



Weak asymmetric interspecific aggression and divergent habitat preferences at an elevational contact zone between tropical songbirds

SAMUEL E. I. JONES^{1,2*}  JOSEPH A. TOBIAS,³ ROBIN FREEMAN² & STEVEN J. PORTUGAL¹ 

¹School of Biological Sciences, Royal Holloway University of London, Egham, Surrey, TW20 0EX, UK

²Institute of Zoology, Zoological Society of London, Regents Park, London, NW1 4RY, UK

³Department of Life Sciences, Imperial College London, Silwood Park, Buckhurst Road, Ascot, Berkshire, SL5 7PY, UK

Closely related tropical bird species often occupy mutually exclusive elevational ranges, but the mechanisms generating and maintaining this pattern remain poorly understood. One hypothesis is that replacement species are segregated by interference competition (e.g. territorial aggression), but the extent to which competition combines with other key factors such as specialization to distinct habitats remains little studied. Using vegetation surveys and reciprocal playback experiments, we explored the dynamics of interspecific aggression between two Nightingale-Thrushes *Catharus* sp. in Central America. We show that lower-elevation Black-headed Nightingale-Thrushes *Catharus mexicanus* are aggressive towards higher-elevation Ruddy-capped Nightingale-Thrushes *Catharus frantzii* where they meet at contact zones. However, interspecific aggressive responses were weak and unidirectional, and the two species were associated with different habitats. We conclude that the contact zone is maintained and located primarily by habitat selection, and is probably reinforced by interspecific aggression. This has important implications for understanding how montane species will respond to climate change because the pace and extent of range shifts will not depend solely on habitat shifts or interspecific competition, but instead on interactions between these two factors.

Keywords: *Catharus*, ecotone, habitat preference, species interactions, territoriality, tropical mountains.

Tropical mountains offer unique opportunities to study the drivers of community composition owing to their exceptional biodiversity and rapid changes in environmental factors within relatively small spatial scales (Whittaker 1975, Jankowski *et al.* 2013a). Striking patterns of elevational parapatry – where related taxa have contiguous, but non-overlapping, elevational distributions (Bull 1991) – have long been observed throughout the tropics (e.g. Wallace 1876). The elevational ranges of species on tropical mountains are often relatively narrow, with abrupt transitions from one population to another, creating a pattern of elevational parapatry, a rapid ‘turnover’ whereby a

given species is replaced at higher or lower elevations by another ecologically similar congener (e.g. Terborgh 1971, Patterson *et al.* 1998, Jankowski *et al.* 2009, Pycrz *et al.* 2009). Previous theoretical and empirical studies have offered multiple explanations for these spatial patterns, including interspecific competition, climatic niche partitioning and divergent habitat preferences (e.g. Janzen 1967, Terborgh 1977, Jankowski *et al.* 2013a). However, the primary mechanisms maintaining elevational parapatry remain unresolved.

Two long-standing hypotheses for these contact zones (where the elevational range limits of two species abut) on tropical mountains are that they are maintained by abrupt habitat transitions (e.g. ecotones; Terborgh 1985) or interspecific competition (e.g. competitive exclusion; Diamond 1973). The ecotone hypothesis proposes that the limits of

*Corresponding author.

Email: samuel.jones.2016@rhul.ac.uk

Twitter: @samuel_ei_jones

a species' elevational range are caused by rapidly changing habitat transitions on elevation gradients and are therefore simply a reflection of divergent habitat specialization among related species (Cadena & Loiselle 2007, Jankowski *et al.* 2009). By contrast, the competition hypothesis predicts that aggressive behavioural interactions (interference competition) between related species place limits on their elevational ranges by competitive exclusion (Price & Kirkpatrick 2009, Grether *et al.* 2017).

Specialization on different habitats provides the most parsimonious explanation for the spatial segregation of species (e.g. Wiens 1989) and has been shown to correlate with the location of contact zones on some tropical elevation gradients (Jankowski *et al.* 2013b). On the other hand, interspecific competition is often inferred from non-overlapping range limits (e.g. Terborgh 1985), yet its role as a primary mechanism maintaining contact zones has been questioned (Cadena & Loiselle 2007, Sexton *et al.* 2009). Nonetheless, previous studies have suggested that interspecific competition may be widespread in tropical bird communities (Robinson & Terborgh 1995, Jankowski *et al.* 2012) and its influence on setting geographical range limits in tropical birds has gained increasing empirical support (Remsen & Graves 1995, Jankowski *et al.* 2013a, Pigot & Tobias 2013, Freeman 2015a, Grether *et al.* 2017, Freeman *et al.* 2019).

Behavioural studies focusing on pairs of related bird species in tropical mountains have shown interspecific aggression at contact zones in Costa Rica (Jankowski *et al.* 2010), Ecuador (Dingle *et al.* 2010), Colombia (Caro *et al.* 2013), Malaysia (Boyce & Martin 2019) and New Guinea (Freeman *et al.* 2016). This is generally interpreted as evidence that interspecific competition maintains spatial parapatry of populations through aggressive territorial behaviour, a form of 'behavioural interference' (Grether *et al.* 2017). In addition, interspecific aggression may be reduced when small elevational gaps separate species ranges, suggesting that aggressive behaviours intensify with direct contact in some species (Freeman *et al.* 2016). Although these studies have provided empirical evidence that interspecific competition may contribute to the pattern of species turnover (Terborgh & Weske 1975, Terborgh 1985), it remains unclear whether contact zones can be maintained by interspecific interactions alone or in concert

with other factors (Jankowski *et al.* 2013a, Srinivasan *et al.* 2018).

