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RESEARCH ARTICLE

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

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ABSTRACT

Bicknell's Thrush (*Catharus bicknelli*) is a threatened species that inhabits high-elevation spruce–fir forests in the northeastern United States. Bicknell's Thrush populations are predicted to shift upslope in response to global warming, leading to local extinctions on mountains that lack the elevational extent to accommodate such shifts. However, biotic interactions may influence how montane species respond to changing abiotic conditions. In territorial songbirds, for example, aggression from dominant low-elevation species has been hypothesized to combine with warming temperatures to "push" populations of subordinate montane species upslope at a faster rate than in the absence of interspecific aggression. This "push" hypothesis could apply to Bicknell's Thrushes: the related Swainson's Thrush (*Catharus ustulatus*) inhabits lower elevations, Bicknell's Thrushes are largely confined to mountaintops, and interspecific aggression by Swainson's Thrushes toward Bicknell's Thrushes has been anecdotally reported. We used reciprocal playback experiments to test whether patterns of interspecific aggression in Swainson's and Bicknell's thrushes along an elevational gradient in the Adirondack Mountains were consistent with the "push" hypothesis. We found weak asymmetrical interspecific aggression: Some Swainson's Thrush individuals at high elevations where the 2 species co-occurred responded aggressively to Bicknell's Thrush playback, and Bicknell's Thrushes did not respond aggressively to Swainson's Thrush playback. While Swainson's and Bicknell's thrushes appeared to regularly occupy overlapping home ranges, asymmetrical interspecific aggression from a lower-elevation species is consistent with the "push" hypothesis and suggests that interspecific aggression from Swainson's Thrushes may be a factor limiting Bicknell's Thrush populations in the Adirondack Mountains. More broadly, this case example supports the recent call to incorporate biotic interactions in models that predict montane species' responses to climate change.

Keywords: asymmetrical aggression, distributional limit, elevational distribution, elevational replacement, interspecific competition, playback experiments, range margin

Las agresiones interespecíficas por parte de *Catharus ustulatus* podrían limitar la distribución de la especie amenazada *Catharus bicknelli* en las montañas Adirondack

RESUMEN

Catharus bicknelli es una especie amenazada que habita bosques de abetos de elevaciones altas en el noreste de Estados Unidos. Se predice que las poblaciones de *C. bicknelli* se moverán hacia tierras más altas en respuesta al cambio climático, lo que llevaría a extinciones locales en las montañas que no sean tan elevadas como para permitir dichos cambios. Sin embargo, las interacciones bióticas podrían afectar cómo las especies de montaña responden a las condiciones abióticas cambiantes. Por ejemplo, se ha propuesto que en aves territoriales, la agresión por parte de especies dominantes de elevaciones bajas se combina con el calentamiento para "empujar" a las poblaciones de especies subordinadas de montaña hacia zonas altas a un ritmo más rápido que en la ausencia de la agresión interespecífica. Esta hipótesis del "empuje" podría aplicarse a *C. bicknelli*; *C. ustulatus* es una especie cercanamente relacionada que habita menores elevaciones mientras que *C. bicknelli* está restringida principalmente a zonas altas, y se ha reportado anecdóticamente agresión interespecífica de *C. ustulatus* hacia *C. bicknelli*. Usamos experimentos recíprocos de reproducción de sonidos previamente grabados para evaluar si los patrones de agresión interespecífica en *C. ustulatus* y *C. bicknelli* a lo largo de un gradiente de elevación en las montañas Adirondack concuerdan con la hipótesis del empuje. Documentamos agresión interespecífica asimétrica y débil, consistente en que algunos *C. ustulatus* de zonas de coexistencia con *C. bicknelli* en alta montaña respondieron agresivamente a los sonidos previamente grabados de *C. bicknelli,* pero los *C. bicknelli* no respondieron agresivamente a los sonidos previamente grabados de *C. ustulatus*. Aunque las áreas de hogar de ambas especies parecían estar regularmente superpuestas, la agresión interespecífica asimétrica de la especie de zonas bajas concuerda con lo esperado de acuerdo a la hipótesis

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de "empuje" y sugiere que la agresión interespecífica por parte de *C. ustulatus* podría ser un factor que limita las poblaciones de *C. bicknelli* en las montañas Adirondack. En general, este caso sustenta los llamados recientes a incorporar las interacciones bióticas en los modelos que predicen las respuestas al cambio climático de especies de montañas.

