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Squeezed at the top: Interspecific aggression may constrain elevational ranges in tropical birds

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Abstract. Tropical montane species are characterized by narrow elevational distributions. Recent perspectives on mechanisms maintaining these restricted distributions have emphasized abiotic processes, but biotic processes may also play a role in their establishment or maintenance. One historically popular hypothesis, especially for birds, is that interspecific competition constrains ranges of closely related species that "replace" each other along elevational gradients. Supporting evidence, however, is based on patterns of occurrence and does not reveal potential mechanisms. We experimentally tested a prediction of this hypothesis in two genera of tropical songbirds, *Catharus* (Turdidae) and *Henicorhina* (Troglodytidae), in which species have nonoverlapping elevational distributions. Using heterospecific playback trials, we found that individuals at replacement zones showed aggressive territorial behavior in response to songs of congeners. As distance from replacement zones increased, aggression toward congener song decreased, suggesting a learned component to interspecific aggression. Additionally, aggressive responses in *Catharus* were asymmetric, indicating interspecific dominance. These results provide experimental evidence consistent with the hypothesis that interspecific competitive interactions restrict ranges of Neotropical birds. Our results also underscore the need to consider biotic processes, such as competition, when predicting how species' ranges will shift with climate change. Asymmetric aggression could be particularly important. For example, if warming in montane landscapes allows upslope range expansion by dominant competitors, then high-elevation subordinate species could be forced into progressively smaller mountaintop habitats, jeopardizing viability of their populations.

Key words: biotic interactions; climate change; cloud forest; competition; gradient; range limits; species replacement.

Introduction

Tropical montane plants and animals are typically restricted to narrow, belt-like elevational distributions, often only a few hundred meters wide (Stotz et al. 1996, Vásquez and Givnish 1998, Jankowski et al. 2009). This elevational specialization of species leads to high species turnover or "beta-diversity" along tropical elevational gradients, making these landscapes important centers of global biodiversity and endemism (Stotz et al. 1996, Myers et al. 2000). Although distributions of tropical montane species are becoming increasingly well documented through investigation of species richness and turnover patterns (Patterson et al. 1998, Herzog et al. 2005, Jankowski et al. 2009, Romdal and Rahbek 2009), there is little understanding of the processes acting at range boundaries to maintain these species' narrow elevational distributions. Research focused on understanding species' range limits, however, is of immediate importance in the context of climate change; our ability to predict how climate changes will drive range shifts and possible extinctions hinges on understanding the factors that determine where a given species occurs. In particular, species with restricted distributions along elevational gradients may be highly vulnerable (Parmesan 2006, Colwell et al. 2008, Sekercioglu et al. 2008).

Range boundaries are generated by multiple abiotic and biotic factors that influence the persistence of populations (see Holt and Keitt 2005); a combination of such factors could lead to narrow distributions of tropical montane species. Recent studies have emphasized abiotic, physiologically based explanations, in

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which small seasonal variation in thermal regimes leads to physiological specialization, as classically proposed by Janzen (1967; see also Ghalambor et al. 2006, McCain 2009). Tropical ectotherms, for example, appear less able than temperate ectotherms to tolerate widely varying thermal conditions and may be at greater risk from global climate change (Tewksbury et al. 2008, Huey et al. 2009).

Likewise, range boundaries may be influenced by biotic interactions (Case et al. 2005, Price and Kirkpatrick 2009). In the tropics, direct interspecific competitive interactions at range boundaries constitute another classic hypothesis of what limits species' distributions in montane landscapes (Terborgh 1971, Diamond 1973). Such interactions should result in elevational gradients that are partitioned into nonoverlapping ranges of competing species, compressing the distributions of any single competitor. Along many tropical mountainsides, there is strong evidence for such "replacements" between closely related species (Bull 1991), especially in birds (Terborgh 1971). Demonstration of range compression of species in areas with competitors present, and range expansion where competitors are absent, is consistent with this hypothesis (Terborgh and Weske 1975, Remsen and Graves 1995), but experimental support for competitive interactions between species in replacement zones is still lacking.