There are several ways that competition could interact with habitat differences. For example, habitat preferences may predict interspecific dominance relationships (or vice versa), such as when a dominant congener restricts the elevational range of a subordinate species by limiting it to a specific habitat (Grether *et al.* 2017). This type of asymmetric interspecific aggression between elevational replacement bird species appears to be widespread, often when (generally smaller) higher elevation species are subordinate to their (generally larger) lower elevation replacement (Dingle *et al.* 2010, Jankowski *et al.* 2010, Freeman *et al.* 2016, Boyce & Martin 2019). These asymmetric competitive interactions theoretically restrict space or resources available for the subordinate species (e.g. habitat or foraging niches; Price & Kirkpatrick 2009, Martin *et al.* 2017). Aggressive interactions of this kind are thought to drive or maintain divergence in habitat preferences between species pairs in the tropical and temperate lowlands (Robinson & Terborgh 1995, Martin & Martin 2001a, 2001b), but this possibility has rarely been examined in montane systems.

To assess the role of interspecific aggression and habitat selection in maintaining an elevational contact zone, we conducted vegetation surveys and playback experiments in and near the territories of two species of Nightingale-Thrush *Catharus* sp. on an elevation gradient in Central America. The two species – Black-headed Nightingale-Thrush *Catharus mexicanus* and Ruddy-capped Nightingale-Thrush *Catharus frantzii* – provide a classic example of parapatric elevational distributions with very limited spatial overlap. We used vegetation surveys to quantify the extent of habitat divergence, and behavioural responses to interspecific song playback to assess the strength and directionality of interspecific aggression.

Our approach allowed us to evaluate the influence of both habitat preference and interference competition on elevational segregation in this study system. Understanding the relationship between these factors is important for interpreting the mechanisms underlying the 'escalator to extinction', whereby climate-driven upslope movements result in species extirpations (Freeman *et al.* 2018) as a product of either lower-elevation behaviourally dominant species 'pushing' a subordinate

higher (Grether *et al.* 2017) or the expansion/contraction of specialized habitat types (Fadrique *et al.* 2018).

METHODS

Field site and study species

Fieldwork was undertaken in Cusuco National Park in the Merendon mountains, north-western Honduras (approximately 15.552°N, 88.296°W). The national park encompasses an elevational range of *c.* 700–2300 m asl. General vegetation types range from moist broadleaf forest at lower elevations (up to 1200 m), pine–oak and tropical montane cloud forest at mid-to upper elevations (*c.* 1200–2000 m) and elfin forest on mountain tops (above 2000 m; Batke *et al.* 2014, Martin *et al.* 2016).

Both species of Nightingale-Thrush have abutting/non-overlapping spatial ranges at the study site, with territories of the two species frequently adjacent. Both species are common, strongly territorial year-round residents of the forest understorey, with Ruddy-capped Nightingale-Thrushes 'replacing' Black-headed Nightingale-Thrushes at higher elevations. Black-headed Nightingale-Thrushes have a broader elevational range (down to at least 1000 m), whereas Ruddy-capped Nightingale-Thrushes occur up to the highest points of the park (*c.* 2250 m). The exact elevation of the contact zone varies but is generally at *c.* 1850 m. Black-headed Nightingale-Thrushes are, on average, slightly heavier (mean \pm sd mass = 30.4 ± 1.87 g, $n = 242$) than Ruddy-capped Nightingale-Thrushes (27.8 ± 1.59 g, $n = 32$; Supporting Information Table S1 and Fig. S1). Neither species has discernible differences in densities throughout their respective elevational ranges. They are closely related, but not sister species, evolving in separate clades that diverged *c.* 3.9 million years ago: Black-headed Nightingale-Thrush in the *mexicanus* clade and Ruddy-capped Nightingale-Thrush in the *bicknell-occidentalis* clade (Voelker *et al.* 2013).

Elevational range limits and territory mapping

We established elevational range limits of both species using *ad hoc* transects across an elevational range from 1225 to 2183 masl in undisturbed

primary forest. This was undertaken at two research camps at the field site where elevational range limits of the two species differed slightly (Fig. 1). We then mapped the contact zone by marking locations of territorial males of both species using a GPS unit (Garmin GPS MAP 62s) to an accuracy of 3–9 m. Initially, we marked the locations of singing males with increasing distance from their contact zone over a 3-week period in early June 2016 between 05:30 and 12:00 h (when territorial activity is strongest). This mapping exercise was repeated on a minimum of 4 days, following recommendations in Gregory *et al.* (2004). Singing males that were not present on all visits were considered non-territorial and were no longer considered for playback experiments. Both species defend territories through continual song bouts from obvious locations and it is unlikely that locations of territories were inadvertently removed as a result of this protocol. In areas of high territorial density, we made careful observations of counter-singing between neighbouring birds to ensure that territories were discrete. We marked locations of each territory in their approximate centre after observations of the movements of the territory-holder. Subsequently, a distance (m) from the interspecific contact zone was measured in QGIS (QGIS Development Team 2016) as the distance from the centre of each territory to the closest heterospecific.

Habitat assessments

After territory mapping, we made a qualitative assessment of habitat types occupied by each species and mapped the approximate borders of these habitat transitions (Fig. 1). Although the edges of habitat transitions were approximated, transitions between them occur over short distances (frequently < 50 m) and territories of each species are adjacent to one another. As such, within the immediate spatial range of our study, a transition zone of co-occurring territories does not exist. However, we classified habitats as transition habitat in cases where obvious forest types did not change rapidly over small spatial scales (generally where topography was not as steep; see Fig. 1).

