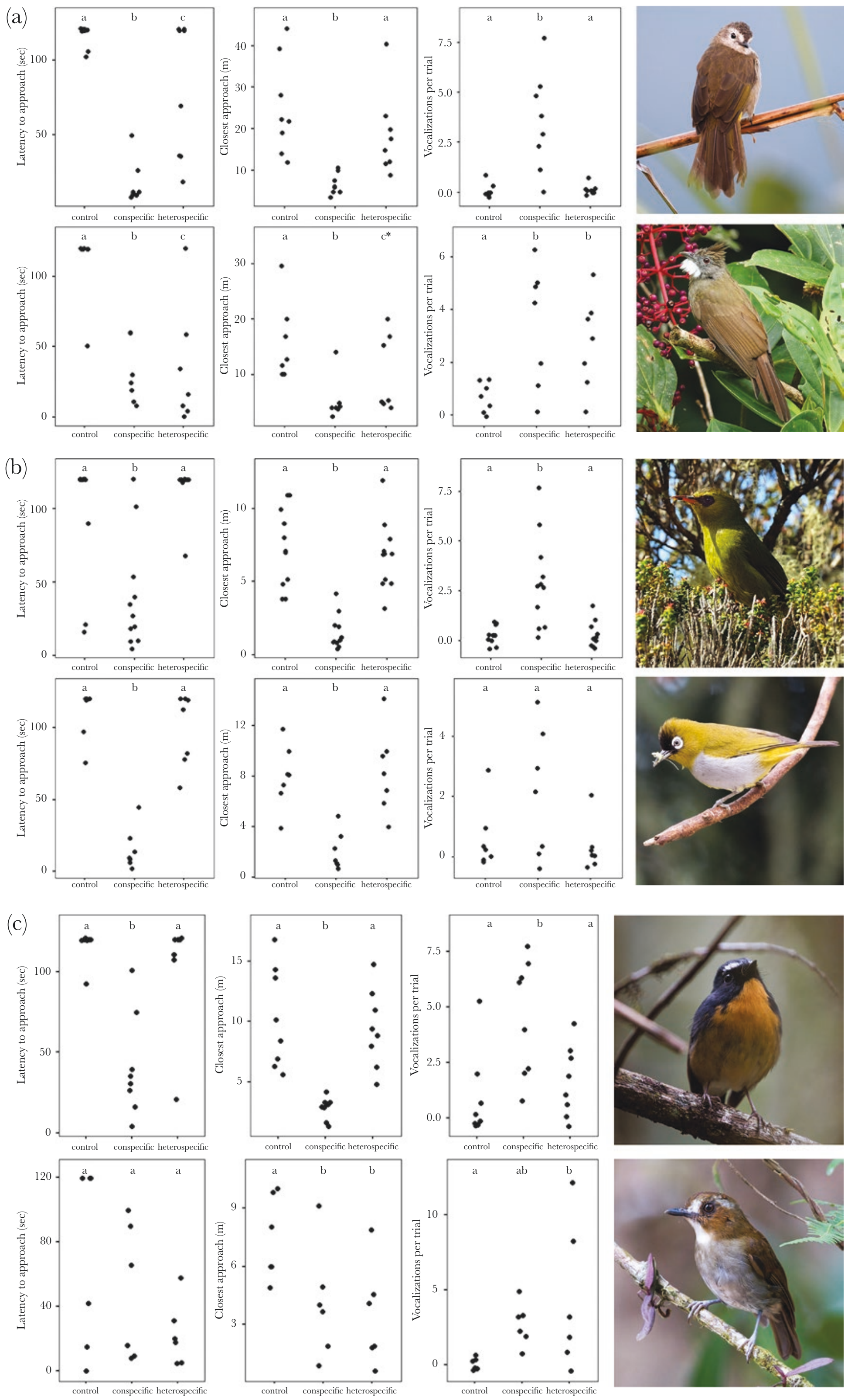

Figure 1

Behavioral responses (distance of closest approach, latency to approach, and number of calls) to control, conspecific and heterospecific playback stimuli in 2 elevationally parapatric species pairs (A, B) and one sympatric species pair (C). Letters above boxplots indicate significant behavioral differences ($P < 0.05$) between stimuli based on post hoc Tukey multicomparison tests. An asterisk (*) indicates a difference with marginal significance ($0.05 < P < 0.10$). For parapatric pairs, high elevation species are shown in the upper panels. For sympatric flycatchers, *Ficedula hyperythra* is in the upper panel, *Vauriella gularis* in the lower panel. Photo credits: *Alophoixus ochraceus*; Chien Lee, *Chlorocharis emeliae*; Cede Prudente.

