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Competition between a migrant and resident passerine
during the non-breeding season

A dissertation submitted in partial satisfaction of the
requirements for the degree Doctor of Philosophy
in Biology

by

Kathryn Peiman

2014

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ABSTRACT OF THE DISSERTATION

Competition between a migrant and resident passerine
during the non-breeding season

by

Kathryn Peiman

Doctor of Philosophy in Biology

University of California, Los Angeles, 2014

Professor Gregory F. Grether, Chair

Migrant birds spend half their lives coexisting with residents during the non-breeding season and their populations may be limited by environmental conditions during this time, yet the degree to which interspecific interactions affect both migrants and residents is still not well known. I studied the ecologically similar migrant White-eyed Vireo (WEVI: *Vireo griseus*) and the resident Thick-billed Vireo (TBVI: *V. crassirostris*), sister taxa that only coexist during the non-breeding season. The intensity of resource competition is expected to depend on resource availability, which can vary spatially and temporally. I used a spatial habitat contrast (forest vs scrub) and a temporal seasonal contrast (fall vs winter) to assess whether variation in resource abundance affected competitive interactions. In order to test for adaptive responses to interspecific competition, I also compared locations allopatric and sympatric with the heterospecific vireo. In chapter 1, I found that TBVI had higher aggression in sympatry than

allopatry and were dominant to WEVI yet territories between the species still overlapped. In chapter 2, I showed that there were more food resources in forest than scrub habitats, and that food resources declined from fall to winter. Using stable isotopes as indicators of diet, I also found that the two species had diets that were more similar to each other in sympatry than in allopatry, opposite to predictions under ecological character displacement. In chapter 3, I measured corticosterone as an indicator of stress and documented higher levels of stress in male TBVI sympatric with WEVI compared to allopatric TBVI; body condition was also lower in sympatric than allopatric TBVI. These results indicate that there is little niche partitioning between species, and this has negative physiological consequences at least for the resident species.

The dissertation of Kathryn Peiman is approved.

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2014

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Peiman, KS. 2013. Thick-billed Vireo (*Vireo crassirostris*), Neotropical Birds Online (TS Schulenberg, Editor). Ithaca: Cornell Lab of Ornithology; retrieved from Neotropical Birds Online:
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Poster presentation: Interspecific aggression and winter habitat use in a migrant and resident passerine

Chapter 1. Interference competition between the migrant White-eyed Vireo (*Vireo griseus*) and resident Thick-billed Vireo (*V. crassirostris*) during the non-breeding season

Abstract

Interference competition can occur both within and between species, but comparisons of conspecific and heterospecific aggression during the breeding season are confounded, as conspecific aggression includes mate competition and thus includes non-shared mate requirements within a species in addition to shared resource requirements between species. To focus solely on interference competition due to shared resources, I examined behavioral interactions between the resident Thick-billed Vireo (TBVI: *Vireo crassirostris*) and migratory White-eyed Vireo (WEVI: *V. griseus*) during the non-breeding season. I tested for both evolutionary (sympatry versus allopatry) and ecological (temporal and spatial differences in resource abundance) effects on aggression and territory overlap. Simulated territorial intrusions showed that TBVI were more aggressive than WEVI, and that both species were more aggressive towards conspecifics than the heterospecific vireo and towards vireos than a non-competitive control species. There was no consistent seasonal change in the levels of aggression. Mean differences suggest TBVI are under directional selection for higher aggression in sympatry, and patterns of correlation suggest that both species are under correlational selection for sociability towards conspecifics and heterospecifics in sympatry. These behaviors resulted in exclusive territories within species, yet territories between species overlapped. Conspecific density, as measured by territory size, did not differ between allopatry and sympatry or between forest and scrub habitats. However, sympatric WEVI did not establish territories in low-quality scrub habitats, and there were more adults in allopatry than sympatry and more females in

sympatry than allopatry, suggesting that competitive interactions within and between species may affect small and large-scale geographic distributions. By combining evolutionary and ecological contrasts in the non-breeding season, this is the most comprehensive assessment of interspecific interference competition over purely shared resources.

Introduction

Interactions both within and between species can have profound effects on community structure and on the ecology and evolution of the interacting species (Gotelli & McCabe, 2002). Competition is one of the main types of ecological interactions (Keddy, 1989) and is classified according to how interactions are mediated among individuals. To date, most studies have focused on the ecological and evolutionary effects of interspecific exploitative competition (Brown & Wilson, 1956; Schluter, 2000; Schoener, 1983). Recent reviews have highlighted the prevalence of interspecific interference competition (Grether et al. 2009; Peiman & Robinson 2010; Ord & Stamps 2009; Grether et al. 2013), yet it has received much less theoretical and empirical attention than other types of species interactions.

Interference competition is often mediated through aggressive interactions. Most studies of competition focus on sympatric populations, and so only measure current ecological interactions. To test evolutionary responses to competition, a comparison with allopatric populations is critical (Peiman & Robinson 2010). Heterospecific aggression is not naturally expressed in allopatry and so in those locations selection can only act conspecific aggression, while in sympatry selection can act on both conspecific and heterospecific aggression. However, we can stimulate the expression of heterospecific aggression in allopatric individuals by presenting these individuals with live or model stimuli of heterospecifics they have never

encountered before. This allows us to estimate levels of this selectively neutral behavior and test hypotheses about how selection is acting in sympatry versus allopatry (Fig. 1-1). If simulated levels of heterospecific aggression in allopatry are due to a common genetic basis with conspecific aggression, then the two behaviors will be correlated. If the expression of heterospecific aggression in sympatry also results from this common genetic basis and so is non-adaptive, the same correlation will be present in sympatry as in allopatry (Fig. 1-1a; Peiman and Robinson 2012; Bell 2005). Alternatively, heterospecific aggression may have evolved in response to the presence of a competing species when resources are defensible (Gill 1974; Hairston 1980; Abrams 1987; Abrams & Matsuda 1994; Melville 2002; Adams 2004; Murray 1981; Grant et al. 2002). There are two non-exclusive ways selection can act on heterospecific aggression in sympatry. If directional selection has acted independently on heterospecific aggression and heterospecific aggression increases access to economically defensible resources (Ortiz & Jenssen, 1982; Werner & Hall, 1977), then heterospecific aggression should be higher in sympatry than allopatry while conspecific aggression should not differ (Fig. 1-1b; Peiman & Robinson 2007; Hess & Losos 1991). Correlational selection, however, acts on both conspecific and heterospecific aggression, resulting in multiple combinations of aggression that are equally fit and thus an adaptive behavioral syndrome. Though most studies assume that conspecific and heterospecific aggression is positively correlated (Peiman and Robinson 2010), this has rarely been tested (Peiman & Robinson 2012). Since correlational selection by definition acts on both behaviors, it can only occur in sympatry (Dingemans & Réale, 2005), resulting in stronger correlations between conspecific and heterospecific aggression in sympatry than in allopatry (Fig. 1-1c; Peiman & Robinson 2012). Directional and correlational selection can also act concurrently (Fig. 1-1d). Thus the relative level of heterospecific aggression and the strength of

the correlation between conspecific and heterospecific aggression in sympatric versus allopatric populations can be used to infer evolutionary selective processes. Interference competition is also predicted to result in interspecific territoriality (Case & Gilpin, 1974). When resources are located within a spatially discrete area, the area itself may be defended against intruding conspecifics and heterospecifics. If the two species are ecologically similar and have not evolved other strategies to reduce competition, they should defend mutually exclusive territories.

Most birds face the problem of potentially conflicting selective pressures on their breeding and wintering grounds. This is true both for migrants that overwinter with residents not encountered during the breeding season, and for residents that face up to a 50% increase in total bird density when migrants overwinter. Migrant birds spend up to three-quarters of the year on the wintering grounds potentially interacting with residents, and migrant populations may be limited by environmental conditions during this time (Sherry & Holmes 1996; Sillett et al. 2000; Dugger et al. 2004; Newton 2004; Saino et al. 2004; Marra et al. 1993). By using natural variation in ecological conditions, we can test for the effects of resource abundance on competition. Wetter forest habitats often have more food resources than drier scrub habitats (Bearhop et al. 2004; Murphy et al. 1998; Chapter 2), leading to stronger exploitative competition and therefore larger territories in scrub habitats (Johnson 2007; Parrish & Sherry 1994; reviewed in Adams 2001; Marra & Holberton 1998). Additionally, rainfall and therefore arthropod abundance declines temporally from the fall to the winter (Poulin et al. 1992; Strong & Sherry 2000; Diggs et al. 2011; Chapter 2), leading to stronger competition in the winter than in the fall. Since territory size should not vary seasonally in landscapes saturated by competitors (Gorrell et al. 2005; Hixon, 1980), seasonal declines in resource abundance should lead to increased aggressive interactions (Dolman 1995; Ewald & Orians 1983; Kaiser et al. 2014).

However, few studies have utilized these ecological contrasts even in intraspecific contexts, and none have used both ecological (spatial and temporal) and evolutionary (allopatry/sympatry) contrasts to examine interspecific interactions outside the breeding season.

To examine the effects of interspecific competition, an ideal system consists of species that only interact over shared resources. Comparisons of intraspecific to interspecific interactions are often conducted during the reproductive season, which confounds breeding requirements within a species (such as mate acquisition, guarding, and nesting sites) and selection to reduce reproductive interference, with resources that are truly shared between species (such as food) (Peiman & Robinson 2010). Thus, the more accurate test of the intensity of interspecific interactions over solely shared resources will occur outside the breeding season, when individuals are only defending food resources. The White-eyed Vireo (WEVI: *Vireo griseus*) and Thick-billed Vireo (TBVI: *V. crassirostris*) only coexist during the non-breeding season and only in parts of their range. Since these species do not co-exist anywhere during the breeding season, there is no selection for reducing hybridization or other forms of reproductive interference; selection only acts directly on traits related to non-breeding interactions. These species are likely sister taxa that diverged 110,000 ybp (Slager et al. 2014; Walker, 1998). The northern migratory population of WEVI (subspecies *V. g. noveboracensis*) breeds in the southeastern United States and winters in some parts of the Caribbean and Central America (Hopp et al. 1995). TBVI are resident in the Caribbean, and The Bahamas subspecies (*V. c. crassirostris*) occurs on all the islands and cays of The Bahamas (Walker, 1998).

WEVI and TBVI are similar in morphology, song and ecology (Hopp et al. 1995; Smith et al. 1990; Walker 1998), though TBVI are on average larger than WEVI in all dimensions (Chapter 2). TBVI pairs maintain territories year-round, with the male active in defense (Peiman

2013) while male and female WEVI establish separate winter territories (Greenberg et al. 1993). Only the males of these species consistently sing, and both sexes emit a chatter call. Song is similar between species but distinguishable, and chatter calls are very different. Both species are insectivores, though they also eat fruit, particularly of the *Bursera simaruba* tree, during the winter (Greenberg et al. 1995; Hopp et al. 1995; pers. obs.). Habitat use is similar, with WEVI occupying different stages of secondary growth, forest, scrub, and mangroves (Estrada et al. 2000; Franklin & Steadman, 2013; Hopp et al., 1995; Lynch, 1989; Murphy et al., 2001) and TBVI in forest, coppice, scrub and mangroves (Bearhop et al., 2004; Bradley, 1994; Currie et al. 2005), and both species forage primarily from 0-6 m (Barlow, 1980; Bradley, 1994; Greenberg et al. 1993; Kirkconnell & Garrido, 1991; Rappole & Warner, 1980). Thus, these two species have the potential to interact over arthropod and fruit resources during the winter.

To investigate interference competition between these species during the non-breeding season, I utilized the evolutionary contrast of allopatric and sympatric locations and the ecological contrasts of spatial differences in habitat quality and temporal changes in resource abundance. (1) Under directional selection on independently expressed heterospecific aggression, I predict that heterospecific aggression will be higher in the dominant species in sympatry than allopatry (Hess & Losos, 1991) while conspecific aggression will not differ between locations. (2) As multiple types of selection may act concurrently, I also predict that both species will experience correlational selection leading to stronger correlations between conspecific and heterospecific aggression in sympatry than in allopatry (Peiman & Robinson 2012). (3) Individuals maintaining territories in areas of lower resource abundance should need larger territories to meet their energetic demands (Eccard et al. 2011). Thus territories should be larger in scrub than forest habitats, and in the presence of the competing species compared to

allopatry. (4) If resources decline seasonally, territorial owners are likely to experience more challenges by floaters and neighbors (Rappole & Warner, 1980) and so aggression should increase from the fall to the winter. (5) Last, heterospecific aggression is predicted to result in mutually exclusive interspecific territories (Leisler 1988).