We quantified potential habitat differences using vegetation data (collected over the same study period) from 37 survey plots (used for REDD + carbon assessments) situated along study transects covering the spatial and elevational

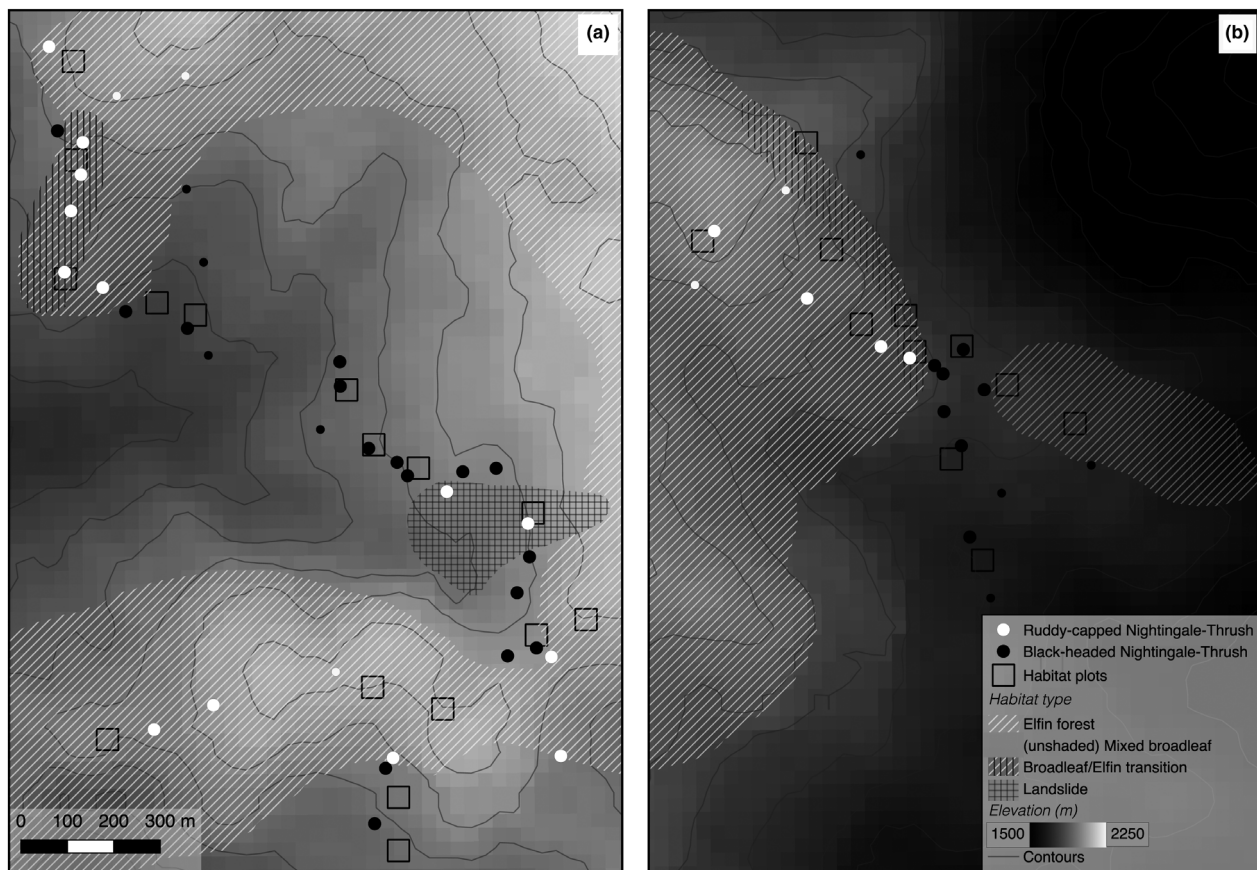


Figure 1. Territory locations in relation to habitat and elevation at two localities in Cusuco National Park, Honduras: (a) Cantiles camp; (b) Capuca camp. Larger points show whether playbacks were conducted on territorial Black-headed *Catharus mexicanus* or Ruddy-capped Nightingale-Thrushes *Catharus frantzii* and smaller points show additional territories of each species at which playback experiments were not conducted. Mapped habitat boundaries away from the immediate vicinity of habitat plots are approximated. Eight playback locations and 10 habitat plots were situated outside the areas shown.

extent of all territory locations (Fig. 1). Habitat assessments were undertaken in a standardized $20 \times 20 \text{ m}^2$, bisected by two separate lines at 10 m (forming four quarters of the larger 20-m^2 plot). The following attributes were measured within each plot: tree type, tree density, tree circumference, understorey density, sapling density, leaf-litter depth and soil density. Because habitat plots were at pre-existing locations and were not always immediately within territories, in occasional ambiguous cases at the range edges we only ascribed habitat to a species where habitat was or was not being used by nearby territory holders (as informed by observations during territory mapping). Because our study was not undertaken across the entire breadth of each species' elevational range, we cannot rule out the possibility that habitat traits gradually change throughout

their ranges. However, because the two species are parapatric, we were more interested in the possible habitat determinants that may immediately influence this (along with interspecific aggression).

Tree type, tree density and tree circumference were measured by recording all trees (defined as any woody plant with a circumference of $\geq 15 \text{ cm}$ at 1.3 m height) within the overall 20-m^2 plot. Each tree was categorized to a crude species level of 'broadleaf', 'fern', 'pine' or 'palm'. Tree types for each survey plot were then calculated as a percentage of total trees present. Tree density was measured as the total number of trees present in the plot and tree circumference was a mean of all tree circumferences within the plot. To measure understorey density, a 3-m pole, marked at 50-cm increments (forming six bands), was placed vertically at pre-marked 1-m increments along the

bisecting lines. At each 1-m increment along this line, the number of foliage 'touches' per 50-cm band on the vertical pole was recorded. This gave a score of six numbers (one per 50-cm band on the vertical pole) to each 1-m increment along the bisecting line, which were summed. The mean of these 40 scores (20 on each bisecting line) then gave an overall underscore density 'score' for the plot as a whole, with higher scores representing denser forest understoreys and lower scores more open understorey.