Palabras clave: agresión asimétrica, competencia interespecífica, distribución en elevación, experimentos de reproducción de sonidos previamente grabados, límites de distribución, márgenes de la distribución, reemplazo en elevación

INTRODUCTION

Bicknell's Thrush (*Catharus bicknelli*) is a migratory songbird that breeds in dense, high-elevation red spruce–balsam fir forests in the mountains of the northeastern United States and at both low and high elevations in Quebec and the Maritime Provinces in Canada (Atwood et al. 1996, Rimmer et al. 2015). Now considered a separate species from Gray-cheeked Thrush (*C. minimus*; Oullet 1993), Bicknell's Thrush is classified as vulnerable by the IUCN due to observed population declines and threats to its habitat such as climate change (Lambert et al. 2008). Global warming is causing most montane species across the globe to shift upslope (Chen et al. 2011), and upslope shifts driven by temperature increases are predicted to lead to local extinctions of species currently restricted to mountaintop environments, such as Bicknell's Thrush (Sekercioglu et al. 2008, La Sorte and Jetz 2010). Bicknell's Thrush populations have declined or disappeared from some smaller mountains in the northeastern United States, possibly in relation to recent climate change (Lambert et al. 2008), and climatic niche models predict that Bicknell's Thrushes will disappear from the northeastern United States by 2080 in response to continued warming (Lambert et al. 2005, Rodenhouse et al. 2008, Ralston and Kirchman 2013).

However, the prediction that climate change will lead to the extinction of Bicknell's Thrushes in the northeastern United States assumes that abiotic factors (and not biotic interactions or interactions between biotic and abiotic factors) are the dominant factors limiting the elevational distribution of Bicknell's Thrush. In general, relatively little is known about how biotic factors influence species' warming-associated elevational shifts (Thomas 2010, HilleRisLambers et al. 2013, Wisz et al. 2013). One biotic factor that could potentially influence the distribution of Bicknell's Thrushes is interspecific competition. Several *Catharus* species live in northeastern North America, and patterns of broad-scale distributions suggest that interspecific competition can influence *Catharus* elevational distributions (Noon 1981). For example, *Catharus* species inhabit distinct elevational zones with relatively small zones of overlap on many mountain slopes in this region (Able and Noon 1976). The widespread Swainson's Thrush (*Catharus ustulatus*) replaces Bicknell's Thrush at lower elevations along some transects in the Adirondack Mountains in the northeastern United States, a pattern hypothesized in part to reflect interspecific competition (Able and Noon 1976). Moreover, interspecific aggression between Bicknell's and Swainson's thrushes has been reported, with preliminary data suggesting that Swainson's Thrush is behaviorally dominant in this interaction (Able and Noon 1976). One hypothesis that could explain these observations is that the elevational distribution of Bicknell's Thrushes is limited by interspecific competition from Swainson's Thrushes mediated by interspecific aggression. In the context of global warming, if the outcome of interspecific competition is directly or indirectly dependent on temperature (Davis et al. 1998, Helland et al. 2011, Carmona-Catot et al. 2013), aggression from a dominant lowland species could "push" a subordinate montane species upslope over time as temperatures increase (alternatively, if the montane species is behaviorally dominant, it could persist as a "king of the mountain"; Jankowski et al. 2010).

If the "push" scenario is occurring in interspecific interactions between Bicknell's and Swainson's thrushes, we can make 3 primary predictions: (1) interspecific aggression exists between Swainson's and Bicknell's thrushes; (2) interspecific aggression is asymmetrical, with Swainson's Thrushes dominating Bicknell's Thrushes; and (3) asymmetrical interspecific aggression from Swainson's Thrushes interacts with abiotic factors (i.e. temperature) to influence the elevational distribution of Bicknell's Thrushes. We used reciprocal playback experiments to test whether the first 2 predictions of the "push" hypothesis were supported in interspecific interactions between Swainson's and Bicknell's thrushes in the Adirondack Mountains in New York State, USA.

METHODS

Study Species

Swainson's and Bicknell's thrushes, the 2 focal species of this study (Figure 1), both breed in the Adirondack Mountains in New York State (McGowan and Corwan 2008). The 2 species defend home ranges through physical (approaching and chasing intruders) and vocal (singing and calling) behavior, with vocal activity concentrated at

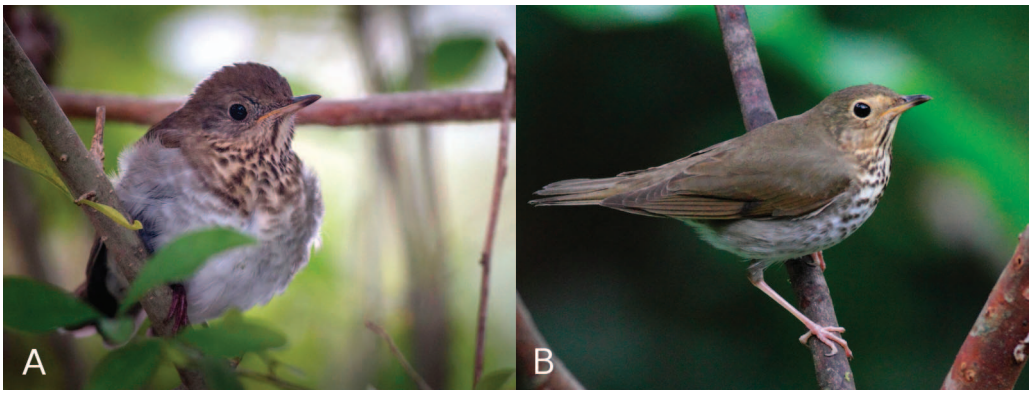


FIGURE 1. (**A**) Bicknell's Thrush (*Catharus bicknelli*) and (**B**) Swainson's Thrush (*C. ustulatus*) co-occur in the mountains of northeastern North America. They are phenotypically similar, but differ in song, elevational distribution, and habitat preference. Photo credit: (**A**) Ian Davies, and (**B**) Graham Montgomery