Here we test a prediction of the hypothesis that competitive interactions, in the form of interspecific aggression, determine species' range limits along an elevational gradient in the Tilarán Mountains of Costa Rica. We focus our study on two passerine genera with species that show distinct elevational replacements: wood-wrens (*Henicorhina*, Troglodytidae) and nightingale-thrushes (*Catharus*, Turdidae). Using a series of song playback experiments to detect aggressive territorial behaviors, which may reflect underlying competitive interactions (Martin and Martin 2001), we tested whether territorial individuals in species with elevational replacements respond aggressively to songs of congeners where their ranges meet. We analyzed each species' reaction to congener songs at increasing distances from replacement zones to determine whether responses were learned or, alternatively, whether they might reflect misdirected intraspecific aggression (the "mistaken identity" hypothesis of Murray 1971). Finally, we evaluated whether interspecific responses of species pairs at the replacement zone were asymmetric in their level of aggression, a likely indication of interspecific behavioral dominance (Robinson and Terborgh 1995).

METHODS

Study area and target species

The Tilarán Mountains of northwestern Costa Rica (10°18′ N, 84°45′ W; maximum altitude 1850 m) run northwest to southeast, with the continental divide separating the leeward Caribbean slope from the drier Pacific slope. The 36-km^2 study area ranges from 1000 to 1700 m altitude on the Pacific slope within 3.6 km of the continental divide. The study area shows dramatic changes in moisture, averaging 4000–6000 mm rainfall annually at the ridge top cloud forest and declining approximately 1000 mm/km downslope (see Jankowski et al. 2009 for more details).

Congeneric species with adjacent, nonoverlapping elevational distributions in the study area were selected for their patterns of replacement, relatively high local population densities, and accessibility of their replacement zones along the mountainside. Our focal species were two wood-wrens, *Henicorhina leucosticta* (White-breasted Wood-Wren), and *H. leucophrys* (Gray-breasted Wood-Wren), and three nightingale-thrushes, *Catharus aurantiirostris* (Orange-billed Nightingale-Thrush), *C. mexicanus* (Black-headed Nightingale-Thrush), and *C. fuscater* (Slaty-backed Nightingale-Thrush; see Plate 1). All of these species are largely restricted to forest understory and are partially to entirely insectivorous (Stiles et al. 1989). Along the elevational gradient, *H. leucosticta* and *C. aurantiirostris* inhabit drier, more seasonal low-elevation forest, whereas *H. leucophrys* and *C. fuscater* inhabit high-elevation moisture-saturated cloud forest. *C. mexicanus* has a narrow elevational distribution on the Pacific slope of 75–125 m (maximum 600 m horizontal distance) between the other two nightingale-thrushes.

Territory mapping, playback stimuli, and experiments

Territories of target species were located at their replacement zones, where individuals of each species are in daily contact with congeners, and at varying distances from replacement zones, up to 1.5 km (horizontal distance) within species' elevational ranges. For *C. mexicanus* no territories were more than 600 m from the replacement zone because of this species' extremely narrow range. Territories of *C. fuscater* were not studied away from the replacement zone because of the lack of behavioral responses toward its lower elevation congener, *C. mexicanus*, at the replacement zone (see *Results*). Prior to playback experiments, transects within the study site were walked daily, and the locations of singing individuals of target species were marked using a GPSMap 60CSx GPS unit (with an accuracy of ±6 m in forest; Garmin International, Olathe, Kansas, USA). These territory locations were revisited on multiple days thereafter. During this time, individuals' movements within their territory and simultaneous singing events with neighbors were noted to estimate the territory's center and to approximate its boundaries. Because our target species regularly sing throughout the morning from well-defined areas, we are confident that our method of territory mapping by simultaneous singing events with neighbors, coupled with observations of individuals' movements, is a reliable approach to distinguish territories of unbanded birds. Each territory along the gradient was assigned a proximity value to the replacement zone, defined by the distance between the

Plate 1. Two species of nightingale-thrushes used in song playback experiments in the Tilarán Mountains of Costa Rica: (left) *Catharus aurantiirostris* is found in drier forest at lower elevations, and (right) *C. fuscater* occupies high-elevation cloud forest. *C. mexicanus* (not shown) occurs at middle elevations between these two species. Photo credits: Aaron Spalding..

territory center and that of the nearest congener using ArcGIS 9.2 (Environmental Systems Research Institute 2007).

Songs used for playback stimuli were recorded within the study area in May of 2007 and 2008. Recordings were made from within 20 m of singing individuals not involved in interactions with neighbors, using a parabolic dish and microphone and an Edirol R-09 digital recorder (Roland Corporation U.S., Los Angeles, California, USA). Songs were filtered to remove low-frequency noise, generally below 750 Hz, and other unwanted noises such as other singing birds using Raven Pro 1.3 (Cornell Lab of Ornithology 2003). Waveforms in some recordings were amplified so that all recordings could be broadcast at equal volume. Each recorded song was presented as a playback stimulus to only one individual per species following recommendations by Kroodsma et al. (2001).