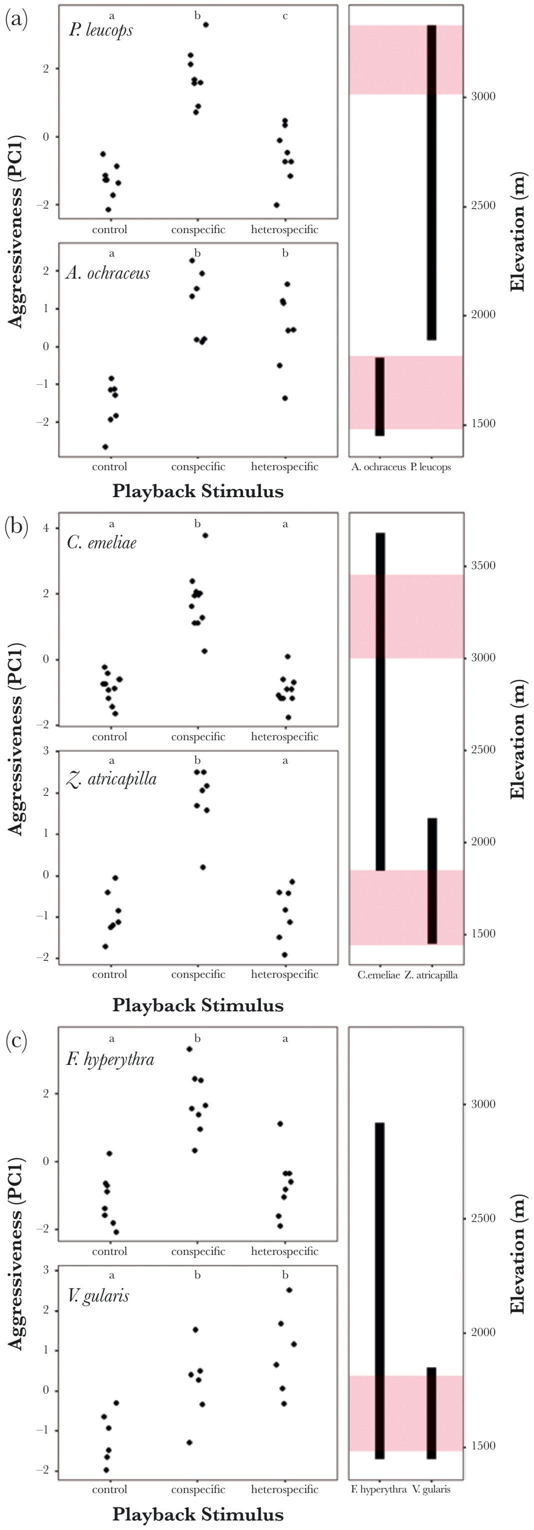

Figure 2

Aggressive responses to control, conspecific and heterospecific playback stimuli in 2 elevationally parapatric species pairs (A, B) and 1 sympatric species pair (C). Higher aggression scores indicate a stronger response. Letters above strip charts indicate significant differences between stimuli based on post hoc Tukey multicomparison tests ($P < 0.05$). High elevation species are shown in the upper panels and vice versa. Elevational distributions within our study site based on point count surveys are depicted in the vertical panel. These ranges are artificially constrained at ~1450 m at the lower park boundary and do not represent the full elevational ranges of these species.

explained 67% of the total variance in behavioral variables for *A. ochraceus* and 75% of total variance for *P. leucops*. *A. ochraceus*, the low-elevation species, responded aggressively to both conspecific playback and heterospecific playback compared with the control ($P < 0.01$, $P = 0.02$) and with equal intensity to both ($P = 0.12$). *Pycnonotus leucops*, the high-elevation species, frequently flew up to an exposed perch affording longer sightlines and sometimes engaged in short approach flights in response to heterospecific playback, such that the response differed significantly from a control (Figure 1A, $P = 0.04$). However, the response to conspecific playback was stronger ($P < 0.01$) and was characterized by frequent vocalizations and a rapid, close approach.