dawn and dusk (Mack and Yong 2000, Rimmer et al. 2015). The territorial system of Swainson's Thrushes remains poorly studied, while Bicknell's Thrush has an unusual mating system in which multiple paternity appears to be common and nestlings are fed by multiple males (Goetz et al. 2003). Related to this system, Bicknell's Thrush males have large home ranges that are not necessarily strictly defended, while females hold exclusive territories (Goetz et al. 2003). During the breeding season, both species forage for insects on or near the forest floor (Mack and Yong 2000, Rimmer et al. 2015), although Swainson's Thrushes also use gleaning and hawking to capture insects more readily than Bicknell's Thrushes (Holmes and Robinson 1988). Swainson's Thrushes are slightly larger than Bicknell's Thrushes (e.g., for after-hatch-year [AHY] males in northeastern North America, average mass = 29.1 g vs. 27.8 g; Mack and Yong 2000, Rimmer et al. 2015).

The 2 species have somewhat divergent habitat preferences and elevational distributions in the northeastern United States. Bicknell's Thrushes nest in dense, high-elevation (>915 m) red spruce–balsam fir forests (see Lambert et al. 2005 for details), and Swainson's Thrushes reach their highest densities in northeastern North America at middle elevations of ca. 800–1,200 m (Able and Noon 1976, Noon 1981). While Swainson's and Bicknell's thrushes co-occur in coniferous montane forests of the northeastern United States, Swainson's Thrushes inhabit relatively lower elevations than Bicknell's Thrushes, with variable amounts of elevational overlap (Able and Noon 1976; see Nixon et al. 2001) for a Canadian study site.

TABLE 1. The number of playback experiments completed for Swainson's and Bicknell's thrushes. Some playback experiments elicited behavioral responses from both species in a comparison, and are denoted as species = "Both." "Elevational range" is the range of elevations at which we conducted playback experiments for a given species within a particular species pair, not the overall elevational distribution of the species at our study site.

Species	Playback experiments	Elevational range
Swainson's Thrush	36	715–1,434 m
Bicknell's Thrush	16	984–1,484 m
Both	13	1,039–1,418 m

Playback Experiments

We conducted reciprocal playback experiments (Table 1) from June 1 to June 13, 2014, on 2 mountains in the High Peaks region of the Adirondack Mountains in New York State (Porter Mountain and Mt. Marcy; respective coordinates: 44.2156, –73.8444 and 44.1172, –73.9153). Song playback experiments are an appropriate method to measure interspecific aggression in *Catharus*, as aggression in this group is primarily based on vocal (rather than visual) signals (Dilger 1956, Noon 1981). We first compiled natural vocalizations recorded from northeastern North America for both species from the Macaulay Library (Cornell Lab of Ornithology, Ithaca, New York, USA; www.macaulaylibrary.org) and xeno-canto.org (n = 6 and n = 9 songs for Bicknell's and Swainson's thrushes, respectively). To minimize pseudoreplication, we arbitrarily selected specific recordings for use in individual playback trials (Kroodsma 1989). We assumed that singing birds were defending home ranges (because Bicknell's Thrushes do not adhere to typical territorial behavior for passerines, we use the term "home range" rather than "territory"), and initiated playback experiments by placing a Pignose amplifier (Pignose-Gorilla, Las Vegas, Nevada, USA; hereafter, "speaker") within ~25 m of where we had located a singing bird, typically within 5 min of detecting the singing bird. The speaker was attached to an iPod (Apple, Cupertino, California, USA) via a 12 m audio cable, allowing observers to document the behavioral response (if any) of individuals to playback trials while hiding ~10 m from the speaker. We

conducted most playback experiments in the morning (04:45–11:00), but also performed a small number of evening experiments (17:45–20:45).

Playback experiments included 3 trials: control, conspecific, and heterospecific. The control trial was performed first, and consisted of 2 min of playback of the song of a resident chickadee (*Poecile*) species followed by 5 min of behavioral observation. *Poecile* species are unlikely to compete with *Catharus* species due to differences in diet, foraging behavior, and foraging strata. In our study area, Black-capped Chickadees (*P. atricapillus*) are largely replaced by Boreal Chickadees (*P. hudsonicus*) above 1,000 m. We thus used Black-capped Chickadee recordings ($n = 8$) as our control for sites located below 1,000 m, and Boreal Chickadee recordings ($n = 5$) at sites above 1,000 m. We then conducted conspecific and heterospecific trials, alternating the relative order of trials (conspecific before heterospecific and vice versa) between playback experiments. These trials also consisted of 2 min of playback followed by 5 min of behavioral observation. All playback trials for a given location were performed sequentially in a single 21-min session.