Methods

Data were collected during the fall (Sept-Nov) and winter (Jan-Mar) in three locations: allopatry for TBVI (San Salvador Island, The Bahamas: 2011-2012), sympatry (Abaco Island, The Bahamas: 2010-2011) and allopatry for WEVI (Los Tuxtlas, Mexico: 2011-2012). I included additional data for age and sex distributions from all three locations gathered in 2012-2013. WEVI overwinter in variable numbers throughout the range of TBVI, and thus TBVI do not occur completely allopatric from WEVI. However, since WEVI density is variable among islands, I used an island with a low density of WEVI (San Salvador) instead of a completely allopatric location for TBVI, as has been used in previous studies of competition when the range of one species is completely within the other (Goldberg & Lande 2006; Kirschel et al. 2009; Pfennig & Murphy 2002; Tynkkynen et al. 2004; Anderson & Grether 2010). For brevity, San Salvador will be referred to as an allopatric TBVI location. Both scrub (scrub/early second-growth/disturbed) and forest (coppice/mature forest) habitats were used in all locations. All individuals were color-banded, aged (Pyle 1997; Peiman 2013; individuals aged as hatch-year in the fall or second-year in the winter are hereafter referred to as first-years; individuals aged as after-hatch year in the fall or after-second year in the winter are hereafter referred to as adults) and sexed (by observing males singing or genetically in the lab). Sex and age effects could only be tested with WEVI (only male TBVI participated in territory defense, and only adult TBVI

were used in territory and behavior assessment).

Sexing: I used the shaft from breast or tail feathers to obtain tissue for sex determination. DNA was extracted following the instructions in QIAGEN's DNeasy blood and tissue kit (catalog number 69506). PCRs were carried out using 2.5µl DNA with 5µl Multiplex Mix, 1ul Q solution, 0.4µl BSA, and 1µl primer. Primers used were 2550F and MSZ1R (Fridolfsson & Ellegren, 1999; McCormack & Smith, 2008). The PCR program ran as follows: 95°C for 15 minutes, 94°C for 30 seconds, 12 cycles of 59°C for 90 seconds, 72°C for 60 seconds, 94°C for 30 seconds, 32 cycles of 55°C for 90 seconds, 72°C for 60 seconds, then 60°C for 30 minutes. Amplified products were resolved on 1% agarose gel stained with ethidium bromide, displaying two bands for females and one band for males.

Aggression: I assessed aggression in territory holders of both species towards conspecifics, the heterospecific vireo, and in some cases an American Redstart (AMRE: *Setophaga ruticella*) non-competitive control. AMRE are common at all locations, but have a different foraging style (sallying vs gleaning in the vireos), rarely eat fruit during the winter, and are smaller (7 g) (Sherry & Holmes, 1997) which should reduce competition between them and vireos. I used taxidermy mounts and vocal playback to simulate territorial intrusions. Individuals used as mounts were caught locally (except that WEVI mounts used for trials in allopatric locations were obtained from the U.S.) and taxidermied in a perched posture on a branch. Songs and calls used for vocal playback were recorded locally using a Marantz PMD670 solid state recorder and parabolic microphone, except for WEVI and AMRE songs which were obtained from online sources. Vireo playback consisted of a single song repeated every 6 seconds for 30 seconds, followed by 10 seconds of chatter, repeated for 3 minutes (the trial duration). AMRE playback consisted of a single song repeated every 6 seconds for the 3 minute trial duration.

Three mounts each of WEVI and TBVI were used, as were 3-4 vocal playback exemplars for each species (Kroodsma, 1989). No mounts were used for AMRE trials.

After locating an individual bird, it was randomly assigned a trial order sequence. If the individual was vocalizing, I waited until it was silent for 30s before starting the trial. I secured the mount in a tree and placed the speaker at ground level under the mount. I recorded behaviors that occurred within 5m of the mount during the 3 minute trial. Regardless of whether the focal individual approached to 5m during the first trial, after it ended the mount was removed and a 3 minute interval of silence ensued, followed by the second 3 minute trial with the next species in the trial order. In trials with AMRE, a 3 minute interval of silence followed the second trial before the third trial with the final intruding species was performed. When possible, individuals were later retested with a different trial order and different mount and playback exemplars, with at least 2 days between testing. Individuals were tested in both the fall and winter to examine seasonal effects.

Behaviors recorded were number of songs and chatters within 5m of the mount, time spent within specified distances to the mount (0-2m and 2-5m), and time spent attacking the mount. Behaviors were spoken into a voice recorder during trials and then transcribed using JWatcher 1.0 (Blumstein et al. 2006). Vocalizations from the focal bird were recorded electronically during trials and also transcribed using JWatcher. When female TBVI chattered during trials, I used my spoken notes from the voice recorder to distinguish between and only transcribe focal male chatters.

Statistical analysis: For response rates (whether individuals approached within 5m of the mount), I fit a generalized linear mixed model with logistic link and subject-level random intercepts to account for the repeated measurements within birds in SAS. For aggressive

responses (level of aggression for individuals that approached within 5m of the mount), I analyzed each behavior separately using linear mixed models fit in SAS Proc Mixed with subject-level random intercepts. All data were transformed to $\log(n+1)$ to improve normality prior to analysis. I tested whether the following factors affected aggressive responses or response rates: competitor (sympatry/allopatry), season (fall/winter), trial type (conspecific/heterospecific/AMRE), trial order (conspecific then heterospecific vireo/heterospecific vireo then conspecific), and (for WEVI only) sex (male/female) and age (first-year/adult). Two analyses were run for response rates and aggression: one restricted to conspecific and heterospecific vireo trials; and a second comparing conspecific, heterospecific vireo, and AMRE trials. The analyses for AMRE only compared response rates/aggression to conspecific and heterospecific vireo trials that were conducted with an AMRE trial. As AMRE trials did not use a mount, I conducted a subset of conspecific and heterospecific vireo trials without mounts when part of an AMRE sequence. The presence of a mount for the conspecific and heterospecific vireo trials was thus also included as a factor in AMRE analyses. AMRE trials were only conducted in the winter, so season was not included as a factor. Non-significant interactions ($p > 0.06$) were removed in a backward step-wise fashion from the models until only significant interactions remained. Main effects always remained in each model, as assessing their effects was the primary goal.

To assess whether behavior towards conspecific and heterospecific vireos were related, I used a principle components analysis (PCA) to reveal suites of correlated behaviors that may represent behavioral syndromes (Sih et al. 2004). I only included data from individuals that had a behavioral response (approached the mount) for at least one conspecific and one heterospecific trial. I averaged behaviors for multiple trials within individuals, transformed them to $\log(n+1)$ and then subjected them to a correlation-based PCA within each species. For WEVI, songs were

not included in the PCA as females do not sing, and attacks were not included as no WEVI attacked the mount (see Results). I assessed Spearman correlations between conspecific and heterospecific behavior on each PC axis for allopatric and sympatric populations separately.

Territories: I mapped territories of both species using conspecific playback and GPS receivers. As territories often occurred along non-linear habitat edges, creating a single minimum convex polygon would include areas that contained no resources. Thus, I combined all GPS points for an individual into multiple minimum convex polygons to exclude water, fields, or areas with no vegetation, using the Animal Movement extension in ArcView 3.2 (Hooge et al. 2000). In a few cases, I included areas up to the edge of usable habitat, even if the territory holder had not been sighted there. Only individuals with at least 8 points, and only individuals for which I was reasonably certain I had established most boundaries, were used in the analysis. Territory overlap was calculated as the percentage of the focal bird's territory overlapped by all other birds. Individuals were excluded from territory overlap analyses when neighbors had not been mapped and so overlap had not been accurately assessed. I also used Pearson correlations to assess relationships between multivariate behavior (the same PCA as above), body mass, and territory size. Data met the assumptions of normality and linearity.

Results

I conducted 902 playback trials, of which 55.7% resulted in an individual approaching within 5m of the mount (Table 1-1). At the individual level, 22 sympatric and 32 allopatric TBVI and 26 sympatric and 27 allopatric WEVI approached during at least one trial. Mount and playback exemplar had no effect on any behavior (Table 1-2), and so were not included in the subsequent analyses.

Response rates to conspecifics versus heterospecific vireo

The full models of effect tests for whether individuals responded ('any response') are shown in the associated tables. TBVI responded to more trials than did WEVI (Table 1-3). Within species, TBVI responded more often to conspecific than heterospecific trials (Table 1-4). WEVI also responded more often to conspecific than heterospecific trials, and responded more often in allopatry than sympatry in the fall while in the winter locations did not differ (Table 1-5).

Aggression: TBVI versus WEVI

TBVI were much more aggressive towards both species of vireo than were WEVI (Table 1-3). TBVI spent more time close to the mount than did WEVI and attacked the mount in 30% of trials where individuals approached (82/270 trials), while WEVI never attacked the mount in 161 trials with approaches. To reduce the number of higher-order statistical interactions, aggression by TBVI and WEVI were analyzed separately.

Aggression to conspecifics versus heterospecific vireo: TBVI

The full models of effect tests for the level of aggression are shown in Table 1-4, with the direction of significant main effects of interest (location, season, trial type) and their interactions reported here. TBVI were more aggressive towards conspecifics than heterospecific vireos: they sang more, spent more time close to the mount (within 2m), and spent longer attacking conspecifics than heterospecifics. TBVI behaved differently in the fall vs winter: they were more likely to chatter in the fall than the winter, yet spent longer attacking in the winter than the fall.

Coexistence with WEVI also affected TBVI's behavior: TBVI spent more time closer (within 2m) and less time farther (2-5m) from the mount and spent longer attacking in sympatry than allopatry. Location and seasonal effects also interacted for two variables: TBVI were more likely to sing in the winter than in the fall and this was more pronounced in sympatry than allopatry; and they spent more time close to the mount in the winter than fall in allopatry, while in sympatry the seasons were similar (Fig. 1-2).

The first three principle components accounted for 79.5% of the variation in behavior (Table 1-5). PC1 captured 35.4% of variation, with positive scores reflecting more time attacking and more time spent within 2m of the mount, and less time spent within 2-5m of the mount. This describes overt aggression. PC2 captured an additional 24% of behavioral variation. Positive scores were associated with more songs and more time spent within 5m of the mount, and may describe sociability (Sih et al. 2004; Réale et al. 2007). PC3 captured 20% and was heavily associated with the number of chatters, which is an aggressive vocal response (Bradley 1980). Conspecific and heterospecific behaviors were correlated in both allopatric (n=29) and sympatric (n=22) populations for PC1 (allopatry: $p=0.0004$, sympatry: $p=0.0014$; Fig. 1-3) and only in allopatry for PC3 (allopatry $p=0.045$; sympatry $p=0.076$), while PC2 was only correlated in sympatry (allopatry: $p=0.35$; sympatry: $p=0.0019$).

Aggression to conspecifics versus heterospecific vireo: WEVI

The full models of effect tests for the level of aggression are shown in Table 1-6, with the direction of significant main effects of interest (location, season, trial type, age and sex) and their interactions reported here. WEVI were more aggressive to conspecifics than towards TBVI, as they spent more time close to the mount during conspecific than heterospecific vireo trials. The

sexes and ages behaved differently: females chattered more than males; males sang more often in the winter than the fall; and adults spent more time within 2-5m of the mount than first-years. WEVI were also affected by coexistence with TBVI: WEVI spent less time within 2-5m during heterospecific compared to conspecific trials in sympatry but not allopatry (Fig. 1-4), and first-years spent less time within 2-5m in sympatry than allopatry. Seasonal responses also interacted with location and species-specific responses for one variable: there were more chatters in the fall than winter towards conspecifics but in the winter than fall towards heterospecifics, a pattern which was accentuated in sympatry (Fig. 1-5). WEVI never attacked the mount.

The first two principle components accounted for 81.2% of the total variation in behavior (Table 1-7). PC1 captured 50.1% and higher values reflected more chatter and more time spent within 2m of the mount (overt aggression), whereas PC2 was heavily associated with more time spent within 2-5m of the mount and more chatters (sociability). Conspecific and heterospecific aggression were correlated in allopatry (n=23) but not sympatry (n=11) for PC1 (allopatry p=0.0003; sympatry p=0.47) but were only correlated in sympatry for PC2 (allopatry: p=0.31; sympatry p=0.051; Fig. 1-6).

Response rates to AMRE versus conspecifics and heterospecific vireo

TBVI were more likely to respond to AMRE than were WEVI (Table 1-8). Both species were less likely to respond to AMRE than to conspecific or heterospecific vireo trials and this difference was greater when a mount was present.

Aggression to AMRE versus conspecifics and heterospecific vireo

Males sang less during AMRE than during conspecific trials and individuals chattered less during AMRE vs conspecific and heterospecific vireo trials (Table 1-8). The presence of a mount during the conspecific/heterospecific trials increased the number of chatters. All individuals spent less time close to the speaker during AMRE than conspecific or heterospecific vireo trials.