Among parapatric white-eyes, interspecific aggression was completely absent (Figures 1B and 2B). The first principal component explained 72% and 68% of total variance in behavioral variables for *Z. atricapilla* and *C. emeliae*, respectively. *Zosterops atricapilla*, the low-elevation species, responded aggressively to conspecific playback ($P < 0.01$), but did not show any difference in behavior in response to heterospecific playback and the control ($P = 0.92$). Similarly, *C. emeliae*, showed a strong aggressive response to conspecific playback ($P < 0.01$), but was unresponsive to heterospecific playback ($P = 0.68$).

Among sympatric flycatchers, interspecific aggression was strongly asymmetric (Figures 1C and 2C). The first principal component explained 79% and 61% of total variance in behavioral variables for *F. hyperythra* and *V. gularus*, respectively. *Ficedula hyperythra*, responded aggressively to conspecific playback ($P < 0.01$), but did not show a difference in aggression in response to heterospecific playback compared with the control ($P = 0.31$). *Vauriella gularis*, showed a strong aggressive response to both conspecific ($P = 0.02$) and heterospecific playback ($P < 0.01$) compared with the control.

DISCUSSION

Interspecific competition mediated by interspecific aggression is thought to drive parapatric distributions of closely related vertebrate species on environmental gradients (Terborgh and Weske 1975; Robinson and Terborgh 1995; Jankowski et al. 2010). Here, we found interspecific aggression between 1 pair of elevationally parapatric species but a complete absence of aggression in another. Furthermore, we detected strong interspecific aggression between broadly sympatric species. In the one case where interspecific aggression was present among parapatric species, we found it to be asymmetric such that the low elevation species was more aggressive toward its high-elevation counterpart than vice versa. This pattern fits with predictions from theory (MacArthur 1972) and observations in other systems (Jankowski et al. 2010) that low elevation species occupying abiotically benign habitat are likely to be competitively dominant over high elevation species tolerating abiotic challenges. However, the absence of aggression between another parapatric pair suggests that interspecific aggression is not a prerequisite for, nor an inevitable result of elevational parapatry.

An absence of aggression has been observed in parapatric species pairs with significant elevational gaps, leading to the suggestion that frequent interactions may be a necessary prerequisite for interspecific aggression (Freeman 2016a).While that possibility remains, our results in white-eyes suggest that spatial separation is not required to facilitate benign interactions between closely related species (Figure 1B). More importantly, if interspecific aggression consistently evolves in the presence of interference competition, we can rule out interference competition as a driver of elevational parapatry in white-eyes.

Causes for the variation in heterospecific response between bulbuls and white-eyes are not readily apparent. Theory predicts that interspecific competition should be strongest between species with the greatest niche overlap (MacArthur and Levins 1967). We did not attempt to quantify niche overlap between species pairs, but due to niche conservatism, niche overlap is generally expected to be highest between close relatives (Peterson et al. 1999). Of the 3 pairs studied here, white-eyes share the most recent common ancestor at no more than 2.3 mya (Moyle et al. 2009). In contrast, our focal pairs of bulbuls and flycatchers are far more phylogenetically distant (Zuccon and Ericson 2010; Shakya and Sheldon 2017). Therefore, it seems unlikely that niche divergence explains variation in heterospecific responses in these groups. Larger species are typically dominant when interpecific aggression is assymetric (Robinson and Terborgh 1995; Martin and Martin 2001a, 2001b; Martin and Ghalambor 2014). In parapatric bulbuls and sympatric flycatchers, the larger species was indeed dominant. However, size disparities do not explain the lack of aggression in white-eyes, as high-elevation *C. emeliae* is significantly larger than *Z. atricapilla*.

Phylogenetic relatedness may not provide the best proxy for expected intensity of heterospecific interactions. The abundance and distribution of resources can also influence the degree of aggression between species such that highly dispersed or clustered resources may not be easily defendable and lead to selection against territorial aggression (Brown 1964; Peiman and Robinson 2010). For example, both white-eyes are primarily nectarivorous and rely on flowers that are typically patchy and ephemeral food sources, but also frugivorous on small fruits that are also typically patchy and ephemeral. Aggression may not be favored in this situation if these characteristics mean that resources are not easily defendable and thus interspecific aggression may play a weaker role in influencing elevational range limits in this group.