We quantified the following behavioral responses to playback for each trial: closest approach to the speaker (m; hereafter "closest approach"), latency to approach the speaker (s), latency of vocal response (s), and number of vocalizations (summed songs and calls; Jankowski et al. 2010, Freeman 2015). We measured closest approach as a continuous variable bounded by 0 m (if the responding bird perched on the speaker) and 15 m (the maximum distance at which we could reasonably detect an individual approaching the speaker in dense understory vegetation). We estimated closest approach by eye during the course of playback trials and later checked our visual estimates by pacing off the distance between the speaker and the location of the responding bird's nearest approach. We measured latency to approach as the time elapsed prior to the first approach made to within 15 m of the speaker by an individual of the focal species. We quantified latency to vocalize as the time elapsed before the first vocalization (song or call) of the focal species that we heard after initiating playback, and the number of vocalizations as the summed total of songs and calls given by the responding individual(s) of the focal species. When we did not observe individuals approach the speaker in response to playback, we categorized the closest approach to the speaker as 15 m and the latency to approach the speaker as 420 s (the summed total of the 2 min of playback and 5 min of observation). Similarly, we categorized latency of vocal response as 420 s when we did not hear vocalizations in response to playback trials.

During a portion of the playback experiments at elevations where the 2 thrush species co-occurred, individuals of both species approached the speaker within an experiment. For example, in an experiment designed to test Bicknell's Thrush responses to conspecific vs. heterospecific song, Bicknell's Thrushes approached the speaker in response to Bicknell's Thrush playback, however Swainson's Thrushes approached the speaker in response to Swainson's Thrush playback (and vice versa). We did not include these experiments in our statistical analyses for 2 reasons. First, we could not identify which species to designate as the putative home-range owner. Second, we could not distinguish between behavioral response to heterospecific playback and behavioral response to the physical presence of a congeneric individual(s). However, such trials indicated spatial overlap between thrush species and also brought individuals of 2 species into close proximity, offering opportunities to observe direct interspecific aggression (e.g., chases). We thus report the frequency of trials in which both thrush species responded (Table 1), as well as observations gleaned from such events (see Results).

Statistical Analysis

We conducted all statistical analysis in R (R Development Core Team 2014). We constructed a linear mixed regression model to analyze species' behavioral responses to playback trials. We used a principal components analysis (PCA) to collapse variation in multiple behavioral response variables (closest approach, latency to approach, latency to vocalize, and number of vocalizations) into a single metric. The first PC axis (PC1) explained ~61% of the variance (PC1 loadings: closest approach to the speaker = –0.56, latency to approach the speaker = –0.57, latency to vocalize = –0.44, number of vocalizations = 0.40); high PC1 values were associated with playback trials that resulted in close approaches, low latencies to approach and vocalize, and a greater number of vocalizations. We therefore considered PC1 to be representative of a composite aggression score, and used PC1 as our response variable in linear mixed models. We included the following fixed effects: category, a categorical variable with 6 factors (conspecific, heterospecific, and control trials for both Swainson's and Bicknell's thrushes); a category × elevation interaction to test whether responses to playback varied along the elevational gradient for different categories; and trial order (conspecific before heterospecific and vice versa), to evaluate whether the order of playback trials influenced behavioral responses. Using "category" as a fixed effect facilitates the interpretation of model parameters, and is statistically equivalent to an alternative formulation that includes species, trial, and a species × trial interaction as predictor variables instead of as a "category." To account for the fact that individuals may vary in their responses to playback (given that each individual received 3 playback trials), we included experiment location as a random effect. To test whether playback order influenced behavioral

TABLE 2. Behavioral responses of Swainson's and Bicknell's thrushes to playback trials. Means and standard deviations for each behavioral response variable for each playback trial are shown. To facilitate comparisons, behavioral responses of Swainson's Thrushes to heterospecific trials are presented separately for responders ($n = 9$) and nonresponders ($n = 27$). All individuals approached the speaker in response to conspecific trials; individuals that did not respond to a heterospecific or control trial were classified as closest approach = 15 m and latency to approach and vocalize = 420 s.