Playback experiments were conducted in May–June of 2007 and 2008 during the peak of the local breeding season when birds are actively singing and defending established territories. Each individual was tested on two days, usually within a five-day period. Tests consisted of an 8-minute observation period of the focal bird, during which no stimulus was given, followed immediately by either an 8-minute heterospecific (hereafter "congeneric") or conspecific playback broadcast by a speaker within the territory. The second test consisted of another 8-minute observation period followed by whichever playback was not performed on the first visit. The order of presentation of congener and conspecific playback stimuli was randomized. Observation and playback periods for each trial were recorded using an Edirol R-09 digital recorder and Sennheiser ME-66 microphone (Sennheiser Electronic Corporation, Old Lyme, Connecticut, USA) mounted on a tripod. Playback songs were played from a second recorder connected to a playback speaker (Dean Markley GT1000 Micro Amp; Dean Markley Strings, Santa Clara, California, USA) placed 5 m from the observers and approximately 15 m from the focal individual. Song stimuli were broadcast at approximately 70–80 dB SPL at 5 m (varying slightly across species) for up to 3 minutes or until the focal bird approached to within 5 m of the speaker.

Playbacks were conducted from 05:30 to 14:00, avoiding periods of heavy wind or rain. First, territorial males were located, usually by song. If the individual was involved in a counter-singing bout with a neighbor, we delayed the trial for several hours. If disputes persisted, no trials with that individual were attempted that day. If non-target individuals (congeneric or conspecific neighbors) approached the territory in response to the playback stimulus, we were thereafter unable to distinguish whether the target individual was responding to our playback or the presence of a non-target bird. In these situations, the playback was aborted and attempted on a different day. During the 8-minute observation and playback periods, all movements of the focal bird were mapped by noting the distances of the bird from the speaker and the amount of time spent in each location. Behavioral variables summarized from these data included closest approach to speaker and latency to approach the speaker to within 10 m.

In 2008, we used the same protocol as in 2007, except that we also conducted "control playbacks" for target individuals to evaluate use of pre-playback observation periods as a negative control. Stimuli for control playbacks used locally recorded songs from one of two common species: *Basileuterus culicivorous* (Golden-crowned Warbler, Family Parulidae) or *Hylophilus decurtatus* (Lesser Greenlet, Family Vireonidae). These species have wide elevational distributions and are sympatric but not known to interact with the target species. For all behavioral variables examined, we found no differences between control playbacks and observation periods prior to control playbacks nor between control playbacks and observation periods prior to congener or conspecific playbacks (Kruskal-Wallis nonparametric ANOVA; for all species and variables, χ^2 values range from 0.28 to 6.0, df $= 3$, P range from 0.11 to 0.96). Therefore, we pooled the behavioral data recorded during observation periods prior to congener and conspecific playbacks to use as a comparative stimulus type (hereafter "control") in statistical models of behavioral response to playback.

Statistical analysis

We analyzed behavioral response to playbacks for each species pair using both general and generalized linear mixed models performed in SAS/STAT v. 9.2 (SAS Institute 2008) for two groups: (1) individuals close to the replacement zone (wood-wrens $\leq$ 100 m; nightingale-thrushes $\leq$ 200 m) and (2) all individuals, at varying distances from the replacement zone. Each response variable (i.e., closest approach to speaker, and latency to approach to within 10 m) was analyzed separately for each pair of congeners sharing a range boundary. The response variable "closest approach to the speaker" was square-root transformed to achieve normality and was modeled using a general linear mixed model for individuals close to the replacement zone and for all individuals. The response variable "latency to approach the speaker" was analyzed using a logistic regression, which modeled the probability of a response during the playback period, given the explanatory variables. We used this procedure because many individuals did not approach to within 10 m (i.e., no response). Then, using only responding individuals close to the replacement zone, we performed a second analysis using a general linear mixed model to examine the time to approach to within 10 m (log transformed), given the explanatory variables. We report mixed-model results for time to approach for individuals close to the replacement zone, and we report logistic regression results for the probability of a response during the playback period when including all individuals. Explanatory variables for all models included stimulus (congener, conspecific, or control), species of the target individual, distance of the target individual's territory from the replacement zone (only for models including all individuals), and interaction terms. Individual was included as a repeated subject. For models with all individuals, if species was a significant term in the model ($P < 0.05$), each species was then analyzed separately to avoid modeling three-way interactions. Post-hoc tests for direct effects or interactions with categorical explanatory variables used least-squares mean difference with a Tukey adjustment to test for significant differences among levels. Contrast statements were used to test for significant differences among levels in the distance-stimulus interaction term, with distance as a continuous variable. See Appendix A for sample sizes of individuals tested for each species.