Sapling density, leaf-litter depth and soil density were all measured in five 2 × 2-m quadrats. These 2-m² quadrats were placed in the centre of the quarters formed by the bisecting lines, and one in the central cross of the bisecting lines. Sapling density was measured by counting the number of woody saplings < 15 cm in circumference at 1.3 m height, in each of the quadrats. The aggregate sapling count for all five quadrats was then divided by 20 to give a density per m². Leaf-litter depth was measured by pushing a steel ruler through the leaf-litter until it hit topsoil. Depth was then measured as the height of the highest dead leaf in each quadrat, and averaged across the five measures. Soil density was measured by dropping a standardized 1-kg spherical cone weight (cone end facing the soil) from a height of 1.5 m onto a patch of earth cleared of leaf-litter. Soil depth was measured in millimetres from the topsoil to the centre (deepest part) of the depression (and averaged across the five measures).

Playback experiments

We conducted a total of 47 playback experiments ($n = 29$ Black-headed Nightingale-Thrushes; $n = 18$ Ruddy-capped Nightingale-Thrushes) between June and August (2016), the time of year at which both species are breeding and territorial defence is at its strongest (Howell & Webb 1995, Taylor & Komar 2010). *Catharus* thrushes are strongly territorial, counter-singing against neighbouring territorial birds and chasing off intruders. Accordingly, playback experiments simulating territorial invasions by rival males are an appropriate test of territorial aggression (Jankowski *et al.* 2010, Freeman & Montgomery 2015).

We recorded natural territorial songs of Black-headed Nightingale-Thrushes ($n = 14$) and Ruddy-capped Nightingale-Thrushes ($n = 9$) at the study site to use as experimental stimuli, using a

directional microphone rig (Sennheiser ME66 microphone/Olympus LS-11 recorder). Recordings were free from prominent background song and occasionally edited (amplified and filtered) for clarity. Each recording was numbered arbitrarily and used in the experiments in numerical sequence to minimize pseudoreplication following recommendations by Kroodsma (1989). We recorded vocalizations of two other sympatric species, Slate-throated Whitestarts *Myioborus miniatus* ($n = 5$) and Collared Trogons *Trogon collaris* ($n = 2$), to use as control trials. These species were treated as controls because they are ecologically, vocally and phylogenetically divergent mid-storey foragers, which appear not to interact with Nightingale-Thrushes.

We began experiments by placing a wireless UE Roll speaker (hereafter 'speaker') in the approximate centre of the focal territory at a height of c. 1 m above the forest floor. The speaker was wirelessly paired to an mp3 player (iPod touch), which was controlled from a concealed position c. 10 m away. Experiments were conducted during the peak of territorial activity both early (06:00–12:00 h) and late in the day (15:00–17:30 h). If a bird was engaged in a counter-singing bout with neighbouring territories on arrival at the focal territory, the experiment was postponed for at least 2 h. No experiments were conducted during rain or windy conditions.

Each playback experiment comprised three separate 8-min trials. Each trial was made up of 3 min of playback through the speaker, followed by 5 min of observation time. The control trial was always conducted first, followed by conspecific and heterospecific trials which were alternated in sequence between experiments (per species) to avoid response bias dependent upon the preceding trial. We broadcast playbacks at a volume similar to that of natural vocalizations (78–84 decibels). We measured five behavioural responses to quantify territorial aggression to each trial: closest approach to the speaker (m), latency to approach the speaker (s), time spent within 15 m of the speaker, latency to vocalize within 15 m of the speaker and number of vocalizations within 15 m of the speaker. The 15-m area surrounding the speaker represents the greatest distance it was feasible to observe the focal bird in the forest understorey and ensured that all responses were indeed in response to the experimental trial.

We measured close approach to the speaker between 0 (where the responding bird stood on the speaker) and 15 m, where all approaches greater than 15 m were bounded to this upper limit. We estimated approach distances visually during trials and paced out distances from the speaker after the experiment ended to check accuracy. We measured latency to approach the speaker as the time elapsed between initiation of the playback trial to the first approach of the focal bird within 15 m of the speaker. We measured latency to vocalize as the time elapsed before the first vocalizations (calls or songs) made by the focal individual within 15 m of the speaker, with the number of vocalizations a sum of all songs and calls given by the focal individual also within this radius. Finally, we measured time spent within 15 m of the speaker as the elapsed period between first arrival and leaving this boundary (there were no incidences of responding birds leaving and re-returning). The radius surrounding the speaker was used to bound territorial responses because we wanted to ensure measured behaviours were genuine aggressive responses to the trial in question, rather than just bouts of spontaneous territorial song. Both species are vocal for extended periods during the breeding season and in pilot studies we found unbounded vocal responses artificially inflated aggressive responses to playbacks. One experiment was cancelled when both *Catharus* species responded to a playback trial, as it became impossible to distinguish the cause of behavioural responses.

Statistical analysis

We conducted all analyses in R (R Core Team 2016). We first compared structural habitat variables (log-transformed where appropriate) between approximate habitat types with one-way ANOVA. Then, to interpret behavioural responses to playback trials, we collapsed observed responses into a single composite aggression score using a principal component analysis (PCA). Because different measurement units were used to measure these behavioural responses (metres and seconds, respectively), we scaled variables using the argument `scale = TRUE` in the `prcomp` function. The first axis (PC1) explained the majority of the overall variance (84%; PC1 loadings: close approach to speaker = -0.45; latency to approach speaker = -0.46; time in recording area = 0.46; latency to

vocalize in the recording area = -0.44; number of vocalizations in the recording area = 0.41). High PC1 scores were typified by closer and faster approaches, greater time spent in the proximity of the speaker, and quicker and more extensive vocal responses in the proximity of the speaker. Accordingly, PC1 loadings per trial were considered to be a representative composite aggression score and we subsequently used these values as the response variable for statistical analyses.