Species	Playback trial	Percentage approached	Closest approach (m)	Latency to approach (s)	Latency to vocalize (s)	Number of vocalizations
Swainson's Thrush ($n = 36$)	Control	6%	14.4 ± 1.4	401.5 ± 77.4	212.6 ± 185.2	22.0 ± 34.6
	Conspecific	100%	1.9 ± 2.1	60.8 ± 70.6	102.6 ± 140.1	30.4 ± 34.0
	Heterospecific (responders)	25%	4.4 ± 5.1	72.2 ± 53.2	146.1 ± 127.2	34.1 ± 34.9
	Heterospecific (nonresponders)	0%	15.0 ± 0.0	420.0 ± 0.0	252.1 ± 186.5	16.9 ± 25.8
Bicknell's Thrush ($n = 16$)	Control	6%	14.8 ± 0.8	419.4 ± 2.5	121.0 ± 132.4	16.0 ± 14.9
	Conspecific	100%	2.6 ± 2.7	73.8 ± 46.8	77.1 ± 84.3	35.1 ± 19.6
	Heterospecific	6%	14.1 ± 3.5	418.1 ± 7.5	231.8 ± 175.7	12.7 ± 15.4

responses, we evaluated models using Bayesian Information Criteria (BIC; Burnham 2004) to determine whether models with the order term outperformed models lacking this term. We then conducted all analyses using the model that was best supported by BIC.

RESULTS

Both Swainson's and Bicknell's thrushes responded to conspecific playback by rapidly approaching the speaker to within a few meters and subsequently vocalizing (Table 2).

TABLE 3. Parameter estimates with standard errors (SE) for fixed effects in the linear mixed regression model predicting aggression score (PC1) in response to playback trials for Swainson's and Bicknell's thrushes. Interpretation of trial-type parameter estimates requires care, as "Intercept" is the mean of a factor level (in this case "Bicknell's Thrush conspecific"), and other "category" factors describe deviations from this intercept value.

Parameter	Estimate	SE
Intercept	0.36	2.39
Bicknell's Thrush heterospecific	−0.95	3.01
Bicknell's Thrush control	−2.18	3.01
Swainson's Thrush conspecific	−0.72	2.54
Swainson's Thrush heterospecific	−5.71	2.54
Swainson's Thrush control	−1.84	2.54
Bicknell's Thrush conspecific: Elevation	0.01×10^{-2}	0.19×10^{-2}
Bicknell's Thrush heterospecific: Elevation	-0.42×10^{-3}	0.19×10^{-2}
Bicknell's Thrush control: Elevation	0.75×10^{-3}	0.19×10^{-2}
Swainson's Thrush conspecific: Elevation	0.18×10^{-2}	0.78×10^{-3}
Swainson's Thrush heterospecific: Elevation	0.44×10^{-2}	0.78×10^{-3}
Swainson's Thrush control: Elevation	0.49×10^{-3}	0.78×10^{-3}

A minority of Swainson's Thrush individuals (25%; 9 out of 36) approached the speaker in response to heterospecific playback, with similar latencies to approach and vocalize to those in response to conspecific playback (Table 2). In contrast, only 1 out of 16 (6%) Bicknell's Thrushes approached the speaker in response to heterospecific trials (Table 2). Individuals rarely approached the speaker in response to control playback of chickadee song, but frequently vocalized during control trials (Table 2), most likely because our fieldwork occurred during the early breeding season when thrush species are highly vocal (and because we used the presence of singing birds to locate sites for playback experiments). Thus, vocal response to control trials appears to represent the background rate of vocalization. Still, aggressive responses were characterized by increased vocalization; individuals sang more songs in response to conspecific playback than control playback, and the number of songs loaded positively on PC1 (our aggression score).

The model without the trial order term was preferred in model selection (without order term, BIC = 477.33; with order term, BIC = 485.61), indicating that the relative order of conspecific vs. heterospecific playback trials did not significantly influence behavioral response to playback. We thus used the simpler model that did not include the order term (Table 3), and found a strong positive relationship for the interaction between elevation and Swainson's Thrush response to heterospecific playback (Table 3; approximate 95% confidence interval of slope = 0.0028–0.0059). This finding indicates that Swainson's Thrushes at higher elevations showed greater aggression to Bicknell's Thrush playback than Swainson's Thrushes at lower elevations. Swainson's Thrushes also showed a weaker, but statistically significant, positive relationship between response to conspecific playback and elevation (Table 3; approximate 95% confidence interval of slope = 0.0002–0.0034), suggesting that Swainson's Thrushes at