RESULTS

Individuals of each genus (*Henicorhina* and *Catharus*) responded aggressively to playbacks of congener songs. In wood-wrens, individuals with territories close to the replacement zone responded aggressively to playbacks of their congeners' songs, approaching on average 71% closer to the speaker and responding 85% faster compared to the control period (Fig. 1; Appendix B: Table B1; $t_{11} = 6.8$ and 7.8, respectively, both $P < 0.0001$). Wood-wrens responded to congener songs by approaching the speaker quietly with short flights through the understory, then singing near the speaker for several minutes. These responses to congener songs were not significantly different from responses to conspecific songs (closest approach, $t_{11} = 2.2$, $P = 0.11$; latency to approach, $t_{11} = 1.04$, $P = 0.32$). When considering individuals at varying distances from the replacement zone, we found that wood-wrens located farther from the replacement zone showed a decreased response to congener playbacks (Fig. 2; Appendix B: Table B2; contrasts of congener to control and conspecific playbacks, for closest approach, $F_{1,49} = 39.01$, $P < 0.0001$; for latency, $F_{1,141} = 12.2$, $P < 0.0006$). At distances > 1 km from the replacement zone, responses to congener playback did not differ from the control period (for closest approach and latency, $t_8 = -1.7$, both $P > 0.26$).

The low-elevation *C. aurantiirostris* and its middle-elevation congener, *C. mexicanus*, likewise responded to congener playbacks (Fig. 1; Appendix B: Table B1). These responses were strongest for *C. aurantiirostris*, which approached 69% closer to the speaker and responded 75% faster compared to control periods ($t_{11} = 5.8$ and $t_{22} = 3.5$, respectively, both $P < 0.02$). In this species, responses to congener and conspecific playbacks were similar, in both the closest approach and latency to respond ($t_{12} = 0.83$ and $t_{22} = -0.06$, respectively, both $P > 0.95$). *C. mexicanus*, on average, approached 27% closer and responded 57% faster to congener playbacks compared to controls ($t_{11} = 4.0$ and $t_{22} = 3.2$, respectively, both $P \leq 0.04$), but the response to congener playback in this species was not as aggressive as the response to conspecific playback (closest approach, $t_{12} = 4.0$, $P = 0.02$; latency, $t_{22} = 4.27$, $P = 0.004$). When considering individuals at varying distances from the replacement zone, we found that these two species of nightingale-thrushes showed weaker responses to congener playbacks farther from the replacement zone (Fig. 2; Appendix B: Table B2; closest approach *C. aurantiirostris*, $F_{1,25} = 10.8$, $P = 0.0003$; *C. mexicanus*, $F_{1,25} = 7.8$, $P = 0.01$; latency to approach significant for *C. aurantiirostris* only, $F_{1,50} = 7.1$, $P = 0.01$).

The middle-elevation *C. mexicanus* and its high-elevation congener, *C. fuscater*, responded differently