Territories

I estimated territory sizes for 20 WEVI males (12 first-years, 7 adults, 1 unknown age), 16 WEVI females (9 first-years, 7 adults) and 48 adult male TBVI. Territories within species were mutually exclusive: $3.9 \pm 1.0\%$ overlap for TBVI and $5.8 \pm 2.5\%$ overlap for WEVI. In sympatry, focal WEVI territories had $30.6 \pm 7.5\%$ overlap with TBVI. However some WEVI established territories in fragments that were too small to support a TBVI pair. Analyzing only WEVI territories that occurred in larger segments revealed that these WEVI ($n=11$) experienced 70.1% overlap with TBVI. Similarly, focal TBVI in sympatry experienced $10.4 \pm 5.3\%$ territory overlap with WEVI. Since no WEVI established territories in scrub, analyzing only forest habitat gave a more accurate estimate of focal TBVI overlap by WEVI of $24.6 \pm 11.2\%$. One individual WEVI had a territory almost twice as large as the next largest territory. As this large size may have resulted from a mid-season shift (he was recorded from one area in the fall and another in the winter), he was excluded from the remaining analyses. Territory size was not related to average body mass in WEVI ($n=33$, $p=0.127$) or TBVI ($n=48$, $p=0.093$). Overt conspecific aggression (PC1) had a positive trend with territory size in allopatric TBVI ($r^2=0.11$, $n=24$, $p=0.11$) yet had a negative trend in sympatric TBVI ($r^2=0.15$, $n=19$, $p=0.10$), and ANCOVA revealed overt conspecific aggression and territory size had a significantly different slope

between allopatric and sympatric populations (location X PC1: $F_{1,39} = 4.17$, $p=0.048$). There was no relationship between overt conspecific aggression and territory size in sympatric or allopatric WEVI (all $p>0.24$), and overt heterospecific aggression was not related to territory size in either species (all $p>0.26$). Neither overt aggression nor sociability towards either species was related to average body mass in TBVI (all $p>0.25$). In sympatric WEVI, body mass was positively related to conspecific sociability (PC2: $r^2=0.59$, $n=8$, $p=0.025$) but not to overt conspecific aggression, overt heterospecific aggression or heterospecific sociability, or to any behavior in allopatry (all $p>0.24$).

TBVI territory size did not differ between habitats (scrub: 1.51 ± 0.13 ha; forest: 1.47 ± 0.15 ha; $F_{1,47}=0.019$, $p=0.89$) or location (allopatry: 1.39 ± 0.14 ha, sympatry: 1.64 ± 0.13 ha; $F_{1,47}=1.41$, $p=0.24$). In sympatry, I initially caught WEVI in both types of habitat but they only established territories in forest, even though allopatric WEVI used both habitat types. WEVI territory size also did not differ between sympatry (0.23 ± 0.022 ha) and allopatry (0.19 ± 0.032 ha; $F_{1,29}=1.38$, $p=0.25$) but adults in allopatry had smaller territories than first-years, while age had no effect in sympatry (age X location: $F_{1,29}=3.96$, $p=0.056$), and males tended to have larger territories than females ($F_{1,29}=3.57$, $p=0.069$). I did not obtain territory sizes from WEVI in scrub in allopatry, so cannot test the effect of habitat for this species. Neither sex nor age affected territory overlap of conspecifics (sex: $p=0.30$, age: $p=0.15$) or heterospecifics (sex: $p=0.11$, age: $p=0.39$) in WEVI.

Age and sex-related settlement: WEVI

Adults were more common in allopatry (48% adults) compared to sympatry (21% adults; Pearson's $\chi^2_{1,211}=16.35$, $p<0.0001$), and females tended to be more common in sympatry (44%

females) compared to allopatry (31% females; Pearson's $\chi^2_{1,169}=3.22$, $p=0.073$) (Table 1-9). First-years were more common in scrub than forest habitat in sympatry (Pearson's $\chi^2_{1,127}=6.56$, $p=0.010$). There were no other age or sex-related habitat effects (all $p>0.23$). Not all individuals were sexed, and so sample sizes are lower for sex than for age comparisons.

Discussion

Evolutionary effects: aggression and territories

The mutually exclusive territories within each species are indicative of strong intraspecific interference competition. However, when the two vireo species occurred in the same habitat their territories overlapped, showing that even high heterospecific aggression does not necessarily result in exclusive interspecific territories. The highly aggressive TBVI had 25% territory overlap by WEVI, but this is an underestimate as some unbanded WEVI were also present on focal TBVI territories. Toms (2011) found even higher interspecific overlap (87%) between interspecifically aggressive resident Adelaide's warblers (*Setophaga adelaidae*) and migrant American redstarts in the non-breeding season. As TBVI territories were present in all habitats and in every area large enough to accommodate them and were about six times larger than WEVI territories, it is not surprising that TBVI had less overlap with WEVI than WEVI did with TBVI, as WEVI did not saturate the landscape. Thus the effects of interspecific behavioral interactions may be more intense in WEVI than in TBVI, especially since each TBVI territory contains two individuals, and male TBVI were extremely physically aggressive towards simulated intruders of both vireo species; several individuals ripped out feathers and some even plucked out eyes from the mounts, whereas the smaller WEVI never attacked and only one individual performed a flyover. In contrast, Greenberg et al (1993) found that WEVI performed

aggressive flyovers to song playback of the smaller resident Mangrove Vireo (*Vireo pallens*) in the Yucatan, and chased *V. pallens* from fruiting *Bursera simaruba* trees. Thus resident status alone is not sufficient for dominance. Body size may be a more important factor in establishing dominance hierarchies (Morse, 1980), and TBVI are larger than WEVI. However, some WEVI established territories in small fragments; this may be a strategy to avoid interactions with the aggressive TBVI. Subordinate species may also coexist with dominant species by avoiding them temporally rather than spatially. In my study, WEVI spent less time in close proximity to the TBVI mount in sympatry than in allopatry (Fig. 1-4) and were less likely to respond to trials in sympatry than allopatry during the fall. This indicates that the subordinate WEVI may be actively avoiding the aggressive TBVI temporally by moving away when they hear or see them on the overlapping part of their territory, and when they do approach they spend less time nearby (Case & Gilpin 1974; Carothers & Jaksic 1984; Kaufmann 1983; Toms 2013). I also found that response rates and aggression were significantly higher in both species towards heterospecific vireos than towards AMRE, and did not differ between populations allopatric and sympatric with the heterospecific vireo. This pattern supports the hypothesis that the frequency and intensity of heterospecific aggression is related to resource overlap (Peiman & Robinson 2010), and that behavioral differences between populations were not due to a general difference in the responsiveness of individuals.

Directional and correlational selection

By comparing behaviors between sympatry and allopatry, we can distinguish non-adaptive from adaptive heterospecific aggression (Peiman & Robinson 2010). While I found that heterospecific aggression was higher in sympatry than allopatry for the dominant TBVI, conspecific aggression showed the same pattern between locations. This suggests that sympatric

TBVI are under directional selection for higher values of either conspecific aggression, heterospecific aggression, or both, or that allopatric TBVI are under directional selection for lower values of conspecific aggression. As territory size did not differ between allopatry and sympatry, I infer that the density of conspecifics was the same in both locations, and so is not an explanation for higher conspecific aggression in sympatry. With my current data I cannot distinguish on which behavior selection acted. Additionally, I found stronger correlations in allopatric than sympatric populations for overt aggression (PC1; TBVI and WEVI) and vocal aggression (PC3; TBVI). Because heterospecific behaviors are not naturally expressed in allopatry, this indicates these behaviors may be driven by non-adaptive genetic co-variation between conspecific and heterospecific expression. The stronger correlation in sympatry than allopatry for sociability (PC2; TBVI and WEVI) indicates the presence of correlational selection, resulting in an adaptive sociability syndrome. Sociable individuals spend more time with the intruder than non-sociable individuals (Réale et al. 2007), and highly social individuals may have both higher benefits (gaining information about both species of intruder) and costs (direct aggression) than non-social individuals that interact less with both species of intruder. If this syndrome is adaptive, then both social and non-social individuals should do equally well (Dingemanse & Réale, 2005); these fitness consequences remain to be tested. Sociability syndromes have rarely been considered in the literature (Conrad et al. 2011; Peiman & Robinson 2012) yet are heritable (Wright et al. 2003) and so may respond to selection. However, it is unclear why sociability and not aggression was under correlational selection. Perhaps only one aggressive type had the highest fitness, as would happen in individuals that were consistently less aggressive towards intruders acquired fewer resources. Here, I present the first evidence for an adaptive conspecific and heterospecific sociability syndrome due to interspecific interference

interactions in birds, a pattern which was consistent in both the dominant and subordinate species. Most studies focus on the effects of overt aggression, but sociability syndromes may be a more common adaptive response to selection than previously thought. Additionally, most studies of syndromes focus on the effects of predators, ignoring the effects of heterospecific competitors.

Ecological effects: season and habitat

Ecological factors, such as differences in food availability related to intrinsic habitat differences or linked to rainfall, can change the intensity of competition and are predicted to affect behavior and/or territory size. I found that forest habitats had more *B. simaruba* fruit than scrub habitats (Chapter 2). Despite this difference in fruit availability, habitat type did not affect territory size, resulting in an equal density of conspecific competitors across habitats, and therefore potentially more intense competition in scrub habitats at least for fruit. I also found that season had a strong effect on arthropod abundance and affected some aspects of behavior. Arthropod abundance declined from fall to winter in sympatric but not allopatric locations (Chapter 2), and I predicted that this change would be mirrored in the patterns of aggressive behavior. However, there was no evidence that aggression increased in the winter in sympatric but not allopatric populations of either species, except that TBVI did increase singing in the winter in sympatry more than allopatry. Other seasonal effects, like more time spent attacking the mount, occurred in both allopatry and sympatry and so are not clearly related to changes in resource abundance.

Habitat use at small spatial scales (WEVI)

The causes of differential distribution of wintering individuals at both large geographic scales and smaller habitat scales have recently received renewed interest (Komar et al. 2005). At the habitat scale, I initially caught sympatric WEVI in both forest and scrub, but found they predominantly established territories in forest habitats. Since allopatric WEVI used both habitat types, the restricted habitat use in sympatry was not due to an innate preference. This type of distribution is hypothesized to occur when all individuals are equal competitors and select among habitats that differ in quality to settle in those that maximize their fitness, i.e. forest habitats with more food (ideal free distribution: Fretwell 1972). For this to occur, food abundance must vary among habitats (Johnson 2007) as I found for fruit abundance (Chapter 2). This type of distribution usually results from intraspecific exploitative competition, but it has been postulated that interspecific interactions may also lead to this pattern (Case & Gilpin, 1974; Dhondt, 2012; Hughes, 1993). However, without experimental manipulation of individuals in different habitats (i.e., Studds & Marra 2005) the causal mechanism of habitat use remains to be determined. Perhaps due to a similar mechanism, WEVI and the resident *V. pallens* partitioned habitat in the Yucatan (Greenberg et al. 1993), where WEVI predominately settled in forest habitat, therefore avoiding *V. pallens* in pasture and second-growth scrub habitat. Thus, the distribution of WEVI across habitats seems to be explained by interspecific exploitative competition resulting in sympatric WEVI specializing in forest habitats.

Age and sex distributions at large spatial scales (WEVI)

I also found large-scale longitudinal differences in age and sex classes in the migrant WEVI, where the age class predicted to be most socially dominant (adults) occupied locations predicted to be highest quality (allopatry), and the subordinate sex class (females) were in lower

quality locations (sympatry) (Table 1-9). Differential migration between age and sex classes has been detected along latitudinal gradients but is less common longitudinally (Terrill & Able, 1988). Sex and age differences in overwintering latitude have been attributed to dominance, thermoregulatory capacity, and spring departure for breeding (Cristol et al. 1999). Under the dominance hypothesis, intraspecific interference competition results in some individuals establishing territories in better quality habitats and aggressively forcing subordinates into lower quality habitats (ideal despotic distribution: Fretwell 1972), which may happen even at large spatial scales (Payevsky 1995; Gauthreaux 1978; Murphy et al. 1998). However I found little evidence that the sexes or ages differed in their level of aggression to simulated conspecific intrusions, so it seems unlikely that the prevalence of adults in allopatry and females in sympatry were caused by sex or age-specific dominance. An alternative hypothesis is that differences in body size allow large individuals to winter in colder locations due to their increased thermoregulatory capacity. Though adult WEVI have longer wing chords than first-years they otherwise do not differ in size, and there are only minor sex-related morphological differences (males have longer wings and are heavier; Chapter 2). Additionally, allopatry (Mexico) was only cooler than sympatry in the fall (Chapter 2), making the ability to withstand colder winters an unlikely driver of longitudinal patterns. A third possibility is that males winter closer to the breeding area to arrive first and secure territories. As in most passerines, WEVI males arrive at the breeding grounds earlier than females (Hopp et al. 1999). However my study site in The Bahamas is closer to the breeding grounds than my site in Mexico, and so this does not explain why males are less common in The Bahamas. Thus no current hypotheses explain the sex-related distributions.