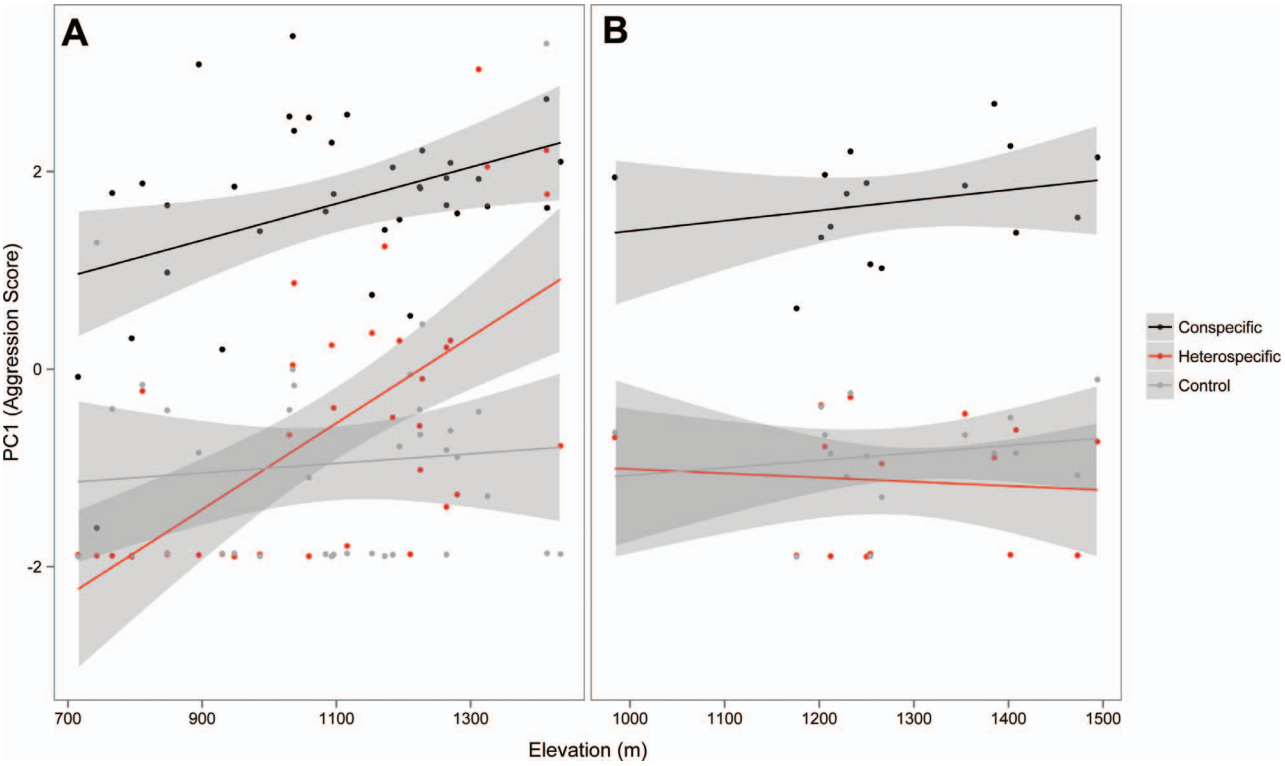


FIGURE 2. Aggression scores for (**A**) Swainson's and (**B**) Bicknell's thrushes by playback trial category. Trend lines with 95% confidence intervals illustrate model predictions for each category. Raw data are plotted as points. Note that *x*-axis (but not *y*-axis) scales differ between panels.

higher elevations are more aggressive than individuals at lower elevations. We displayed these results by plotting the model predictions (and raw data) of aggression scores by category and elevation (Figure 2). In the upper reaches of their elevational distribution (~1,200–1,400 m), Swainson's Thrushes had significantly higher aggression scores in heterospecific trials compared with control trials (but higher aggression scores in conspecific trials than in heterospecific trials; Figure 2; see also Figure 3, which shows a similar pattern in the raw data for closest approach to speaker).

Finally, Swainson's and Bicknell's thrushes both responded to playback in 13 trials at higher elevations (i.e. in an experiment designed to test Bicknell's Thrush responses to conspecific vs. heterospecific song, Bicknell's Thrushes approached the speaker in response to Bicknell's Thrush playback, however Swainson's Thrushes approached the speaker in response to Swainson's Thrush playback (and vice versa) (Table 1). This suggests that Swainson's and Bicknell's thrushes regularly occupy overlapping home ranges in high-elevation coniferous forests in the Adirondack Mountains. Despite this high proportion of our experiments that brought the 2 putative competitors together, we did not observe unequivocal attacks or chases between Swainson's and Bicknell's thrushes, although such interactions may have occurred without our knowledge if they occurred at greater distances from the speaker than we could view.

DISCUSSION

We demonstrated asymmetrical interspecific aggression between Swainson's and Bicknell's thrushes along an elevational gradient in the Adirondack Mountains in northeastern North America. Our results are consistent with the "push" hypothesis—We found that some individuals of the lower-elevation species (Swainson's Thrush) responded aggressively to playback of the upper-elevation species (Bicknell's Thrush), but not vice versa (Figures 2 and 3). This asymmetrical aggression suggests that Swainson's Thrushes are behaviorally dominant to Bicknell's Thrushes, a result that may have implications for Bicknell's Thrush conservation.