Using this response variable, we constructed a linear mixed-effects model using the *lme4* package (Bates *et al.* 2014). Two fixed effects were specified: an interaction term between trial type and distance from the contact zone (where trial type has six levels: control, conspecific and heterospecific responses for both species) and trial order (whether conspecific lures or heterospecific lures were played first in the experiment). Including the interaction between 'trial type' and distance is statistically equivalent to including species, trial and a species \times trial interaction but allows for a clearer examination of the model parameters (see Freeman & Montgomery 2015, Freeman *et al.* 2016). We log-transformed distance from the contact zone to normalize the data distribution and to model the reduction in aggressive responses to heterospecifics with increasing distance from the contact zone. We included focal bird identity (of the territory holder) as a random effect because of the repeated measures each individual received during playback experiments (three treatments). We defined significant cases of interspecific aggression as those in which the confidence intervals (CIs) for control trials and heterospecific trials were non-overlapping in close proximity to the contact zone. Additionally, if aggressive responses to heterospecifics are learned from experience, we expected the strength of the response to decline with distance from the contact zone (Jankowski *et al.* 2010). Although the extent to which responses are learned is not relevant to understanding elevational range limits, a learned response indicates that aggression towards heterospecific playback is not merely misdirected behaviour intended for conspecific receivers (Murray 1971). Finally, to assess whether territorial responses were influenced by the order in which heterospecific and conspecific treatments were presented during playback experiments, we used Wald Chi-square tests in the *car* package (Fox *et al.* 2013) to test for an effect of the 'trial order' term on the strength of responses.

RESULTS

Habitat assessments at the contact zone

We found territories of Ruddy-capped Nightingale-Thrushes in three approximate habitat types. The majority were situated in elfin/dwarf forest typified by stunted trees and an abundance of tree ferns (Cyatheales) and mosses (Bryophyta). Additionally, some territories were situated in a transition habitat at the edge of elfin forest with bamboo stands (Bambusoideae) and an area of successional scrub and *Pinus* (Pinaceae) in a landslide site. By contrast, Black-headed Nightingale-Thrushes exclusively occupied mixed broadleaf cloud forest typified by *Quercus* (Fagaceae), *Liquidambar* (Altingiaceae) and occasional *Pinus* (Pinaceae). The contact zone was at 1890–1964 m at one study site and at 1811–1835 m at the other, but in both areas the two species consistently appeared to occupy different habitats (Figs 1 and 2).

We found relatively little difference in the structural habitat attributes between habitat types except for soil and tree densities (Table 1). Soil density differences were probably driven by the complete removal of topsoil at the landslide site. Differences in tree types were more substantial, with habitats occupied by Ruddy-capped Nightingale-Thrushes being dominated by smaller trees, primarily ferns or a mosaic of ferns/broadleaf trees (Tables 1 and 2).

Playback experiments

Both species responded strongly to conspecific playback, generally approaching the speaker quickly, closely, and remaining within its vicinity for protracted periods while singing in response. Similarly, neither species responded aggressively to control playbacks, with only a single Black-headed Nightingale-Thrush responding to this trial across all experiments conducted (also indicating the control stimuli species had no influence on subsequent responses; ANOVA, $F_{1,139} = 0.04$, $P = 0.84$). Aggression directed towards heterospecifics differed between species, however; the lower elevation Black-headed Nightingale-Thrushes were territorially aggressive towards the higher elevation Ruddy-capped Nightingale-Thrushes, but not vice versa (Fig. 3). This interaction was limited to a

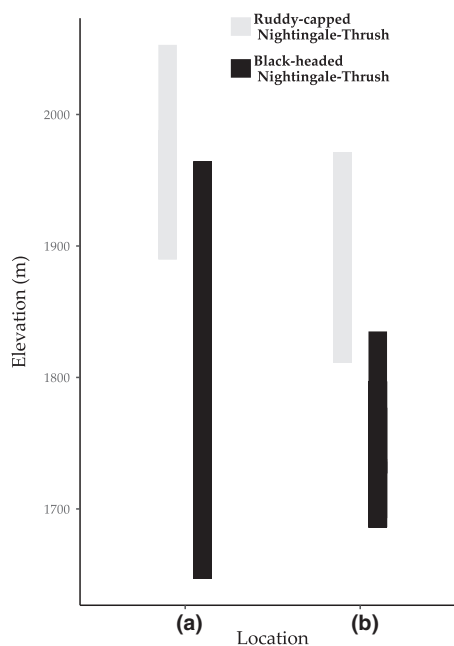


Figure 2. Elevational range limits of Ruddy-capped Nightingale-Thrushes *Catharus frantzii* and Black-headed Nightingale-Thrushes *Catharus mexicanus* at two localities in Cusuco National Park, Honduras (Fig. 1): (a) Cantiles camp; (b) Capuca camp. Plotted elevations represent the territories mapped at two research camps and do not represent the entire elevational ranges of both species (see Methods). Black-headed Nightingale-Thrushes extend to lower elevations (c. 1000 m), whereas Ruddy-capped Nightingale-Thrushes extend to higher elevations (c. 2300 m).

small number of individuals (31% of Black-headed Nightingale-Thrush experiments, $n = 9$), all but two of which were ≤ 141 m to the contact zone (rounded up here to < 150 m for the purpose of interspecific comparisons). In these instances, behavioural responses by Black-headed Nightingale-Thrushes were often as strong towards heterospecifics as to conspecifics, although numerous individuals in close proximity to Ruddy-capped Nightingale-Thrushes did not exhibit any interspecific aggression; of 18 trials < 150 m to the contact zone, 11 (60%) did not respond to heterospecifics (Fig. 3). Response rates of Ruddy-capped Nightingale-Thrushes were even lower; only a single heterospecific trial (5.5% of 18 experiments) elicited a response from a territorial individual.