An additional possibility that may explain the predominance of adults in allopatry is that younger birds face an energetic constraint during fall migration (Prescott & Middleton, 1990). During fall migration, adults and first-years did not differ in date of arrival at a stop-over site, but adults of several species including WEVI had higher fat loads and could make the trans-Gulf flight to Mexico, whereas first-years could not (Woodrey & Moore, 1997). It may be that young birds, migrating at the edge of the range (Kelly & Hutto, 2005; Ralph, 1981) and energetically unable to cross the Gulf (Woodrey & Moore 1997), instead migrate along the coast to Florida and then make the much shorter flight to The Bahamas. Other studies have found that young birds make more short-distance movements compared to adults (Jorge et al. 2011). Thus the observed large-scale distributions of age classes can potentially be explained through physiological constraints.

Conclusions

The ecological and evolutionary effects of interference competition are still widely untested (Grether et al. 2013, 2009). The high level of heterospecific aggression observed here suggests it is an evolutionary response to interspecific interference competition, yet this aggression was not sufficient to maintain exclusive territories between species. This is not completely surprisingly as the resident TBVI used all habitats except smaller fragments, forcing WEVI to settle on their territories. Yet there was some suggestion that WEVI were still able to avoid the aggressive TBVI spatially (by using these small habitat fragments) and temporally (by responding less to trials and spending less time near TBVI mounts). Thus it seems the high level of interspecific aggression may not be adaptive as it does not result in exclusive habitat use, and may in fact have negative physiological consequences as TBVI spend energy in attacking and

WEVI spend energy in retreating, with loss of foraging opportunity for both. The lack of spatial niche partitioning in sympatry predicts that these species should partition other aspects of their niche, such as food, to reduce exploitative competition (Murray 1971). Additionally, the restriction of habitat use in sympatric WEVI may cause a reduction in their overall abundance (Newton 1998), thus fulfilling one of the criteria for interspecific competition (Dhondt 2012). I also found that no WEVI returned to my study plots in the two years following this project in sympatry, whereas at least 8/45 (17.8%) returned to the same territories the following year in allopatry, indicating that sympatry may be less suitable as over-winter habitat. This same pattern was observed in other studies of WEVI: in Los Tuxtlas, 3/16 territorial birds returned the subsequent year (Rappole and Warner 1980); in San Salvador, 0/18 returned (Murphy et al. 2001). Intraspecific competition during the winter has known negative effects on body condition, migration date, and subsequent fitness on the breeding grounds in migrants (Marra 2000; Marra & Holmes 2001; Reudink et al. 2009; Sillett & Holmes 2002; reviewed in Newton 2004) and residents should experience similar effects due to intraspecific competition (Kirk & Gosler, 1994; Tellería & Pérez-Tris, 2003; Toms, 2011), but studies of comparable effects due to interactions between migrants and residents are lacking (Greenberg 1986; Dhondt 2012; Leisler 1990). Recent studies in the Palearctic/African migration system have focused on niche partitioning in sympatric migrant/resident populations (Salewski et al. 2002; Bensusan et al. 2011) but none have used allopatric populations as well and so cannot test for evolutionary responses (Peiman & Robinson 2010). By combining evolutionary and ecological contrasts, researchers will be able to provide a more comprehensive examination of the effects of interspecific competition.

Current interactions are expected to be more intense than historical interactions because over-wintering sites have been subjected to human-caused habitat destruction, resulting in birds sharing smaller areas of habitat, potentially leading to more frequent interactions with ecologically similar species (Sutherland, 1996). By assessing the effects of competition in habitats that differ in quality (Studds & Marra 2011), we can predict whether future habitat degradation, which may mimic current conditions in poor quality habitats, will have the potential to adversely affect populations of migrants and residents. This may be especially critical to some locations in the Caribbean (i.e. San Salvador Island in The Bahamas) that are already marginal over-wintering sites for migrants, but that allow young birds to overwinter their first year and become socially competitive enough to overwinter in a higher-quality location the following year as adults (Murphy et al. 2001). Thus, even marginal habitat should be a conservation concern, which is a departure from the normal recommendation of preserving only the highest-quality habitats (eg. Saracco et al. 2008).

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Table 1-1: Number of individual trials with mounts (for C and H trials) within allopatric and sympatric populations of Thick-billed Vireos (TBVI) and White-eyed Vireos (WEVI) during the fall and winter (includes replicate trials on the same individual). An additional 102 C and H trials were conducted without mounts. Though C and H trials were paired within individuals, differences in sample sizes resulted from a few trials that were not usable due to technical issues. C = conspecific, H = heterospecific vireo, AMRE = American redstart.

Location	Season	Focal species	Trial type	Number of trials	Percentage of trials with approaches $\leq 5m$ of mount
Allopatry	fall	TBVI	C	38	78.9
Allopatry	fall	TBVI	H	36	63.9
Allopatry	fall	WEVI	C	46	69.6
Allopatry	fall	WEVI	H	46	56.5
Allopatry	winter	TBVI	C	61	75.4
Allopatry	winter	TBVI	H	59	61
Allopatry	winter	TBVI	AMRE	51	41.2
Allopatry	winter	WEVI	C	55	58.2
Allopatry	winter	WEVI	H	54	35.2
Allopatry	winter	WEVI	AMRE	47	17
Sympatry	fall	TBVI	C	37	81.1
Sympatry	fall	TBVI	H	37	75.7
Sympatry	fall	WEVI	C	17	23.5
Sympatry	fall	WEVI	H	17	23.5
Sympatry	winter	TBVI	C	48	72.9
Sympatry	winter	TBVI	H	48	68.7
Sympatry	winter	WEVI	C	46	41.3
Sympatry	winter	WEVI	H	46	39.1
Sympatry	winter	WEVI	AMRE	11	45.5

Table 1-2: Summary of tests for the effects of playback and mount exemplars on behavioral response rates and on the level of aggressive responses for Thick-billed Vireos (TBVI) and White-eyed Vireos (WEVI). Season compares the fall to winter, location compares allopatry to sympatry, and trial order compares conspecific then heterospecific trials to heterospecific then conspecific trials. These fixed effects were included in all models to adjust for their effects before testing for playback and mount exemplar (bolded rows). Note the location could not be tested for TBVI mounts as different mounts were used in each location. See text for details about mounts and playback and definitions of behaviors. Species and behaviors are carried down columns until the next entry.

Species	Behavior	Effect	Num DF	Den DF	F value	p-value
TBVI	response rate	Season	1	300	2.57	0.1099
		Location	1	300	1.08	0.2988
		Trial order	1	300	2.36	0.1252
		Playback	8	300	1.28	0.253
	song	Season	1	196	24.64	<.0001
		Location	1	196	0.00	0.9614
		Trial order	1	196	3.07	0.0813
		Playback	8	196	0.87	0.5387
	chatter	Season	1	196	13.49	0.0003
		Location	1	196	0.18	0.671
		Trial order	1	196	0.05	0.8243
		Playback	8	196	1.12	0.3496
	time within 1-2m	Season	1	196	4.77	0.0302
		Location	1	196	2.85	0.0931
		Trial order	1	196	3.12	0.0791
		Playback	8	196	1.03	0.4151
	time within 2-5m	Season	1	196	0.07	0.7931
		Location	1	196	7.17	0.0081
		Trial order	1	196	4.96	0.0271
		Playback	8	196	1.72	0.0949
time attack	Season	1	196	4.67	0.0319	
	Location	1	196	5.23	0.0233	
	Trial order	1	196	6.06	0.0147	
	Playback	8	196	1.01	0.426	
WEVI	response rate	Season	1	250	4.30	0.0392
		Location	1	250	0.36	0.5514
		Trial order	1	250	2.86	0.0921
		Playback	12	250	1.26	0.2423

	song	Season	1	56	17.02	0.0001
		Location	1	56	0.46	0.5008
		Trial order	1	56	1.22	0.2739
		Playback	10	56	1.56	0.1432
	chatter	Season	1	85	1.20	0.2759
		Location	1	85	0.11	0.7451
		Trial order	1	85	0.16	0.6873
		Playback	11	85	1.33	0.2228
	time within 1-2m	Season	1	85	1.17	0.2823
		Location	1	85	0.74	0.3915
		Trial order	1	85	0.02	0.9001
		Playback	11	85	0.62	0.8052
	time within 2-5m	Season	1	85	0.12	0.7284
		Location	1	85	8.54	0.0045
		Trial order	1	85	0.13	0.7186
		Playback	11	85	0.76	0.6765
TBVI	response rate	Season	1	299	1.93	0.1662
		Trial order	1	299	1.92	0.1664
		Mount	9	299	0.93	0.5034
	song	Season	1	195	25.62	<0.0001
		Trial order	1	195	2.69	0.1025
		Mount	9	195	1.02	0.4214
	chatter	Season	1	195	12.75	0.0004
		Trial order	1	195	0.26	0.6117
		Mount	9	195	0.78	0.6345
	time within 1-2m	Season	1	195	4.66	0.0322
		Trial order	1	195	2.53	0.1133
		Mount	9	195	0.94	0.4929
	time within 2-5m	Season	1	195	0.01	0.9335
		Trial order	1	195	6.10	0.0144
		Mount	9	195	1.16	0.3199
	time attack	Season	1	195	4.69	0.0316
		Trial order	1	195	3.87	0.0505
		Mount	9	195	1.05	0.3982
WEVI	response rate	Season	1	252	3.82	0.0516
		Location	1	252	0.16	0.6909
		Trial order	1	252	2.45	0.1189
		Mount	10	252	1.16	0.3203
	song	Season	1	58	15.43	0.0002
		Location	1	58	0.09	0.77

	Trial order	1	58	0.09	0.7693
	Mount	10	58	0.61	0.7962
chatter	Season	1	87	1.00	0.3206
	Location	1	87	6.31	0.0139
	Trial order	1	87	0.19	0.663
	Mount	10	87	1.06	0.4011
time within 1-2m	Season	1	87	1.16	0.2846
	Location	1	87	3.25	0.0748
	Trial order	1	87	0.21	0.6515
	Mount	10	87	1.33	0.2261
time within 2-5m	Season	1	87	0.50	0.483
	Location	1	87	0.03	0.8559
	Trial order	1	87	0.19	0.663
	Mount	10	87	1.47	0.1663

Table 1-3: Analysis of behavioral response rates and the level of aggressive responses for White-eyed Vireos (WEVI) and Thick-billed Vireos (TBVI). Species compares focal WEVI to TBVI, location compares allopatry to sympatry, season compares fall to winter, trial type compares conspecific to heterospecific vireo stimulus, and trial order compares conspecific then heterospecific vireo trials to heterospecific vireo then conspecific trials. See text for definitions of behaviors. Non-significant interactions ($p>0.06$) were removed in a backward step-wise fashion from the models until only significant interactions remained. Main effects always remained in each model, as assessing their effects was the primary goal. Behaviors are carried down columns until the next entry.

Behavior	Effect	Num DF	Den DF	F value	p-value
any response	Location	1	575	1.17	0.2789
	Species	1	575	19.25	<0.0001
	Season	1	575	6.48	0.0112
	Trial type	1	575	10.13	0.0015
	Trial order	1	575	5.89	0.0155
song	Location	1	273	4.74	0.0303
	Species	1	273	6.25	0.013
	Location X Species	1	273	3.39	0.0666
	Trial type	1	273	12.36	0.0005
	Season	1	273	43.47	<0.0001
	Season X Species	1	273	3.5	0.0626
	Location X Season	1	273	5.02	0.0259
	Trial order	1	273	1.21	0.2726
	Location	1	304	7.26	0.0075
	chatter	Species	1	304	15.65
Location X Species		1	304	7.45	0.0067
Trial type		1	304	20.46	<0.0001
Species X Trial type		1	304	8.62	0.0036
Season		1	304	9.88	0.0018
Trial order		1	304	0.26	0.6126
time 0-2m	Species	1	303	54.75	<0.0001
	Season	1	303	0.01	0.9046
	Season X Species	1	303	6.12	0.0139
	Location	1	303	7.94	0.0052
	Location X Season	1	303	4.91	0.0275
	Trial type	1	303	22.94	<0.0001
	Trial order	1	303	1.33	0.2498
time 2-5m	Location	1	304	10.98	0.001
	Species	1	304	14.68	0.0002

Trial type	1	304	0.08	0.7741
Species X Trial type	1	304	4.09	0.044
Season	1	304	0.02	0.8987
Trial order	1	304	5.68	0.0178

Table 1-4: Analysis of behavioral response rates and the level of aggressive responses for Thick-billed Vireos (TBVI) towards conspecifics and White-eyed Vireos (WEVI). Location compares allopatry to sympatry, season compares fall to winter, trial type compares conspecific to heterospecific vireo stimulus, and trial order compares conspecific then heterospecific vireo trials to heterospecific vireo then conspecific trials. See text for definitions of behaviors. Non-significant interactions ($p > 0.06$) were removed in a backward step-wise fashion from the models until only significant interactions remained. Main effects always remained in each model, as assessing their effects was the primary goal. Behaviors are carried down columns until the next entry.