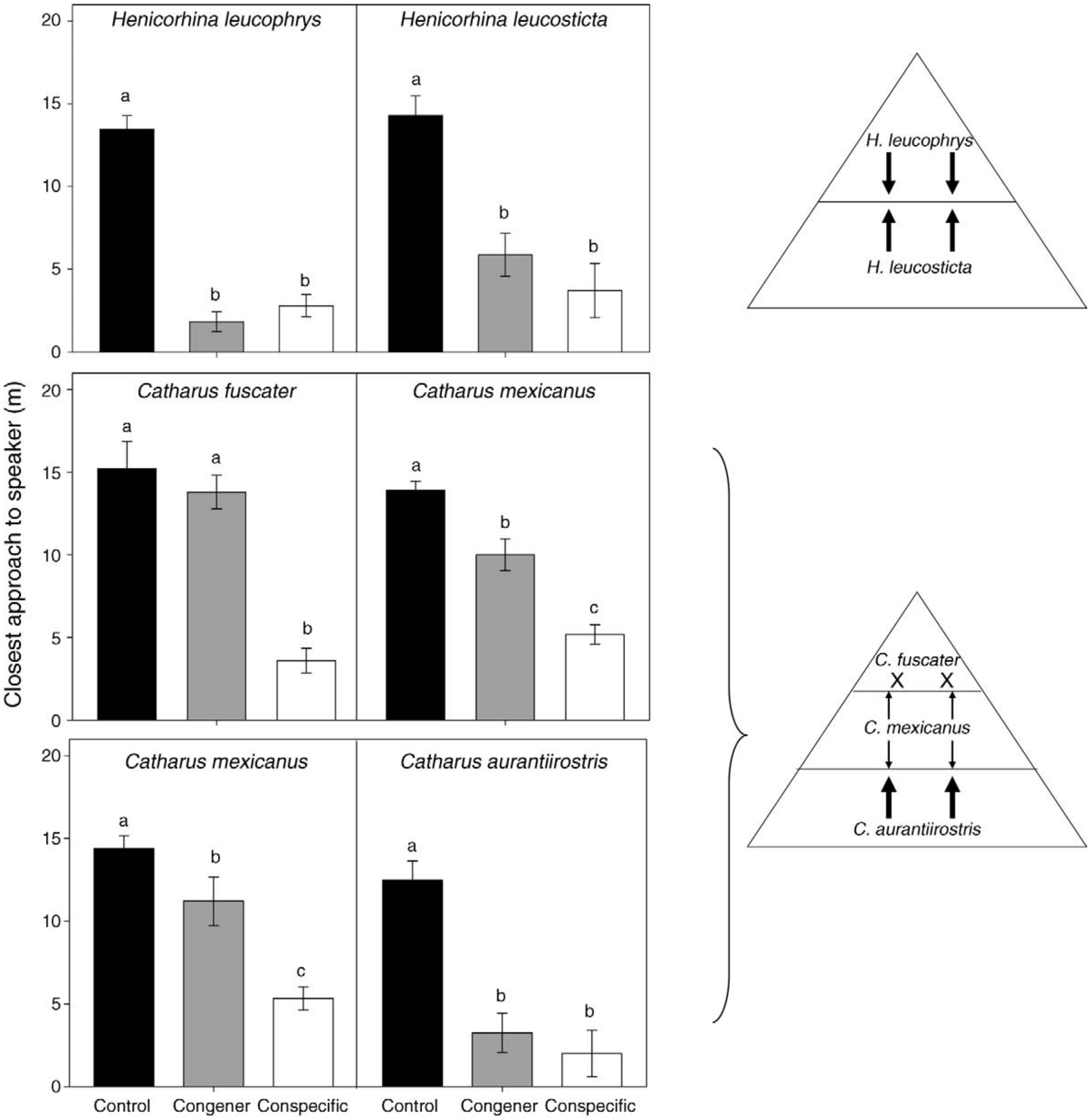

FIG. 1. Response to playback trials by individuals with territories near the replacement zone ($\leq$100 m for wood-wrens [*Henichorina* spp.], $\leq$200 m for nightingale-thrushes [*Catharus* spp.]). Bars show the closest approach to the speaker (mean ± SE) during control (black), congener (gray), and conspecific (white) trials for each pair of species tested. Values with different letters are significantly different for that species ($P < 0.02$; least-squares mean difference with Tukey adjustment). Schematics to right depict the elevational location of species, with arrows of different thickness indicating the relative strength of response to congener playbacks between species pairs at the replacement zone and "×" to indicate species with no response to congeners.

to congener playbacks. Compared to control periods, *C. mexicanus* approached on average 28% closer and responded 51% faster to congener playbacks (Fig. 1; Appendix B: Table B1; $t_{21} = 3.6$ and $t_{41} = 4.5$, respectively; both $P \leq 0.0008$). Its response to congener playbacks was nonetheless weaker than its response to conspecific playbacks (Fig. 1; closest approach, $t_{21} = 4.9$, $P = 0.001$; latency, $t_{41} = 7.5$, $P < 0.0001$). In this species, there was no change in the strength of the response to congener playbacks farther from the replacement zone (Appendix B: Table B2). In *C. fuscater*, response to congener playbacks did not differ from the control period (Fig. 1; Appendix B: Table B1; closest approach, $t_{21} = 0.6$; latency, $t_{41} = -0.28$; both $P = 0.99$), indicating no detectable aggressive response of this species toward *C. mexicanus*.