We found that ‘trial order’ did not have a significant effect on playback responses ($\chi^2_1 = 20.09$, $P = 0.15$), so we examined the full model for parameter estimates (Table 3). At the contact zone, the aggression responses to conspecific and

Table 1. Microhabitat characteristics of habitat transitions between species.

	Black-headed Nightingale-Thrush <i>Catharus mexicanus</i>	Ruddy-capped Nightingale-Thrush <i>Catharus frantzii</i>			Test statistic
	Mixed broadleaf cloud-forest (18)	Elfin/dwarf forest (13)	Broadleaf–elfin forest transition (5)	Landslide/succession scrub (1)	
Tree density (per 20 m ²)	116 ± 35.1 (2088)	151.1 ± 78.8 (1964)	124 ± 131.1 (620)	29 (29)	$F_{3,33} = 2.97$, $P = 0.05$
Tree circumference (cm)	49 ± 12.4 (2088)	41.4 ± 5.91 (1964)	44.5 ± 8.78 (620)	45.9 (29)	$F_{3,33} = 1.35$, $P = 0.28$
Understorey density (touches per m)	1.27 ± 0.43	1.48 ± 1.08	1.24 ± 0.64	1.55	$F_{3,33} = 0.27$, $P = 0.85$
Sapling density (per m ²)	2 ± 1.04	1.39 ± 1.07	1.17 ± 1.19	1.9	$F_{3,33} = 1.24$, $P = 0.31$
Leaf-litter depth (mm)	40.01 ± 16.26	44.6 ± 15.8	54.02 ± 36.7	27.8	$F_{3,33} = 0.88$, $P = 0.46$
Soil density (mm)	29.9 ± 7.47	30.04 ± 9.08	25.33 ± 14.15	2.4	$F_{3,33} = 3.2$, $P = \mathbf{0.04}$

Values are mean ± sd of values per plot. Numbers in parentheses for habitat type and tree density/circumference represent the number of habitat plots and the total number of trees within a habitat type, respectively. Test statistic in the final column refers to ANOVA results. Soil density differences were probably driven by the complete removal of topsoil at the landslide site. Significant term in the model is in bold.

Table 2. Proportions of different tree types between habitat transitions occupied by the study species.

% Tree type	Black-headed Nightingale-Thrush <i>Catharus mexicanus</i>	Ruddy-capped Nightingale-Thrush <i>Catharus frantzii</i>			Test statistic
	Mixed broadleaf cloud-forest (18)	Elfin/dwarf forest (13)	Broadleaf–elfin forest transition (5)	Landslide/scrubby regrowth (1)	
Broadleaf	75.7 ± 16	50.1 ± 20.9	55.2 ± 24.3	6.9	$F_{3,33} = 7.67$, $P < \mathbf{0.01}$
Fern	20.4 ± 16.8	50.2 ± 13.2	43.1 ± 22.7	3.4	$F_{3,33} = 9.31$, $P < \mathbf{0.01}$
Palm	5.7 ± 4	5.8 ± 5.6	3.6 ± 3.5	NA	$F_{3,33} = 0.2$, $P = 0.82$
Pine	<0.01	<0.01	<0.01	89.7	NA

Figures shown in parentheses after habitat categories are sample sizes of habitat plots. Data shown are means ± sd calculated across plots. Test statistic in the final column refers to ANOVA results. NA indicates data were absent or insufficient for statistical analyses. Significant terms in the model are in bold.

heterospecific playback trials were significantly different to controls for Black-headed Nightingale-Thrushes, but were only significantly different for conspecific trials for Ruddy-capped Nightingale-Thrushes (Fig. 3). Thus, responses to heterospecifics by Black-headed Nightingale-Thrushes in close proximity to the contact zone were still significantly different to control trials, despite numerous non-responding individuals. Aggression towards heterospecific playback in Black-headed Nightingale-Thrushes declined rapidly with distance from parapatry (95% CI for the slope: -1.08 to -0.11).

By contrast, aggression directed towards conspecifics in both species did not differ with proximity to the edge of their own elevational ranges (95% CI for the slope: Black-headed Nightingale-Thrushes -0.17 to 0.80 ; Ruddy-capped Nightingale-Thrushes -0.87 to 0.20 ; Table 3, Fig. 3).

DISCUSSION

Our results demonstrate asymmetric interspecific aggression between two Nightingale-Thrush species, showing that lower elevation Black-headed