Behavior	Effect	Num DF	Den DF	F value	p-value
Any response	Season	1	308	2.39	0.1229
	Location	1	308	0.36	0.5479
	Trial type	1	308	5.12	0.0243
	Trial order	1	308	3.29	0.0708
song	Season	1	203	25.84	<0.0001
	Location	1	203	0.12	0.7318
	Location X Season	1	203	5.12	0.0248
	Trial type	1	203	14.28	0.0002
	Trial order	1	203	2.48	0.117
chatter	Season	1	204	12.63	0.0005
	Trial type	1	204	2.33	0.1287
	Location	1	204	0.01	0.9148
	Trial order	1	204	0.17	0.6799
time 0-2m	Location	1	203	3.95	0.0482
	Season	1	203	5.65	0.0183
	Location X Season	1	203	11.16	0.001
	Trial type	1	203	18.86	<0.0001
	Trial order	1	203	2.62	0.1074
time 2-5m	Trial type	1	204	2.72	0.1007
	Season	1	204	0.03	0.864
	Location	1	204	8.04	0.005
	Trial order	1	204	5.96	0.0154
time attacking	Trial type	1	204	13.24	0.0003
	Location	1	204	11.85	0.0007
	Season	1	204	5.22	0.0233
	Trial order	1	204	5.57	0.0192

Table 1-5: Loadings from a principle components analysis of Thick-billed Vireo behavior towards conspecifics and the heterospecific White-eyed Vireo. Values ± 0.4 are bolded to highlight their major contribution to variation on each component.

Behavior	PC1	PC2	PC3
Song	-0.04	0.84	-0.16
Chatter	0.13	0.097	0.97
Time 0-2m	0.52	0.42	-0.026
Time 2-5m	-0.59	0.33	0.16
Time attacking	0.60	0.003	-0.04
Eigenvalue	1.77	1.20	1.00
Cumulative percent	35.44	59.5	79.5

Table 1-6: Analysis of behavioral response rates and the level of aggressive responses for White-eyed Vireos (WEVI) towards conspecifics and Thick-billed Vireos (TBVI). Location compares allopatry to sympatry, season compares fall to winter, trial type compares conspecific to heterospecific vireo stimulus, and trial order compares conspecific then heterospecific vireo trials to heterospecific vireo then conspecific trials. Sex and age (first-year and after first-year) were also included. See text for definitions of behaviors. Non-significant interactions ($p>0.06$) were removed in a backward step-wise fashion from the models until only significant interactions remained. Main effects always remained in each model, as assessing their effects was the primary goal. Behaviors are carried down columns until the next entry.

Behavior	Effect	Num DF	Den DF	F value	p-value
any response	Location	1	252	2.39	0.1237
	Season	1	252	0.3	0.5874
	Location X Season	1	252	4.19	0.0418
	Trial type	1	252	4.93	0.0273
	Age	1	252	1.41	0.2356
	Sex	1	252	1.66	0.1985
	Trial order	1	252	2.08	0.1502
song	Season	1	64	16.14	0.0002
	Location	1	64	2.54	0.1156
	Trial type	1	64	0.02	0.8873
	Age	1	64	0.45	0.5049
	Trial order	1	64	0.7	0.4072
chatter	Season	1	90	0	0.9618
	Location	1	90	0.69	0.4072
	Location X Season	1	90	1.8	0.1826
	Trial type	1	90	23.24	<0.0001
	Season X Trial type	1	90	5.58	0.0203
	Location X Trial type	1	90	5.75	0.0186
	Location X Season X Trial type	1	90	4.88	0.0297
	Age	1	90	0.24	0.6234
	Sex	1	90	6.03	0.016
	Trial order	1	90	0.07	0.7876
time 0-2m	Location	1	94	2.17	0.1444
	Season	1	94	0.8	0.3726
	Trial type	1	94	5.6	0.02
	Sex	1	94	1.47	0.2289
	Age	1	94	0.22	0.6437
	Trial order	1	94	0.1	0.7504
	Location	1	93	0.98	0.3239

time 2-5m	Trial type	1	93	6.62	0.0117
	Location X Trial type	1	93	4.78	0.0313
	Season	1	93	0.28	0.5994
	Age	1	93	4.42	0.0383
	Location X Age	1	93	4.74	0.0319
	Sex	1	93	1.41	0.2384
	Trial order	1	93	0.88	0.3511

Table 1-7: Loadings from a principle components analysis of White-eyed Vireo behavior towards conspecifics and the heterospecific Thick-billed Vireo. Values ± 0.4 are bolded to highlight their major contribution to variation on each component.

Behavior	PC1	PC2
Chatter	0.62	0.43
Time 0-2m	0.68	0.11
Time 2-5m	-0.39	0.89
Eigenvalue	1.50	0.93
Cumulative percent	50.1	81.2

Table 1-8: Analysis of behavioral response rates and the level of aggressive responses for Thick-billed Vireos (TBVI) and White-eyed Vireos (WEVI) towards American redstart (AMRE) playback. Mount refers to whether the associated conspecific and heterospecific vireo trials had a mount present or not, location compares allopatry to sympatry, trial type compares the three stimulus species (conspecific, heterospecific vireo, and AMRE), species compares focal WEVI to TBVI, and trial order compares conspecific then heterospecific vireo trials to heterospecific vireo then conspecific trials. See text for definitions of behaviors. Non-significant interactions ($p>0.06$) were removed in a backward step-wise fashion from the models until only significant interactions remained. Main effects always remained in each model, as assessing their effects was the primary goal. Behaviors are carried down columns until the next entry.

Behavior	Effect	Num DF	Den DF	F value	p-value
Any response	Mount	1	263	19.65	<0.0001
	Trial type	2	263	24.55	<0.0001
	Mount X Trial type	2	263	4.32	0.0143
	Species	1	263	8.77	0.0033
	Location	1	263	3.32	0.0696
	Trial order	1	263	3.47	0.0637
Song	Species	1	109	2.09	0.1508
	Mount	1	109	0.09	0.7666
	Trial type	2	109	3.01	0.0536
	Location	1	109	1.93	0.1676
	Trial order	1	109	0.07	0.7854
	Species	1	127	5.93	0.0163
Chatter	Trial type	2	127	5.68	0.0043
	Mount	1	127	5.56	0.0199
	Location	1	127	15.95	0.0001
	Trial order	1	127	0.72	0.3966
	Species	1	127	38.78	<0.0001
Time 0-2m	Trial type	2	127	34.53	<0.0001
	Mount	1	127	0.22	0.6397
	Location	1	127	1.34	0.2489
	Trial order	1	127	0.25	0.6176
	Species	1	125	11.31	0.001
Time 2-5m	TrialType	2	125	0.6	0.5482
	Mount	1	125	0.29	0.5929
	Mount X Trial type	2	125	3.63	0.0295
	Location	1	125	0.25	0.6193
	Trial order	1	125	4.18	0.0429

Table 1-9: Age and sex of White-eyed Vireos by location and habitat as determined by original capture, which did not always reflect habitat of territory establishment. Sample sizes are lower for the sex categories as not all individuals had their sex determined.

	Location			
	Sympatry		Allopatry	
	Forest	Scrub	Forest	Scrub
Adult	25	2	29	12
First-year	68	32	29	16
Female	35	6	18	6
Male	46	6	33	21

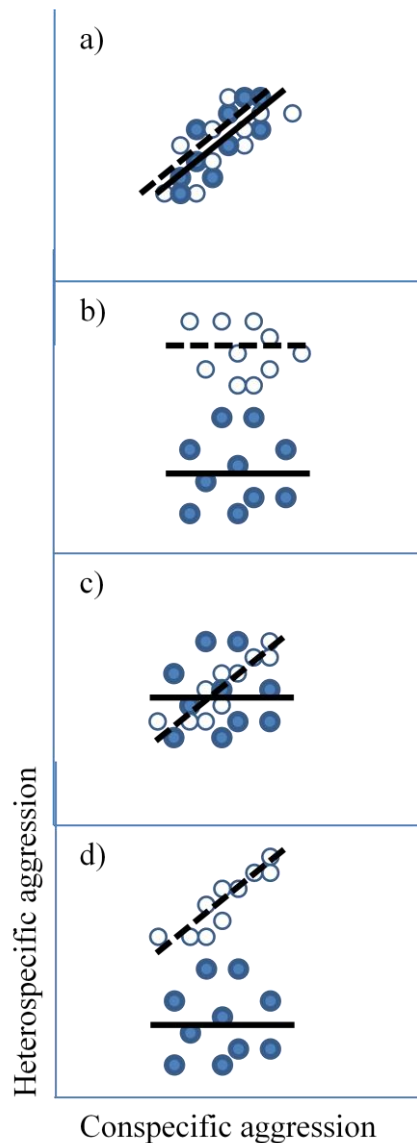


Figure 1-1: Hypothetical distributions of individuals under different types of selection in an allopatric (filled circles, solid line) and a sympatric (open circles, dashed line) population. a) Non-adaptive heterospecific aggression: When the expression of heterospecific aggression is due to a common genetic basis with conspecific aggression, the same correlation will be present between the two behaviors in sympatry and in allopatry. Selection on one behavior will result in the other behavior also changing, but the strength of correlation will be the same across populations regardless. b) Adaptive heterospecific aggression: In the absence of genetic correlations between behaviors, directional selection can act independently on heterospecific aggression, resulting in higher levels of heterospecific aggression in sympatry than allopatry while conspecific aggression will not differ between populations. c) Adaptive heterospecific aggression: Correlational selection acts on both conspecific and heterospecific aggression in sympatry, resulting in an adaptive behavioral syndrome. Since correlational selection by definition acts on two behaviors, it can only occur in sympatry and so results in stronger correlations between conspecific and heterospecific aggression in sympatry than in allopatry. d)

Correlational selection acting concurrently with directional selection, resulting in mean differences in aggression (heterospecific aggression higher in sympatry than allopatry) and also differences in the strength of correlation (stronger correlation in sympatry than allopatry).

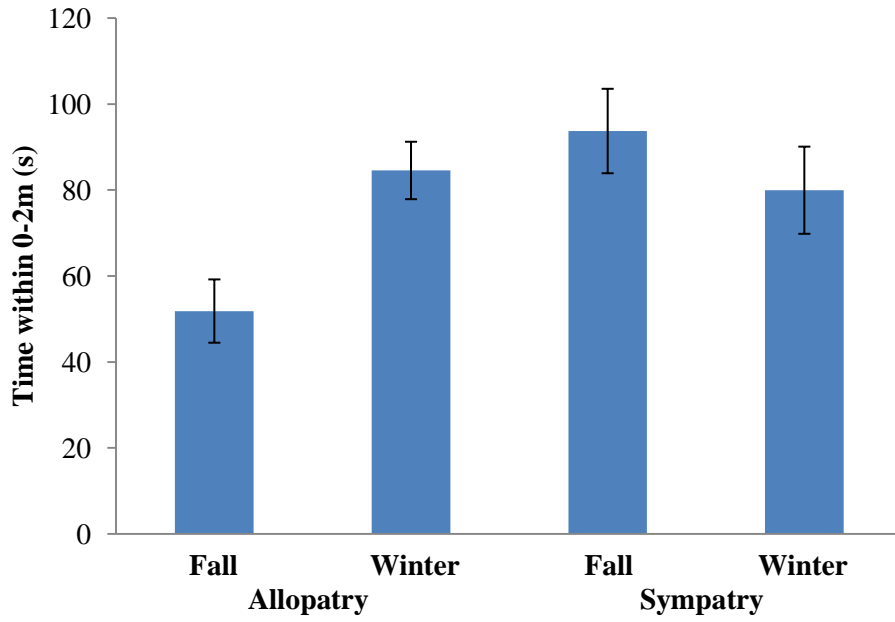


Figure 1-2. Time spent within 2m of the mount (mean \pm SE) during combined conspecific and heterospecific vireo trials for Thick-billed Vireos.