DISCUSSION

These results demonstrate aggressive interactions between species that replace each other along eleva-

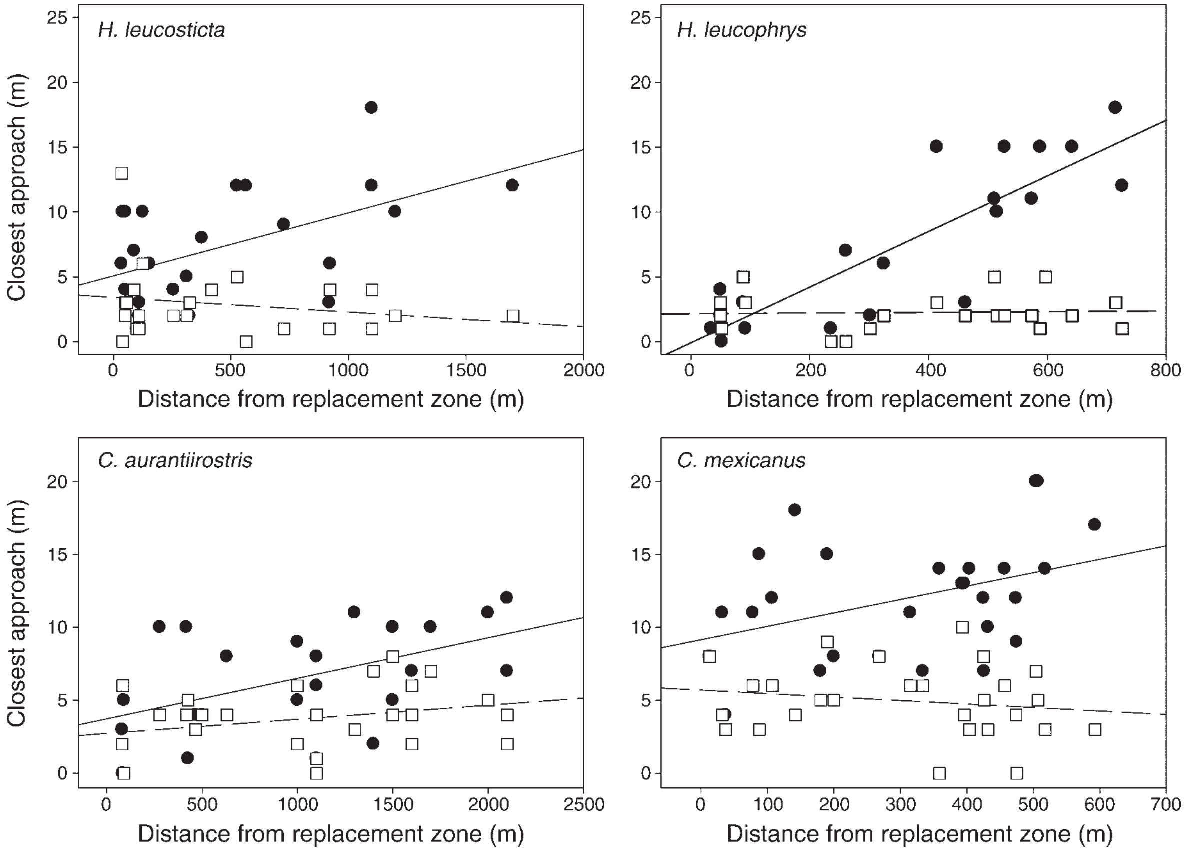

FIG. 2. Closest approach to the speaker in response to congener and conspecific playback trials for individuals found at increasing distances from the replacement zone. Solid circles show responses of each individual to congener playbacks (with solid best fit lines), and open squares show responses of individuals to conspecific playback trials (with dashed best fit lines). Species pairs shown have significant stimulus–distance interactions, where post hoc contrasts of congener response to combined control and conspecific response for each species are significant with $P \leq 0.01$.