The "push" hypothesis predicts that aggression from dominant low-elevation species may accelerate warming-driven upslope shifts of subordinate high-elevation species. At our study site, climatic niche models predict that 14 of 15 breeding montane bird species, including both Bicknell's and Swainson's thrushes, will disappear by 2080 in response to continued warming (Ralston and Kirchman

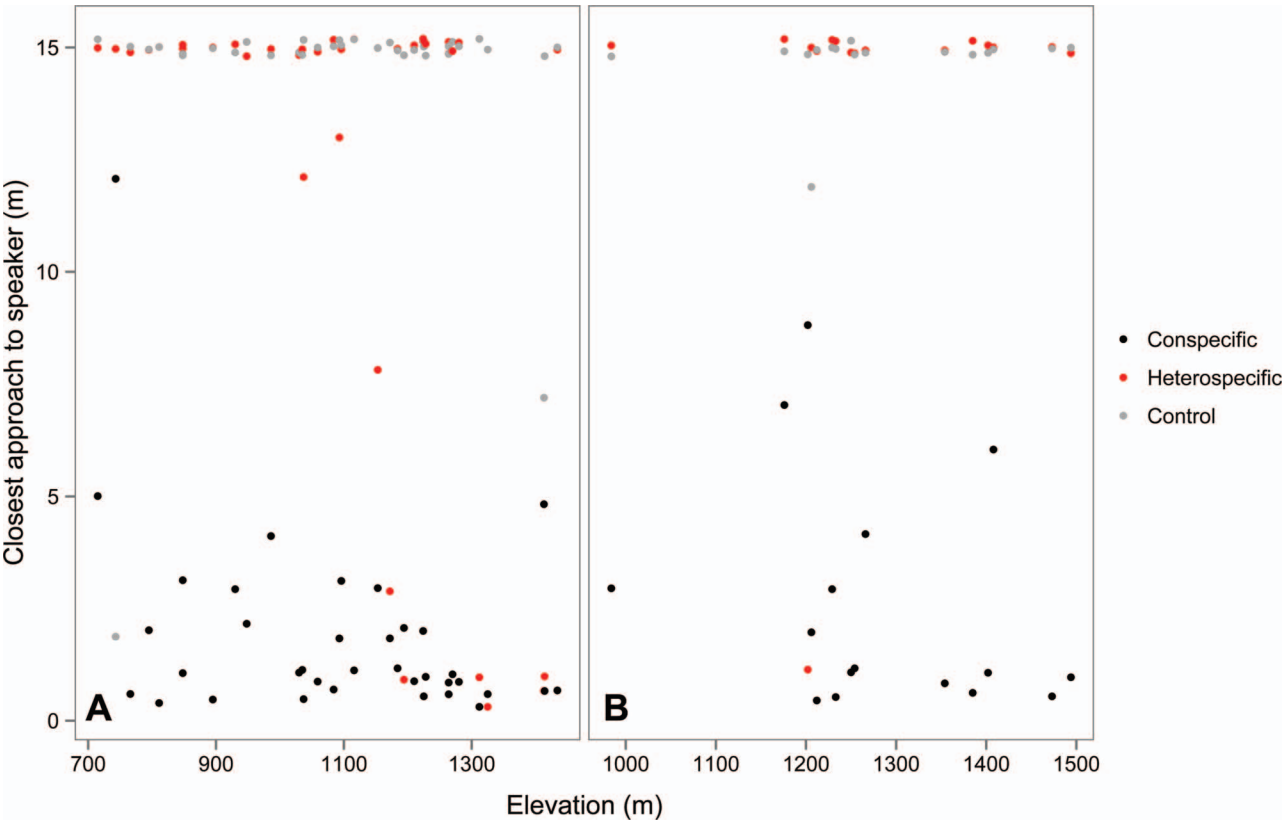


FIGURE 3. Closest approach to speaker by playback trial category for (**A**) Swainson's and (**B**) Bicknell's thrushes. Close approaches represent aggressive responses to playback; trials in which we did not observe an approach to the speaker were coded as 15 m. Note that *x*-axis (but not *y*-axis) scales differ between panels.

2013). These predictions assume that climate alone limits species' elevational distributions. The extent to which *Catharus* species' distributions are limited by abiotic factors remains unknown, although Bicknell's Thrushes appear to be significantly better adapted metabolically to cold temperatures than other *Catharus* species, including Swainson's Thrush (Holmes and Sawyer 1975). In conjunction with our behavioral data, this suggests a scenario wherein biotic (Swainson's Thrushes are behaviorally dominant to Bicknell's Thrushes) and abiotic (Bicknell's Thrushes perform better in cold, high-elevation environments) factors have combined to influence the current elevational distribution of Bicknell's Thrush. While speculative, a warming climate may allow Swainson's Thrushes to compete for high-elevation sites, negating the physiological adaptations to colder climates that have allowed Bicknell's Thrushes to remain the dominant *Catharus* at high elevations up to the present time, a possibility that should be considered when predicting the future distribution of Bicknell's Thrush. We also note that the high-elevation spruce–fir forest preferred by Bicknell's Thrushes has moved downslope in recent decades on mountains in Vermont and New Hampshire, USA, despite temperature increases (Foster and D'Amato 2015). This counterintuitive finding suggests that Bicknell's Thrush habitat may actually be expanding, at least within some montane regions of the northeastern United States, potentially explaining the observation that high-elevation songbirds have moved downslope in recent decades on the White Mountains in New Hampshire (Deluca 2013).