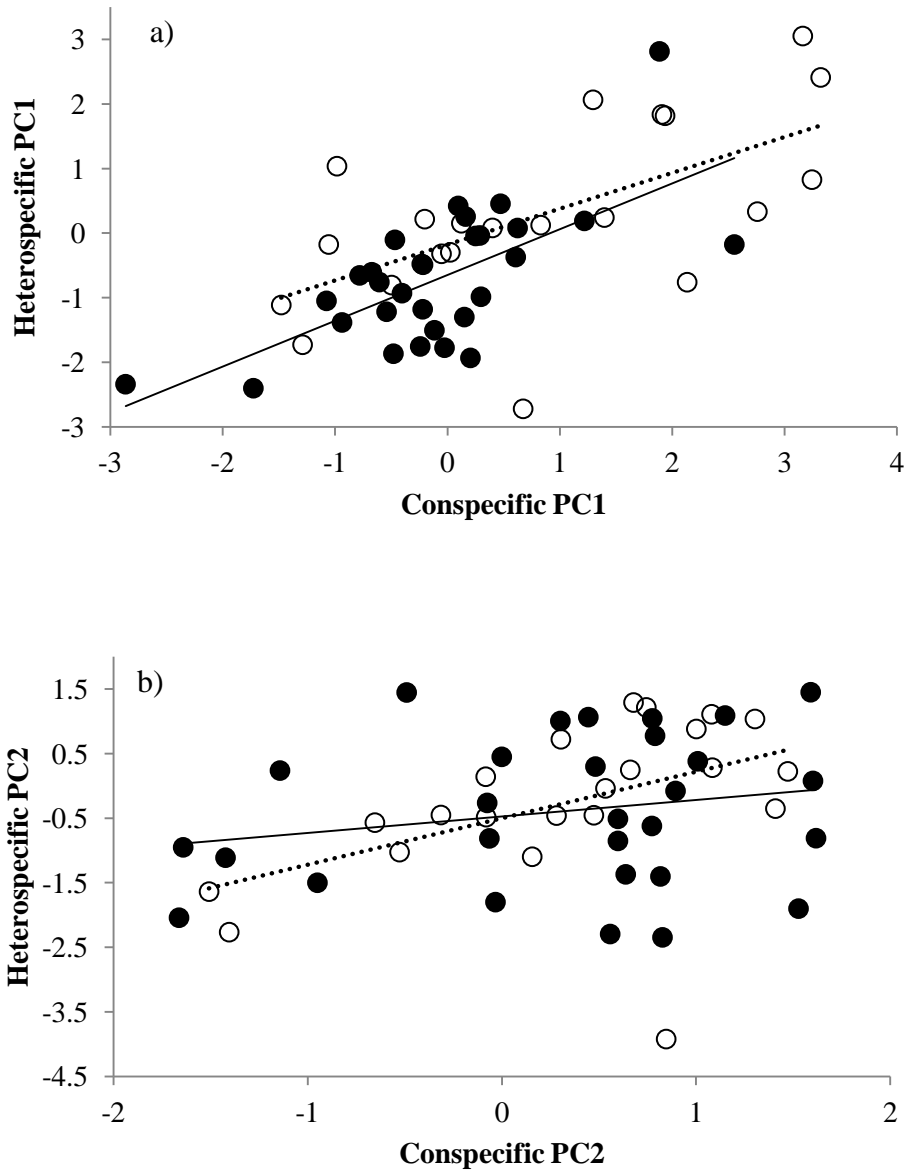


Figure 1-3. The correlation between Thick-billed Vireo aggression towards conspecific and the heterospecific White-eyed Vireo. a) Positive PC1 scores reflect more time attacking and more time spent within 2m of the mount, and less time spent within 2-5m of the mount (overt aggression). Both allopatric and sympatric populations have significant correlations. b) Positive scores on PC2 reflect more songs and more time spent within 5m of the mount (sociability). Only the sympatric population exhibited a significant correlation. Open circles and dashed line are for sympatry, closed circles and solid line are for allopatry.

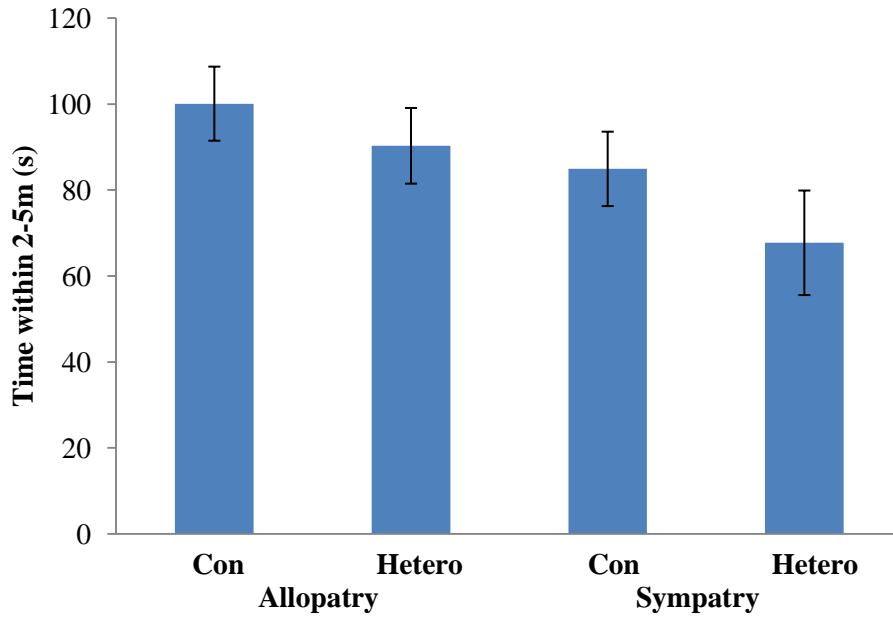


Figure 1-4. Time spent within 2-5m of the mount (mean \pm SE) during trials towards conspecifics (Con) and the heterospecific vireo (Hetero) in populations of White-eyed Vireos allopatric and sympatric with Thick-billed Vireos.

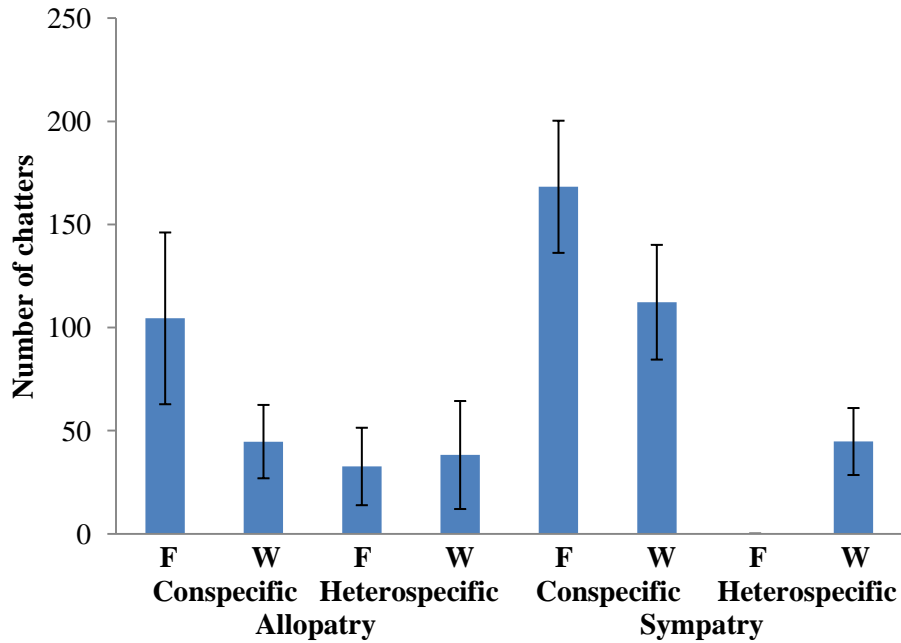


Figure 1-5. Number of chatters (mean \pm SE) emitted by White-eyed Vireos in the fall (F) and winter (W) towards conspecific and the heterospecific Thick-billed Vireo in populations allopatric and sympatric with the Thick-billed Vireo. There is a significant 3-way interaction between fall/winter, conspecific/heterospecific, and allopatry/sympatry (see Table 1-6 for details).

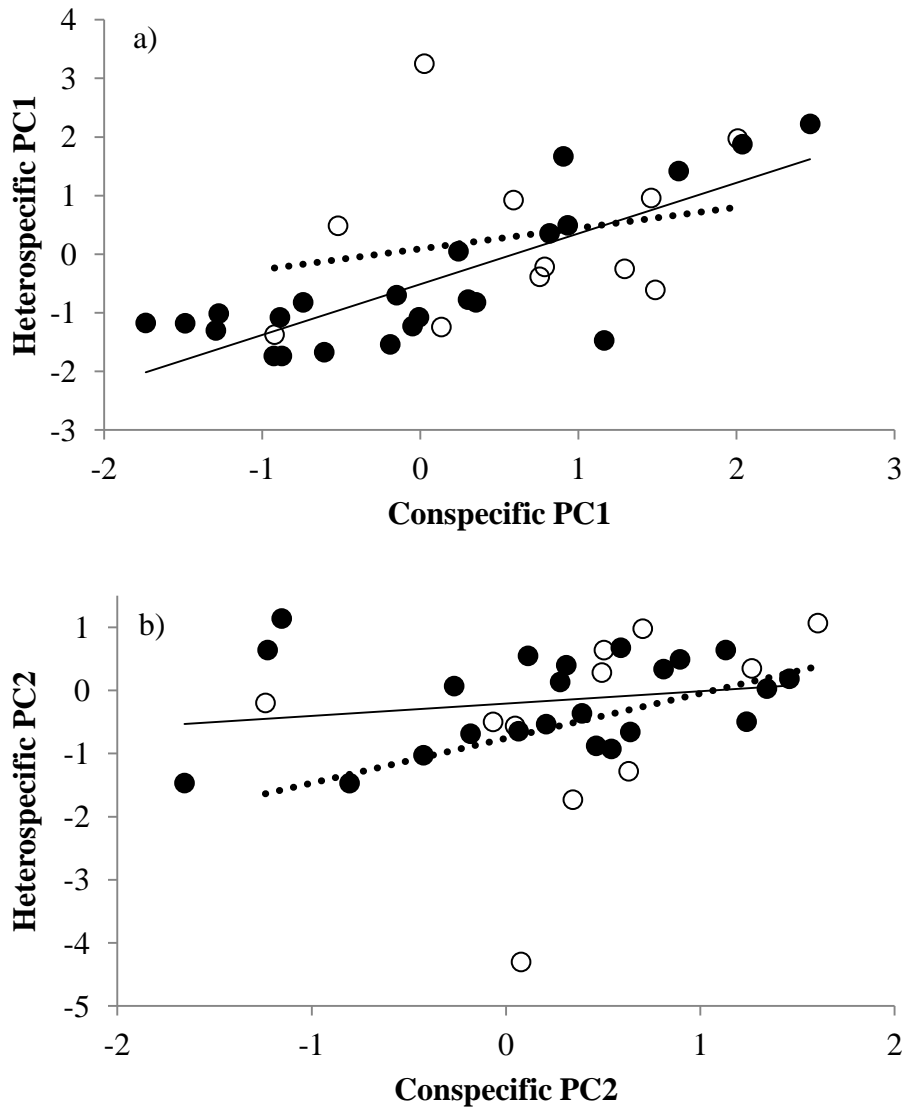


Figure 1-6. The correlation between White-eyed Vireo aggression towards conspecific and the heterospecific Thick-billed Vireo. a) Positive PC1 scores reflect more chatter and more time spent within 2m of the mount (overt aggression). Both allopatric and sympatric populations have significant correlations. b) Positive PC2 scores are heavily associated with more time spent within 2-5m of the mount and more chatters (sociability). Only the sympatric population exhibited a significant correlation. Open circles and dashed line are for sympatry, closed circles and solid line are for allopatry.

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Chapter 2. The effect of resource availability on exploitative competition between resident Thick-billed Vireos (*Vireo crassirostris*) and migrant White-eyed Vireos (*V. griseus*) during the non-breeding season

Abstract

Exploitative competition theory predicts that ecologically similar species will shift their morphology and/or diet in sympatry compared to allopatry to reduce interspecific competition. In addition to a mean diet change, interspecific competition favors reduced population diet variation, while intraspecific competition increases it. However, the effect of competition may be weaker on a species that is composed of generalists, where all individuals consume the full spectrum of resources, than specialists, where each individual uses a subset of the resources that the population uses as a whole, as specialists may be less able to respond to variation in resource abundance or to changes in competitor presence. The intensity of resource competition is expected to depend on resource availability, which can vary spatially and temporally. The migrant White-eyed Vireo (*Vireo griseus*, WEVI) and resident Thick-billed Vireo (*V. crassirostris*, TBVI) only coexist during the non-breeding season and only in parts of their range. They are ecologically similar and have overlapping territories in sympatry, reducing the opportunity for spatial niche partitioning. I measured resource abundance to quantify availability and stable isotopes to quantify diet in relation to seasonal changes, habitat differences, and geographical locations with and without the heterospecific competitor. I found that resources declined from fall to winter, and were more abundant in forest than scrub habitats. Both species were larger in body and bill size in sympatry than allopatry. WEVI consumed higher trophic levels than TBVI in sympatry, but TBVI were more similar in diet composition to WEVI in

sympatry compared to allopatry. The socially subordinate WEVI had higher diet variation than the dominant TBVI, but I found little support for changes in population variance under intraspecific or interspecific competition. However, TBVI had strong evidence of individual specialization between seasons and years, and had stronger correlations between diet and morphology under more intense competition. This specialization may explain the lack of adaptive diet shift in sympatric TBVI, which may have negative consequences for them.