In parapatric species pairs, asymmetric aggression has been interpreted as a force causing spatial segregation (Jankowski et al. 2010). However, interspecific aggression in co-occurring relatives appears to be common, with the vast majority of interactions being asymmetric (Martin and Martin 2001a, 2001b; Freeman 2016b; Martin et al. 2017a; Figure 2C). Because there is no categorical difference between asymmetric aggression in broadly sympatric species pairs and between parapatric pairs near their mutual boundary, interspecific aggression alone is not sufficient evidence to suggest interference competition is the primary driver of parapatric distributions. While interference competition may play a role in driving parapatry, the presence of asymmetric aggression between species that occasionally interact is a reasonable null hypothesis rather than confirmation of particularly intense competition driving complete parapatry. Interspecific aggression may still be important in both contexts. Interspecific aggression can drive niche displacement in co-occurring species with consequences for fitness and demography (Grether et al. 2009; Martin and Martin 2001b). Thus, costs of coexistence mediated by interspecific aggression may act to influence range boundaries in combination with other factors in both sympatric and parapatric species pairs.

The intensity of interspecific aggression often increases with proximity to a zone of interaction, suggesting a learned component as opposed to an evolved response (Jankowski et al. 2010; Freeman 2016b, 2016a). We did not specifically test whether proximity to range boundary was related to response intensity in our focal species, but our results still speak to this question. *Pycnonotus leucops* showed a significant heterospecific response (Figure 1A) during playback trials between 3000 and 3450 m, at least 1200 m above the closest territory of *A. ochraceus*. We find it unlikely that dispersal over such a distance is common in a small, territorial songbird, suggesting that interspecific aggression in songbirds may have both evolved and learned components. Observations of interspecific aggression in completely allopatric populations of sunbirds (Nectarinidae) indicate that evolved aggressive responses may be widespread in songbirds (McEntee 2014).

Increasingly, interspecific interactions are being incorporated into species distribution models and models aiming to predict future range shifts in light of climate or other anthropogenic change (Belmaker et al. 2015; Engler et al. 2017). Our results provide evidence that interspecific aggression is present between some pairs of parapatric species. However, we also show that interspecific aggression is not a prerequisite for parapatry. Thus, workers seeking to identify biotic interactions that may influence range dynamics must be cautious when inferring biotic processes from distributional patterns. Drivers of elevational range boundaries may differ substantially among clades. Understanding the causes and correlates of this variation is critical to accurately predicting range dynamics in light of changing biotic and abiotic conditions.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

FUNDING

This work was supported by the National Science Foundation (DEB-1241041, DEB-1651283, and IOS-1656120 to T.E.M.), an AOU Graduate Student Research Grant and the Wesley M. Dixon Memorial Fellowship to A.J.B.

We are grateful to our lab and 2 anonymous reviewers for helpful comments on the article. We would like to thank Alim Biun, Dr. Maklarin Lakim, Rimi Repin, and Fred Tuh from Sabah Parks, and C.Y. Chung from the Sabah Biodiversity Centre for assistance in Malaysia. A.J.B. would also like to thank Connor Armstad, Adam Mitchell, James Mouton, Ahva Potticary, and Riccardo Ton for invaluable assistance in the field. This work was performed under the auspices of University of Montana IACUC protocol #059-10TMMCWRU. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US Government.

Data Accessibilty: Analyses reported in this article can be reproduced using the data provided by Boyce and Martin (2019).

Handling editor: Andrea Griffin

REFERENCES

Belmaker J, Zarnetske P, Tuanmu MN, Zonneveld S, Record S, Strecker A, Beaudrot L. 2015. Empirical evidence for the scale dependence of biotic interactions. Glob Ecol Biogeogr. 24:750–761.

Bioacoustics Research Program. 2014. Raven Pro: interactive Sound Analysis Software. Ithaca (NY): The Cornell Lab of Ornithology. Available from: http://www.birds.cornell.edu/raven

Boyce AJ, Martin TE. 2019. Data from: interspecific aggression among parapatric and sympatric songbirds on a tropical elevational gradient. Dryad Digital Repository. http://dx.doi.org/10.5061/dryad.gc06qt7.