That Swainson's and Bicknell's thrushes interact aggressively is not unexpected, as previous research has documented that interspecific aggression occurs at least occasionally between these 2 species (Able and Noon 1976). We found that Swainson's Thrushes showed interspecific aggression toward Bicknell's Thrushes only at high elevations where both species were found (Figure 2); Swainson's Thrushes at slightly lower elevations on the same mountain where Bicknell's Thrushes were not present did not show interspecific aggression. This pattern occurred over small spatial scales, and suggests that interspecific aggression by Swainson's Thrushes is a learned response to the presence of a dense population of a competitor (Bicknell's Thrush) at high elevations, rather than misdirected intraspecific aggression (e.g., Murray 1971) or an evolved response to a competitor.

This pattern may also reflect, in part, increased overall aggression of Swainson's Thrushes that live at upper elevations, as high-elevation Swainson's Thrushes also showed greater aggression toward conspecific playback than low-elevation Swainson's Thrushes (Table 3, Figure 2). More study is needed to clarify the degree to which Swainson's Thrushes influence Bicknell's Thrushes, e.g., by measuring whether home-range overlap between the 2 species correlates with Bicknell's Thrush reproductive success, or, if feasible, through small-scale removal experiments. Successful Bicknell's Thrush conservation will ultimately depend on protecting their wintering habitat in Hispaniola (Townsend et al. 2009, Rimmer et al. 2015), improved monitoring (Lambert et al. 2008), and, where possible, mitigating the effects of climate change (Lambert and McFarland 2004, Rodenhouse et al. 2008, Rimmer et al. 2015).

Our results should be interpreted through the lens of the unusual breeding biology of Bicknell's Thrush. For example, playback experiments (including ours in this study) typically take the form of simulated territorial intrusions, but Bicknell's Thrushes do not exhibit typical passerine territorial behavior. Instead, Bicknell's Thrush males call and sing from several perches, but show little physical defense of these areas (Goetz et al. 2003) and have large home ranges (5.5–12.0 ha) that often overlap extensively, while females are territorial and defend home ranges (3.2–5.4 ha) against other females (Collins 2007). While we were unable to determine the sex of Bicknell's Thrushes that responded aggressively to conspecific playback, these data suggest that such individuals may typically have been females rather than males. The fact that Bicknell's Thrushes (typically a single bird, but sometimes 2 or 3 individuals) responded to conspecific playback by approaching the speaker demonstrates that our experiment successfully generated aggressive responses to playback, despite this species' complex breeding and spatial system. We also note that the breeding and spatial system of Swainson's Thrush is poorly understood (Mack and Yong 2000), and may not necessarily be a typical passerine system with social monogamy and male territorial defense.

While Swainson's Thrushes appear to be behaviorally dominant over Bicknell's Thrushes, interspecific interactions between other *Catharus* species are likely more complex. At lower elevations in the Adirondack Mountains, Swainson's Thrushes overlap with Hermit Thrushes (*C. guttatus*), and we recorded incidental observations during the course of our study of Hermit Thrushes responding aggressively to Swainson's Thrush playback, including physically attacking a Swainson's Thrush on one occasion. This suggests the possibility that Hermit Thrushes are behaviorally dominant to Swainson's Thrushes, and future field playback experiments should investigate behavioral interactions between Hermit and Swainson's thrushes, and possibly also Veeries (*C. fuscescens*) and Wood Thrushes (*Hylocichla mustelina*), that occur at low elevations in the Adirondack Mountains and across the northeastern United States (Noon 1981).

In conclusion, we documented asymmetrical interspecific aggression by the lower-elevation Swainson's Thrush toward the upper-elevation Bicknell's Thrush in the Adirondack Mountains that was strongest at the higher elevations where these 2 species co-occurred. We found that both species co-occurred over a wide range of elevations at our study site (Table 1), and that Swainson's and Bicknell's thrushes appeared to regularly occupy overlapping home ranges in dense coniferous habitat at relatively high elevations (as they do on lower-elevation mountains in New Brunswick, Canada; Nixon et al. 2001), demonstrating that interspecific interactions did not lead to complete spatial separation of these 2 species. In light of this, behavioral interaction with Swainson's Thrushes may be one of many factors that limits the current distribution of Bicknell's Thrushes. Further experiments are necessary to test the degree to which interspecific aggression limits the distribution of Bicknell's Thrush, and whether the outcome of aggressive interactions between the 2 species is dependent on temperature. Nevertheless, our results are broadly consistent with the "push" hypothesis, and add to a growing body of evidence suggesting that biotic interactions may limit the distributions of montane birds (Jankowski et al. 2010, Caro et al. 2013, Freeman and Mason 2015) and therefore should be incorporated into models that predict species' responses to climate change.

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