Introduction

The ecological and evolutionary consequences of exploitative competition have been well-documented in several taxa and are theoretically well understood (Grant, 1972; Robinson & Schluter, 2000; Robinson & Wilson, 1994). When two species require the same limited resource, exploitative competition theory predicts that the species will evolve diet (Grant, 1972) and/or phenotypic (Brown & Wilson, 1956) differences that reduce the effects of interspecific competition, leading to the evolution of exaggerated differences in trophic morphology and a shift in diet in sympatry compared to allopatry (Schluter, 2000). In addition to a shift in mean diet between allopatry and sympatry, interspecific competition is predicted to affect the population's dietary niche width, but in an opposite way compared to intraspecific competition (Connell, 1983). During intraspecific competition, preferred resources should decline and individuals should include previously underutilized resources in their diet, increasing population niche width (Bolnick, 2001; Roughgarden, 1972; Svanbäck & Bolnick, 2007; Svanback & Persson, 2004; Wilson & Turelli, 1986). Conversely, during interspecific competition one species limits the availability of certain food items and so each species will have a narrower population niche width (Bolnick et al. 2003; Bolnick et al. 2007). Thus, while intraspecific

competition favors increased population variation, interspecific competition reduces it. The ability of a species to change the mean or variance of their dietary niche under intraspecific or interspecific competition may depend on the level of individual specialization in the population. The effects of competition are predicted to be weaker on a species that is composed of generalists (where all individuals consume the full spectrum of resources) as they may be more able to respond to variation in resource abundance or to changes in competitor presence compared to a species composed of specialists (where each individual uses a subset of the resources that the population uses as a whole) (Bolnick et al. 2003). If specialists occur because morphological variation drives among-individual differences in prey use, as opposed to chance or behavior, morphology and diet should be correlated (Bolnick et al. 2002; Werner & Sherry, 1987), and the correlation should be stronger when competition is more intense (Svanback & Bolnick 2007). Though the theory is well developed, the pattern of diet shifts and degree of individual specialization under both intraspecific and interspecific exploitative competition still lacks empirical examples.

The intensity of resource competition is expected to depend on resource availability (White, 2008). Variation in resource abundance can occur spatially and temporally. Temperature and moisture vary across the landscape and determine the vegetative composition of habitats (Holdridge, 1967). This in turn determines the resource abundance available to consumers (Bale et al. 2002; Janzen & Schoener, 1968; Karr & Freemark, 1983). Evergreen forest or mangrove habitats are typically wetter and have higher arthropod abundance than habitats with scrub-type vegetation (Marra & Holberton, 1998; Parrish & Sherry, 1994; Smith et al. 2010; Wilson et al. 2013). This spatial variation in resource abundance is expected to result in stronger competition in low-resource habitats (Fretwell, 1972). Resource abundance can also vary seasonally. In the

tropics there is a seasonal decline in rainfall from the fall to the winter (Chen & Taylor, 2002; Rappole & Warner, 1980; Valdez-Hernandez et al. 2010) which results in fewer food resources available in the winter than the fall (Strong & Sherry, 2000; Toms, 2011). This temporal change is expected to increase the intensity of competition among all individuals in the winter. These spatial and temporal differences in resource abundance provide a natural experiment to test the effects of both intraspecific and interspecific exploitative competition on population diet and individual specialization.

Stable isotopes reflect an individual's diet and habitat use (Chamberlain et al. 1997; DeNiro & Epstein, 1978, 1981; Hobson & Wassenaar, 1997; Marra et al. 1998; Tieszen & Boutton, 1988). When arthropods consume plants, they incorporate the plant's isotopic signature into their tissues (Marra et al. 1998), and consumers incorporate the isotopic signature of the arthropods they eat (Chamberlain et al. 1997; Hobson & Wassenaar, 1997; Peterson & Fry, 1987). Stable nitrogen isotopes ($\delta^{15}\text{N}$) become enriched as trophic level increases, so that predaceous arthropods have higher $\delta^{15}\text{N}$ values than herbivorous arthropods, which in turn have higher $\delta^{15}\text{N}$ values than fruit (Gagnon & Hobson, 2009; Herrera et al., 2003). This enrichment is consistent from one trophic level to the next (Bearhop et al. 2002; DeNiro & Epstein, 1981; Hobson & Clark, 1992). $\delta^{15}\text{N}$ therefore indicates the trophic position of the consumer. Stable carbon isotopes ($\delta^{13}\text{C}$) are mainly affected by the photosynthetic pathway and water use efficiency of plants (Farquhar et al. 1989; O'Leary, 1981). C_3 plants are associated with cooler, moister habitats, and have lower $\delta^{13}\text{C}$ values than C_4 plants in hotter, drier environments (Lajtha & Marshall, 1994). Even within the C_3 plant communities, trees with higher water use efficiency that are experiencing drier conditions have higher $\delta^{13}\text{C}$ values (Cernusak et al. 2007; Knight et al. 1994; Pate, 2001). Thus $\delta^{13}\text{C}$ reflects the wetness of the habitat the consumer occupies. These

two isotopes can be used to test the effects of intraspecific (Dammhahn & Kappeler, 2010; Forero et al. 2002, 2005) and interspecific (Connan et al. 2014; Cucherousset et al. 2007; LeBrun et al. 2007; Palmer, 2013) competition on diet, habitat use, and population niche width (Bearhop et al. 2004).

The non-breeding diet and habitat use of most passerines have not been well studied (Latta & Baltz, 1997). In particular, little is known about how migrants and residents coexist during the non-breeding season (Faaborg et al. 2010; Greenberg, 1986; Latta, 2012). Here I present the first study to use stable isotopes to assess non-breeding intraspecific and interspecific exploitative competition in any passerine. The migratory White-eyed Vireo (WEVI: *Vireo griseus*) and resident Thick-billed Vireo (TBVI: *V. crassirostris*) are sister taxa (Slager et al. 2014; Walker, 1998). These species only coexist during the non-breeding season and only in parts of their range, providing a geographical contrast in heterospecific presence. Anecdotal evidence suggests they consume similar diets of arthropods and some fruit (Greenberg et al. 1995; Hopp et al. 1995; Nolan & Wooldridge, 1962), and they forage from 0-6m (Bradley, 1994; Greenberg et al. 1993; Kirkconnell & Garrido, 1991; Rappole & Warner, 1980). Both species are territorial during the winter (Greenberg et al. 1993; Hopp et al. 1995; Peiman, 2013) and use diverse habitat types, though WEVI are more common in forest habitats when sympatric with TBVI where they have overlapping territories (Chapter 1). The similarity in diet and habitat use and lack of spatial niche partitioning makes these species an ideal system to study exploitative interspecific competition.

I assessed spatial variation in resource abundance between forest and scrub habitats, and temporal variation in resource abundance from the fall to the winter, to detect places and/or times where the intensity of competition should be higher. I predicted forest habitats would have more

food for vireos than scrub habitats, and all habitats would have more food in the fall than the winter. I then used stable isotope data to determine whether this variation in resource abundance affected the intensity of exploitative competition by comparing diet between habitats and seasons in a location allopatric and sympatric with the heterospecific vireo. If WEVI and TBVI engage in interspecific exploitative competition, they should have similar isotope values and morphology in allopatry but diverge from each other in sympatry (Brown & Wilson, 1956; Grant, 1972). If intraspecific resource competition results in individuals including previously underutilized resources in their diet under reduced resource availability, in allopatry both species should have increased isotopic variance in scrub compared to forest habitat, and in the winter compared to the fall. If interspecific resource competition is more intense than intraspecific resource competition so that one species limits the availability of certain food items, both species should have reduced variance in scrub compared to forest habitat and in the winter compared to the fall within sympatric populations, and have reduced variance in sympatric compared to allopatric populations (Bolnick et al. 2003). Additionally, if individual specialization occurs, the isotopes of individuals should be correlated between seasons and between years, and if morphology causes diet variation among individuals, morphology and isotopes should be correlated and that correlation should be stronger where competition is more intense (scrub habitats, in the winter, and in sympatry) (Svanback & Bolnick 2007).

Methods

The northern migratory population of WEVI (subspecies *V. g. noveboracensis*) breeds in the south-eastern United States and winters in some parts of the Caribbean and Central America (Hopp et al. 1995). TBVI are resident in the Caribbean, and the Bahamas subspecies (*V. c.*

crassirostris) occurs on all the islands and cays of the Bahamas (Walker, 1998). I collected data during the fall (Sept-Nov 2012) and winter (Jan-Mar 2013) in three locations: allopatric TBVI (San Salvador Island, The Bahamas), sympatry (Abaco Island, The Bahamas) and allopatric WEVI (Los Tuxtlas, Mexico). WEVI overwinter in variable numbers throughout the range of TBVI, and thus TBVI are not completely allopatric from WEVI. However, since WEVI density is variable among islands (Wunderle & Waide, 1993), I used an island with a low density of WEVI (San Salvador) instead of a completely allopatric location for TBVI (Murphy et al. 1998), as has been used in previous studies of competition when the range of one species is completely within the other (Goldberg & Lande 2006; Kirschel et al. 2009; Pfennig & Murphy 2002; Tynkkynen et al. 2004; Anderson & Grether 2010) (for brevity, San Salvador will be referred to as an allopatric TBVI location). WEVI captured on San Salvador Island were also considered sympatric, as they encountered many TBVI but TBVI mainly encountered other TBVI. I will refer to location effects as the effect of heterospecific vireo presence and absence, but note that I only used one sympatric and allopatric location for each species and so have no replication at the geographical scale. No other closely-related vireos (the ‘eye-ringed’ clade: Slager et al. 2014) are overwinter residents in any of my study locations (Raffaele et al. 2003; Van Perlo, 2006).

I used measurement data from additional sympatric individuals caught in fall 2010 and winter 2011 and from allopatric individuals (and sympatric WEVI) in fall 2011 and winter 2012, and isotope data from allopatric individuals (and sympatric WEVI) caught in winter 2012. Note this means that I only had one year of isotope data from sympatric TBVI. Individuals were color-banded, aged using molt limits (Peiman, 2013; Pyle, 1997: individuals aged as hatch-year in the fall or second-year in the winter are hereafter referred to as first-years; individuals aged as after-hatch year in the fall or after-second year in the winter are hereafter referred to as adults), sexed

(by observation of singing as only males of these species consistently sing, or genetically in the lab; see Chapter 1 for details about genetic sex determination), measured (see Morphological data below), and 1-2mm of the central claw of each foot clipped for isotope analysis. Claw samples in these species likely represent diet and habitat use two months previous (Hahn et al. 2014). Because some WEVI were captured soon after arriving from migration, fall claw samples for that species may represent diet and habitat use during migration and not local conditions on the wintering grounds.

Within each location, I used two forest and two scrub sites. Forest habitats consisted of coppice (broad-leaved evergreen forest) in The Bahamas and rainforest in Mexico; scrub habitats consisted of human-disturbed habitat or coastal scrub/thickets in The Bahamas and second-growth (acahual) in Mexico. In the Bahamas, scrub habitats are dominated by granny bush (*Croton linearis*), black torch (*Erithalis fruticosa*), horse bush (*Gundlachia corymbosa*), beefwood (*Guapira discolor*) and darling plum (*Reynosia septentrionalis*), while forest habitats are diverse and lack dominant species, although they include sweet torchwood (*Nectandra coriacea*), wild tamarind (*Lysiloma latisiliqua*), haulback (*Mimosa bahamensis*), lignum vitae (*Guaiacum sanctum*), and gumbo limbo (*Bursera simaruba*) (Smith, 1993; Sykes & Clench, 1998). In Mexico, scrub habitats are dominated by species of *Cecropia*, *Piper*, *Ochroma*, and *Cnidoscolus* (Rappole & Warner, 1980; Winker et al. 1992) and forest habitats are extremely diverse (Bongers et al. 1988).

Morphological data

All individuals were measured for unflattened wing chord (from carpal joint to the longest primary with wing closed; right wing) to the nearest 1mm using a metal wing rule, tarsus

length (from the notch at the intertarsal joint to the point created by bending the toes 90° to the tarsus; right leg) to the nearest 0.01mm using dial calipers, bill length, width, and height (at the anterior end of the nares) to the nearest 0.01mm using dial calipers, and mass using an AMW-100 electronic scale to the nearest 0.01g. TBVI were molting during Sept-Oct and so all individuals with primary 7-10 in active molt were excluded from wing chord measurements.

I tested for differences in morphology due to the main effects of age (first-year vs adult), sex and location (sympatry/allopatry), plus all their interactions. Not all individuals were sexed and so sample sizes for sex are lower than those for age comparisons. Morphology was analyzed using linear mixed models with individual ID as a random term to account for repeated captures of some individuals. As the goal was to determine which factors affected the outcome variables, Non-significant interactions ($p > 0.06$) were removed in a backward step-wise fashion from the models until only significant interactions remained. Main effects always remained in each model, as assessing their effects was the primary goal. All morphological analyses were conducted in JMP Pro v11.2, and Tukey's HSD was used to conduct pairwise comparisons when those terms were significant.