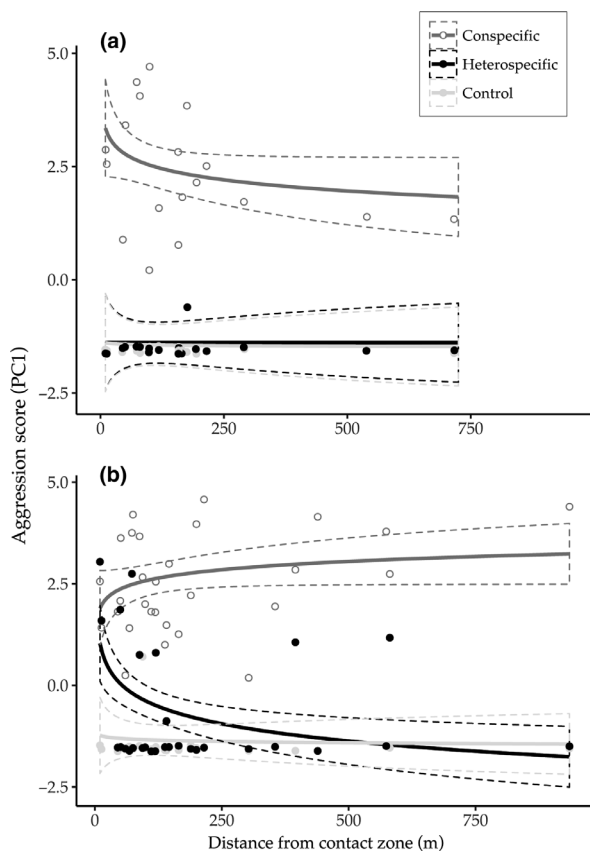


Figure 3. Territorial aggression (PC1 loadings) estimated from playback trials as a function of distance (over ground) from the contact zone in (a) Ruddy-capped Nightingale-Thrushes *Catharus frantzii* and (b) Black-headed Nightingale-Thrushes *Catharus mexicanus*. Data points show responses to playback experiments of conspecific, heterospecific and control treatments (higher PC1 scores denote stronger aggression). Solid lines show generalized linear mixed model (GLMM) fits (log-transformed); dashed lines show confidence intervals (see Methods). The overlapping confidence intervals for control and heterospecific trials in Ruddy-capped Nightingale-Thrushes illustrate the lack of interspecific aggression observed in experiments on this species (compare with Black-headed Nightingale-Thrushes).

Nightingale-Thrushes were dominant over Ruddy-capped Nightingale-Thrushes, their higher elevation congener. The intensity of interspecific interactions was relatively weak, with many individuals present near the contact zone behaving non-aggressively (to heterospecifics). Using playback of heterospecific song, we also showed that the strength of interspecific responses declined rapidly with distance from the contact zone, suggesting that aggressive behaviour reflected a learned response to heterospecifics rather than misdirected

Table 3. Parameter estimates for fixed effects from a linear mixed model of aggression responses to playback experiments for Black-headed Nightingale-Thrushes *Catharus mexicanus* and Ruddy-capped Nightingale-Thrushes *C. frantzii*.

Parameter	Estimate	se	95% CI
(Intercept)	-1.34	0.99	-3.52/ 0.62
Ruddy-capped Nightingale-Thrush conspecific	5.51	1.35	2.94/ 8.19
Ruddy-capped Nightingale-Thrush heterospecific	-0.04	1.35	-2.60/ 2.52
Black-headed Nightingale-Thrush control	0.22	1.29	-2.15/ 2.60
Black-headed Nightingale-Thrush conspecific	2.56	1.29	0.19/ 4.94
Black-headed Nightingale-Thrush heterospecific	3.79	1.29	1.43/ 6.17
Distance to contact zone	-0.19	0.21	-0.40/ 0.36
Playback trial order	-0.24	0.16	-0.54/ 0.05
Ruddy-capped Nightingale-Thrush conspecific × distance to contact zone	-0.33	0.28	-0.87/ 0.20
Ruddy-capped Nightingale-Thrush heterospecific × distance to contact zone	0.01	0.28	-0.51/ 0.55
Black-headed Nightingale-Thrush control × distance to contact zone	-0.02	0.26	-0.51/ 0.46
Black-headed Nightingale-Thrush conspecific × distance to contact zone	0.31	0.26	-0.17/ 0.80
Black-headed Nightingale-Thrush heterospecific × distance to contact zone	-0.59	0.26	-1.08/ -0.11

'Intercept' represents the Ruddy-capped Nightingale-Thrush control parameter estimate. Trial type (control/conspecific/heterospecific per species) × distance to contact zone estimates (log) are approximate slope estimates for the interaction terms. Significant terms in the model are in bold.

aggression intended for conspecifics (Murray 1971). The elevational contact zone of the two species was also strongly linked to habitat differences, suggesting that their elevational ranges are segregated largely by habitat selection, perhaps in combination with interference competition.

Our results broadly mirror patterns observed in previous studies, which overall have identified eight of 13 species-pairs of tropical songbirds with elevational asymmetries in aggressive dominance, with higher elevation species being subordinate (Dingle *et al.* 2010, Jankowski *et al.* 2010, Caro *et al.* 2013, Freeman *et al.* 2016, Boyce & Martin

2019). The same pattern is consistent with other *Catharus* thrushes in temperate (Freeman & Montgomery 2015) and tropical (Jankowski *et al.* 2010) regions. Although these findings indicate that aggressive interactions may play a general role in maintaining elevational range boundaries, the prevalence of asymmetric interactions suggests that they are unlikely to provide a full explanation for elevational parapatry. Evidently, dominant competitors either preferentially do not, or are unable to, occupy the elevational range of a subordinate species.

Some interspecific interactions between related bird species appear to be symmetrical, without any obvious dominance asymmetry (Tobias & Seddon 2009). However, most appear to be asymmetric, with a dominant species using and defending a preferred resource that may in turn limit the spatial distribution or niche breadth of a subordinate (Amarasekare 2002, Martin *et al.* 2017). Finer scale niche shifts in birds can occur when a subordinate species is freed from competition with a dominant one, and thus occupies a wider niche through ecological release (e.g. Alatalo *et al.* 1985, Martin & Martin 2001b). Experimental evidence for the expansion of elevational ranges through ecological release is lacking in birds but has been shown in other tropical montane vertebrates (Pasch *et al.* 2013). Nonetheless, natural observations of range expansions in the absence of competitors has been inferred as evidence for the role of overt competitive interactions limiting the elevational ranges of tropical birds (Terborgh & Weske 1975). In our field site, neither Nightingale-Thrush species has been found to hold permanent territories outside their native elevational/habitat boundaries over a 6-year period. Occasionally, solitary male Black-headed Nightingale-Thrushes have been found singing at higher elevations in elfin forest, but this has never resulted in the establishment of permanent territories. Thus, it appears likely that habitats at higher elevations may be suitable for Ruddy-capped Nightingale-Thrushes but not for Black-headed Nightingale-Thrushes.