Brown JL. 1964. The evolution of diversity in avian territorial systems. Wilson Bull. 76:160–169.

Cadena CD, Kozak KH, Gómez JP, Parra JL, McCain CM, Bowie RCK, Carnaval AC, Moritz C, Rahbek C, Roberts TE, et al. 2011. Latitude, elevational climatic zonation and speciation in New World vertebrates. Proc R Soc B Biol Sci. 279:194–201.

Cadena CD, Loiselle BA. 2007. Limits to elevational distributions in two species of emberizine finches: disentangling the role of interspecific competition, autoecology, and geographic variation in the environment. Ecography. 30:491–504.

Colwell RK, Brehm G, Cardelús CL, Gilman AC, Longino JT. 2008. Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. Science. 322:258–261.

Connell JH. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. Ecology. 42:710–723.

Diamond JM. 1973. Distributional ecology of New Guinea birds. Science. 179:759–769.

Engler JO, Stiels D, Schidelko K, Strubbe D, Quillfeldt P, Brambilla M 2017. Avian SDMs: current state, challenges, and opportunities. J Avian Biol. 48:1483–1504.

Freeman BG. 2015. Competitive interactions upon secondary contact drive elevational divergence in tropical birds. Am Nat. 186:470–479.

Freeman BG. 2016a. Asymmetric interspecific aggression in New Guinean songbirds that replace one another along an elevational gradient. Ibis. 158:726–737.

Freeman BG. 2016b. Strong asymmetric interspecific aggression between two sympatric New Guinean robins. Ibis. 158:75–81.

Freeman BG, Montgomery G 2016. Interspecific aggression by the Swainson's Thrush (*Catharus ustulatus*) may limit the distribution of the threatened Bicknell's Thrush (*Catharus bicknelli*) in the Adirondack Mountains. Condor. 118:169–178.

Gifford ME, Kozak KH. 2011. Islands in the sky or squeezed at the top? Ecological causes of elevational range limits in montane salamanders. Ecography. 34:1–11.

Grether GF, Losin N, Anderson CN, Okamoto K. 2009. The role of interspecific interference competition in character displacement and the evolution of competitor recognition. Biol Rev Camb Philos Soc. 84:617–635.

Harris JBC, Sheldon FH, Boyce AJ, Eaton JA, Bernard H, Langevin A, Martin TE, Wei D. 2012. Using diverse data sources to detect elevational range changes of birds on Mount Kinabalu, Malaysian Borneo. Raffles Bull Zool. S25:197–247.

Heller HC. 1971. Altitudinal zonation of chipmunks (Eutamias): interspecific aggression. Ecology. 52:312–319.

Huey R. 1978. Latitudinal pattern of between-altitude faunal similarity: mountains might be "higher" in the tropics. Am Nat. 112:225–229.

Jankowski JE, Londo GA, Robinson SK, Chappell MA 2012. Exploring the role of physiology and biotic interactions in determining elevational ranges of tropical animals. Ecography. 35:1–12.

Jankowski JE, Robinson SK, Levey DJ. 2010. Squeezed at the top: interspecific aggression may constrain elevational ranges in tropical birds. Ecology. 91:1877–1884.

Kroodsma DE, Byers BE, Goodale E, Johnson S, Liu W-C. 2001. Pseudoreplication in playback experiments, revisited a decade later. Anim Behav. 61:1029–1033.

MacArthur RH. 1972. Geographical ecology. Princeton (NJ): Princeton University Press.

MacArthur R, Levins R. 1967. The limiting similarity, convergence, and divergence of coexisting species. Am Nat. 101:377–385.

Martin PR, Freshwater C, Ghalambor CK. 2017a. The outcomes of most aggressive interactions among closely related bird species are asymmetric. PeerJ. 5:e2847.

Martin PR, Ghalambor CK. 2014. When David beats Goliath: the advantage of large size in interspecific aggressive contests declines over evolutionary time. PLoS One. 9:e108741.

Martin PR, Martin TE. 2001a. Behavioral interactions between coexisting species: song playback experiments with wood warblers. Ecology. 82:207–218.

Martin PR, Martin TE. 2001b. Ecological and fitness consequences of species coexistence: a removal experiment with wood warblers. Ecology. 82:189–206.