tional gradients, consistent with the hypothesis that such biotic interactions are important in determining species' range limits in tropical montane landscapes (Terborgh and Weske 1975). The influence of interspecific competition on the spatial arrangement of species in sympatry has been suggested for many taxa, including fish (Bay et al. 2001), amphibians (Cunningham et al. 2009), reptiles (Langkilde and Shine 2004), and mammals (Brown 1971). In birds, such interactions can determine local habitat selection (Martin and Martin 2001), settlement patterns of migrants arriving to breeding grounds (Fletcher 2007), and spatial partitioning of closely related species along successional gradients (Robinson and Terborgh 1995). In particular, song playback experiments in birds have been shown to be an appropriate method to assess underlying competitive interactions between species; indeed, habitat segregation of species resulting from this behavior can confer higher fitness compared to individuals whose territories overlap with those of congeneric competitors (Martin and Martin 2001). Our observations of interspecific territorial aggression at range boundaries of species with replacements support the presence of competitive interactions and the importance of this biotic interaction in maintaining segregated distributions. Our study is the first to provide experimental support for the hypothesis that such interspecific competitive interactions could reinforce range boundaries that segregate species along large-scale elevational gradients in the tropics.

Our results are also unique in demonstrating that interspecific aggression varies greatly over small spatial scales. In particular, we discovered that interspecific aggression occurs primarily when individuals are in close contact with congeners and weakens with increasing distance from zones of replacement. This pattern is not consistent with the alternative hypothesis of response to congener song—that the responses simply reflect mistaken identity of congeners and misdirected intraspecific aggression (e.g., Murray 1971). Rather, assuming that our populations are not genetically divergent within the 4-km gradient of our site (which would be unlikely at this spatial scale in a primarily forested landscape lacking major dispersal barriers), our results suggest a learned component to aggressive interactions at range boundaries and a behavioral flexibility that allows finely tuned responses corresponding to the likelihood of encountering heterospecifics (see also Richards 1979). In this situation, the development of such behavioral interactions likely depends upon local densities of interacting species along gradients.

Species pairs tested at their replacement zone did not respond equally to playbacks of their congeners' songs. Whereas wood-wrens exhibited symmetric levels of interspecific aggression, nightingale-thrushes showed asymmetry in their territorial responses to congeners. The high-elevation *C. fuscater* showed no response toward songs of the middle-elevation *C. mexicanus*, whereas *C. mexicanus* responded aggressively to *C. fuscater* songs. Such asymmetries suggest that interspecific dominance in the aggressive species could limit some species to portions of the elevational gradient.

In light of climate change, interspecific aggression could have important implications for species with behavior-mediated elevational range limits, especially if high-elevation species were subordinate. If warming in montane climates allows upslope range expansion by dominant competitors, then high-elevation species could be forced to still higher elevations and become dependent on progressively smaller land areas to sustain viable populations. If interspecific aggression between congeners is widespread, many species could face such a scenario. Considering only species that are currently threatened with extinction, we estimate that 108 of 334 tropical montane species occurring at high elevations (approximately 9% of the 1184 threatened species, worldwide) have elevational ranges that are bordered by widespread low-elevation congeners (data from BirdLife International 2000). Dominant congeners at higher elevations could similarly prevent upslope expansion of subordinate species, squeezing middle-elevation species between an expanding suboptimal abiotic environment at the lower boundary and a resistant biotic upper boundary. In this scenario, dominant high-elevation species would be able to hold off upslope movement of lower-elevation species as true "kings of the hill" for much longer than predicted by climate models alone.

In conclusion, our results point to the importance of including biotic interactions in predicting community responses to climate change; doing so may be particularly important for diverse tropical systems. In the Tilarán Mountains, there is already evidence for climate-driven population declines and elevational range shifts across many taxa, including birds (Pounds et al. 1999). Under a moderate warming scenario of 3°C over the next century (IPCC 2007), montane species can be expected to shift their ranges 500 m upslope in response to rising temperatures (assuming an adiabatic lapse rate of 6°C/1000 m altitude; Colwell et al. 2008; Gasner et al., *in press*). For the high-elevation species in our study, this corresponds to shifts nearly as large as their elevational distributions. While range shifts in tropical montane regions will undoubtedly be affected by a changing abiotic environment and species' physiological tolerances (Tewksbury et al. 2008), the constraints imposed by biotic interactions will likely limit the ability of many species to track optimal abiotic conditions.

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APPENDIX A

Number of playback trials conducted and number of individuals tested per species (*Ecological Archives* E091-125-A1).

APPENDIX B

Mixed model results for each species pair for closest approach and latency to approach the speaker (*Ecological Archives* E091-125-A2).