It is not immediately clear what drives these habitat preferences. The most obvious difference in habitat was tree type and tree density characteristics. Potentially important factors such as diet and nesting requirements of both species appear to be similar (Howell & Webb 1995), although no detailed studies have been undertaken. Ruddy-

capped Nightingale-Thrushes can occupy both primary and disturbed montane forest types (Rangel-Salazar *et al.* 2008a), although breeding performance is linked to these habitat types with greater breeding success, resulting in higher population density in primary forest (Rangel-Salazar *et al.* 2008b). It is possible that asymmetries in foraging and breeding success drive divergent habitat preferences in our study species, particularly for Black-headed Nightingale-Thrushes, which appear to breed exclusively in broadleaf-dominated cloud-forest. Comparative ecological studies are needed to clarify the role of ecological specialization, and associated fitness differences, in maintaining discrete elevational ranges or habitat niches in this system.

It is debatable whether non-overlapping spatial distributions can be maintained by interspecific aggression alone (see Martin & Martin 2001b). Even in cases of extremely strong aggression between congeners, there is usually an ecological component to segregation (Tobias & Seddon 2009). In multiple experimental trials, we found that Black-headed Nightingale-Thrushes were unresponsive to playback of heterospecific territorial song despite close proximity to the contact zone, suggesting that behavioural interference is relatively weak and perhaps unlikely to explain divergence in habitat or elevation. More rigorous examination via removal experiments may clarify this (e.g. Pasch *et al.* 2013). In addition, Black-headed Nightingale-Thrushes show substantially reduced levels of territorial aggression in the non-breeding season (S. E. I. Jones unpubl. data), and year-round study would clarify whether the spatial extent of co-occurrence varies by season.

Another possible mechanism for elevational parapatry in tropical mountains is physiological specialism to elevation-specific microclimates (Janzen 1967). Although it is unlikely that our study species are limited by microclimates, their elevational ranges may represent thermal conditions that are preferentially selected owing to aspects of their physiology (e.g. at different life-stages; Jankowski *et al.* 2013a). Evidence in support of elevational range restriction to thermal niches in birds is generally lacking (Freeman 2015b, Londoño *et al.* 2017), but thermal preferences in two parapatric species of Singing Mice (*Scotinomys* sp.) segregated by interspecific aggression have been reported (Pasch *et al.* 2013). Further research is needed to assess whether physiological differences can

contribute to the maintenance of elevational parapatry in tropical birds.

From the perspective of environmental change, understanding the nature of interspecific interactions and habitat preferences has potentially important implications (Grether *et al.* 2017). In Cusuco National Park, Black-headed Nightingale-Thrushes have shown significant upslope shifts in their mean elevational range over the past decade (Neate-Clegg *et al.* 2018). On the one hand, this upslope shift may mean the dominant Black-headed Nightingale-Thrushes are gradually encroaching on higher elevation habitats, resulting in an ever-decreasing spatial range for Ruddy-capped Nightingale-Thrushes, possibly resulting in extirpation (e.g. Freeman *et al.* 2018). On the other hand, boundaries between habitats may represent a hard limit for permanent territorial residency of Black-headed Nightingale-Thrushes and – because habitats shift relatively slowly in response to climate (Jankowski *et al.* 2013b) – they may potentially buffer Ruddy-capped Nightingale-Thrushes against a gradual ‘escalator to extinction’ by delaying upslope shifts of the dominant congener. Whether habitat boundaries have the ability to ‘buffer’ these upslope shifts, however, depends on the extent to which other potentially key factors driving habitat selection are also affected by climate. For example, concurrent shifts in arthropod and bird communities have been documented on the same elevation gradients (Chen *et al.* 2009, Harris *et al.* 2012). As such, understanding the role of a variety of range determinants in combination with species interactions is necessary. This is particularly the case when considering variability in interactions measured in other studies (e.g. where a high-elevation species is dominant or no interaction is present) because an upslope shift does not necessarily mean a dominant species is ‘pushing’ another upslope (e.g. Barve & Dhondt 2017, Boyce & Martin 2019).

Our study shows relatively weak asymmetric interspecific aggression between two tropical Nightingale-Thrushes with elevational ranges segregated by habitat type. Structural habitat differences at the contact zone suggest that divergent ecological niches rather than interference competition are the primary drivers of spatial segregation in this system. However, the aggressive defence of territories against heterospecifics also suggests that overt interactions may help to sharpen and maintain elevational range limits, particularly in areas where the habitat transition is less abrupt. Taken together, these findings support the view that

biotic interactions work in conjunction with other factors to maintain the elevational ranges of species (Jankowski *et al.* 2013a, Srinivasan *et al.* 2018) and, furthermore, that range limits between competing species may be set in ecological and evolutionary time because higher fitness within a given species niche prevents successful exploitation of one directly adjacent (Price & Kirkpatrick 2009). Further studies are needed to explore the relative roles of ecological niches, behavioural interference and competitive dominance in setting elevational range limits and in governing their response to climatic change.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Raw body mass data of Black-headed *Catharus mexicanus* and Ruddy-capped *Catharus frantzii* Nightingale-Thrushes captured at the field site.

Figure S1. Images of Black-headed and Ruddy-capped Nightingale-Thrushes captured at the field site.

Figure S2. A male Black-headed Nightingale-Thrush singing in territorial defence.