Martin TE, Oteyza JC, Boyce AJ, Lloyd P, Ton R. 2015a. Adult mortality probability and nest predation rates explain parental effort in warming eggs with consequences for embryonic development time. Am Nat. 186:223–236.

Martin TE, Oteyza JC, Mitchell AE, Potticary AL, Lloyd P. 2015b. Postnatal growth rates covary weakly with embryonic development rates and do not explain adult mortality probability among songbirds on four continents. Am Nat. 185:380–389.

Martin TE, Riordan MM, Repin R, Mouton JC, Blake WM. 2017b. Apparent annual survival estimates of tropical songbirds better reflect life history variation when based on intensive field methods. Glob Ecol Biogeogr. 26:1386–1397.

McCain CM. 2009. Vertebrate range sizes indicate that mountains may be 'higher' in the tropics. Ecol Lett. 12:550–560.

McEntee JP. 2014. Reciprocal territorial responses of parapatric African sunbirds: species-level asymmetry and intraspecific geographic variation. Behav Ecol. 25:1380–1394.

Merckx VS, Hendriks KP, Beentjes KK, Mennes CB, Becking LE, Peijnenburg KT, Afendy A, Arumugam N, de Boer H, Biun A, et al. 2015. Evolution of endemism on a young tropical mountain. Nature. 524:347–350.

Moyle RG, Filardi CE, Smith CE, Diamond J. 2009. Explosive pleistocene diversification and hemispheric expansion of a "great speciator." Proc Natl Acad Sci USA. 106:1863–1868.

Peiman KS, Robinson BW. 2010. Ecology and evolution of resource-related heterospecific aggression. Q Rev Biol. 85:133–158.

Peterson AT, Soberón J, Sanchez-Cordero V. 1999. Conservatism of ecological niches in evolutionary time. Science. 285:1265–1267.

R Core Team. 2015. R: a language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing. Available from: https://www.r-project.org

Rafiqpoor MD, Nieder J. 2006. Altitudinal zonation of climate and vegetation in a global megadiversity centre, Mount Kinabalu (North Borneo). Erdkunde. 60:362–374.

Remsen JV Jr, Graves WS IV. 1995a. Distribution patterns of Buarremon brush-finches (Emberizinae) and interspecific competition in Andean birds. Auk. 112:225–236.

Remsen JV Jr, Graves WS IV. 1995b. Distribution patterns and zoogeography of Atlapetes brush-finches (Emberizinae) of the Andes. Auk. 112:210–224.

Robinson SK, Terborgh J. 1995. Interspecific aggression and habitat selection by Amazonian birds. J Anim Ecol. 64:1–11.

Sekercioglu CH, Schneider SH, Fay JP, Loarie SR. 2008. Climate change, elevational range shifts, and bird extinctions. Conserv Biol. 22:140–150.

Shakya SB, Sheldon FH. 2017. The phylogeny of the world's bulbuls (Pycnonotidae) inferred using a supermatrix approach. Ibis. 159:498–509.

Sheldon FH. 2015. Gazetteer and site-based history of the ornithlogy of Sabah, Borneo. Occasional Papers Museum Nat Sci, Louisiana State Univ. 86:1–91.

Sheldon FH, Lim HC, Moyle RG. 2015. Return to the Malay Archipelago: the biogeography of Sundaic rainforest birds. J Ornithol. 156:91–113.

Smythies BE. 1999. In: Davison GWH, editors. The birds of Borneo. 4th ed. Kota Kinabalu: Natural History Publications (Borneo).

Stevens GC. 1992. The elevational gradient in altitudinal range: an extension of Rapoport's latitudinal rule to altitude. Am Nat. 140:893–911.

Stotz DF, Fitzpatrick JW, Parker TA, Moskovits DK. 1996. Neotropical birds. Chicago: Chicago University Press.

Terborgh J. 1971. Distribution on environmental gradients: theory and a preliminary interpretation of distributional patterns in the avifauna of the Cordillera Vilcabamba, Peru. Ecology. 52:23–40.

Terborgh J, Weske JS. 1975. The role of competition in the distribution of Andean birds. Ecology. 56:562–576.

Zuccon D, Ericson PGP. 2010. A multi-gene phylogeny disentangles the chat-flycatcher complex (Aves: Muscicapidae). Zool Scr. 39:213–224.