Stable isotopes

Claws were washed in 1:30 detergent:deionized water, air-dried in a fume hood for at least 24 hrs, then washed in 2:1 chloroform:methanol and again air-dried in a fume hood for at least 24 hrs (Paritte & Kelly, 2009). To determine the isotopic signature of the prey base, I collected spiders (Order Araneae), beetles (Order Coleoptera), leafhoppers (Family Cicadellidae) and fruit from *Bursera simaruba* trees from 1-4 different transects (see below) within each habitat and season. No prey samples had lipid removed, as lipids may be an important

contribution to keratinaceous tissue like claws (Newsome et al. 2010). Each sample was weighed on a microbalance, placed in a tin capsule and analyzed by a continuous flow CHNOS Elemental Analyzer interfaced to an IsoPrime100 mass spectrometer at the Center for Stable Isotope Biogeochemistry, UC Berkeley. Long-term external precision is $\pm 0.10\text{‰}$ for carbon isotopes and $\pm 0.15\text{‰}$ for nitrogen isotopes. All stable isotope values are reported in delta (δ) notation in parts per mil (‰) according to: $\delta X = 1000 \times [(R_{\text{sample}}) / (R_{\text{standard}}) - 1]$, where $X = {}^{13}\text{C}$ or ${}^{15}\text{N}$ and $R = {}^{13}\text{C}/{}^{12}\text{C}$ or ${}^{15}\text{N}/{}^{14}\text{N}$.

To determine the causes of mean variation in claw stable isotopes, they were tested for the fixed effects of capture year (winter in allopatry only), habitat, season (2012/13 only), sex, and age. I included individual ID as a random term to account for repeated captures of some TBVI, but not for WEVI as all isotopes were from unique individuals. I tested for mean differences between years using winter samples, as that was the only season where I had claw tissue for both years. I tested for mean differences between seasons using 2012/13 data, as that was the only year I had samples for both seasons. I used Tukey's HSD to conduct pairwise comparisons when terms were significant. To determine if variation in $\delta^{15}\text{N}$ was related to variation in morphology as predicted under competition, I used principle components analysis (PCA) to generate orthogonal PC axes for each species using the five linear measurements described above. Models included fixed effects of location (sympatry/allopatry), habitat, season, sex, age, and morphology (PC1 or 2), with random ID for TBVI but not for WEVI, and claw $\delta^{15}\text{N}$ as the dependent variable. To determine whether interspecific and intraspecific competition affected population niche variance, I compared variation in $\delta^{15}\text{N}$ values between species, and between sympatry/allopatry, habitat and season within each species, using Levene's test (Wilson, et al. 2010). Because some prey isotopes varied by location, and because I did not have data on

prey isotopes in 2011/12 and so could not assess whether baseline values varied between years, analyses on variation in avian $\delta^{15}\text{N}$ were carried out within location and year. All isotope analyses were conducted in JMP Pro v11.2.

Both nitrogen and carbon stable isotope values can differ among microhabitats due to local geochemical processes, so I measured the isotopic signature of the arthropods and fruit at each site (Hansson et al. 1997; Hobson, 1999; Post, 2002). I used ANOVA to test for the effects of habitat, season and location on prey isotope values. Season was ignored in fruit because *B. simaruba* only flower from April-June with fruit setting concurrently and so all fruit were grown during the same time of year (Valdez-Hernandez et al. 2010). Since I found that prey isotope values did vary by location (see Results), I was unable to directly compare WEVI and TBVI isotope values between sympatry and allopatry. I thus used the Bayesian model SIAR (stable isotopes in R) to determine probability distributions of proportional prey contribution to avian tissues (Parnell et al. 2008). There is only one experimental study of trophic fractionation in avian claws, but it used swans and mallards and these large, herbivorous birds likely experience different physiological effects on fractionation than small omnivorous birds (Hahn et al. 2012). $\delta^{13}\text{C}$ shows less fractionation on low-protein diets, while there is little effect of protein on $\delta^{15}\text{N}$ (Pearson et al. 2003). I thus used fractionation values of 3.5‰ for $\delta^{13}\text{C}$ but used a lower $\delta^{13}\text{C}$ fractionation of 3.2‰ for fruit, and used 4.1‰ for $\delta^{15}\text{N}$ in all samples, similar to other avian isotope studies (eg., Hobson & Bairlein, 2003). Results are presented using median proportions of prey, as the median value is the most likely level of prey contribution to diet (Parnell et al. 2010).

Arthropod and fruit abundance

To estimate relative food abundance, I surveyed transects at each site. Transects were 200m apart and each was 50m long perpendicular to the trail. At the 25m and 50m points on each transect, I used a beat sheet and a sticky trap to capture invertebrates. I shook a branch from each of four trees and used tweezers to collect all invertebrates that fell onto a 1m² nylon sheet. Beat sheets are effective at capturing sedentary invertebrates (Hagar et al. 2007; Rorh et al. 2006), and both vireo species are primarily foliage gleaners (Bowen, 2004; Emlen, 1981; Hopp et al. 1995; Williamson, 1971). I also hung a 3x5 inch yellow sticky trap from a branch for aerial arthropods and coated the string with Tangle-trap adhesive to prevent predators crawling onto the trap and consuming the trapped arthropods. Sticky traps were left out for 48 hours. All fruiting *Bursera simaruba* trees within 5m of the transect line were marked and fruit abundance estimated by counting the number of fruits in five clusters, averaging it, and multiplying that by the number of clusters. Each transect was re-sampled after 3 months using the same techniques to measure changes in fruit and arthropod abundance from fall to winter. I also used historical weather data for San Salvador (airport, 7-9 km from study sites), Abaco (Marsh Harbour, 1-10 km from study sites), and Mexico (Catemaco, 19-24 km from study sites) to describe changes in rainfall across years and seasons (accessed from www.worldweatheronline.com). Rainfall data were summed for each day; temperature data was averaged over the four daylight records (0700, 1000, 1300, and 1600).

All invertebrates were identified to taxonomic Order or Family and counted. Beat sheet samples were oven-dried at 60 °C for 48 hrs then weighed within each Order/Family. Because arthropods on sticky traps could not be weighed, lengths were used instead; arthropods less than 1mm were ignored as birds were unlikely to actively consume prey this small. The two beat-sheet and sticky trap samples on each transect were added together (within each collection

method) to determine abundance and biomass. Invertebrate and fruit abundance and invertebrate biomass was analyzed using linear mixed effect models, with season as a repeated measure, location and habitat as fixed effects, and transect as a random effect. Total invertebrate number (all arthropods and snails collected), mass and length data were $\log(n+1)$ transformed to improve normality. To focus on the taxa that seemed to contribute most to vireo diet (K.S.P., unpublished data), I also separately analyzed abundance and biomass of spiders (Order Araneae), beetles (Order Coleoptera), and leafhoppers (Family Cicadellidae). Analysis of abundance (count) data of separate arthropod taxa used Poisson models with the same factors as above. For fruit, I used a mixed effect logistic model with location as fixed effect and site as a random effect to test for the number of trees and the amount of fruit per tree. This analysis was restricted to forest transects as no scrub transects contained fruiting trees. Season was not tested as the number of trees with fruit did not change between fall and winter, and counts were too inaccurate on trees with large numbers of fruit to estimate seasonal changes (see Results).

Results

Morphology

I tested for differences in morphology due to location, sex, and age, plus all interactions. Non-significant interactions ($p > 0.06$) were removed in a backward step-wise fashion from the models until only significant interactions remained. Main effects always remained in each model, as assessing their effects was the primary goal. Details of tests are presented in the associated tables.

Adult TBVI were larger than first-years, and males were larger than females (Table 2-1). Specifically, first-year TBVI had shorter wings and narrower bills than adults, and males had longer wings, had longer, deeper and wider bills, and were heavier than females (Table 2-2).

Adult WEVI were larger than first-years, and males were larger than females (Table 2-3). Specifically, first-year WEVI had shorter wings than adults, and males had longer winger and were heavier than females (Table 2-4). Additionally, first-years in allopatry tended to have shorter wings than in sympatry, and males in sympatry were heavier than in allopatry (Table 2-4).

Individuals of both species in sympatry were larger than those in allopatry. In sympatry, TBVI had longer wings, longer tarsi, and deeper and wider bills, while WEVI had longer and wider bills and were heavier, compared to allopatry (Fig. 2-1). TBVI were larger than WEVI in all dimensions (*t*-tests, ages and sexes combined; wing chord: $t_{467}=707.53$, $p<0.0001$; tarsus length: $t_{506}=707.22$, $p<0.0001$; bill length: $t_{504}=501.14$, $p<0.0001$; bill depth: $t_{506}=550.13$, $p<0.0001$; bill width: $t_{506}=398.34$, $p<0.0001$; mass: $t_{498}=319.44$, $p<0.0001$) (Fig. 2-1).

Isotopes: prey

Prey isotopes were first analyzed for differences among locations, habitat and season and their interactions (Table 2-5). There was no seasonal or habitat effect on $\delta^{15}\text{N}$, and little location effect. The effects of $\delta^{13}\text{C}$ were more complicated, but there was very little seasonal change, forest habitats tended to have lower values, and locations varied depending on prey type.

B. simaruba fruit did not differ in $\delta^{13}\text{C}$ (all $p>0.067$) or $\delta^{15}\text{N}$ (all $p>0.069$) among habitats or locations (season was not tested; see Methods). For leafhoppers, while there was no seasonal effect on $\delta^{13}\text{C}$ within a location, in the fall San Salvador had lower values than Abaco or Mexico

(location X season: $F_{2,15}=3.69$, $p=0.036$; Tukey HSD: fall San Salvador vs fall Mexico $p=0.033$, fall San Salvador vs fall Abaco $p=0.036$, all other $p>0.18$). No factor affected $\delta^{15}\text{N}$ (all $p>0.12$). Beetles had lower $\delta^{13}\text{C}$ in Mexico than San Salvador or Abaco (location: $F_{2,19}=7.50$, $p=0.0040$; Tukey HSD: Mexico vs San Salvador $p=0.0040$, Mexico vs Abaco $p=0.017$; all other $p>0.10$) but no factor affected $\delta^{15}\text{N}$ (all $p>0.096$). Spiders showed a seasonal decrease in $\delta^{13}\text{C}$ on San Salvador only (season X location, $F_{1,14}=4.46$, $p=0.032$). The difference between scrub and forest habitats in spider $\delta^{13}\text{C}$ was larger in the fall than winter (habitat X season, $F_{1,14}=6.22$, $p=0.026$). Spiders in both Abaco and Mexico had lower $\delta^{13}\text{C}$ values in forest than scrub habitat (habitat X location: $F_{2,14}=20.02$, $p<0.0001$). Spider $\delta^{15}\text{N}$ was lowest in Abaco ($F_{2,17}=17.46$, $p<0.0001$; Tukey HSD: Abaco vs San Salvador $p<0.0001$, Abaco vs Mexico $p=0.0006$), though this effect varied among habitats (location X habitat, $F_{2,17}=5.23$, $p=0.017$). Even though the average prey isotope values varied among locations, the variation in available $\delta^{15}\text{N}$ values was similar (Levene's test, $F_{2,79}=0.095$, $p=0.91$; $\delta^{15}\text{N}$ range: Abaco: -2.87 to 4.52, Mexico: -0.13 to 5.90, San Salvador: -1.22 to 8.98) though San Salvador had the lowest variation in $\delta^{13}\text{C}$ (Levene's test, $F_{2,79}=3.71$, $p=0.029$; $\delta^{13}\text{C}$ range: Abaco: -30.4 to -23.48, Mexico: -31.5 to -25.29, San Salvador: -28.62 to -23.67).

Isotopes: vireos

Individual specialization: I tested for consistency in diet across seasons and years in each location using $\delta^{15}\text{N}$ of repeated captures of individual TBVI. Individuals were very consistent in $\delta^{15}\text{N}$ from fall to winter in allopatry ($n=24$, $R^2=0.71$, $p<0.0001$; Fig. 2-2a) but were only weakly consistent in sympatry ($n=18$, $p=0.061$). However, this non-significant pattern in sympatry was driven by one individual with a much higher $\delta^{15}\text{N}$ value in the winter than the fall; with this

individual removed the correlation was highly significant ($n=17$, $R^2=0.54$, $p=0.0008$; Fig. 2-2a). Individuals were also consistent across years (this could only be tested for allopatry: $n=19$, $R^2=0.42$, $p=0.0027$; Fig. 2-2b). To determine if this individual consistency in $\delta^{15}\text{N}$ was related to morphology, I retained the first two PC axes (eigenvalues >1) from a PCA within each species (Table 2-6). PC1 represented overall size, while PC2 represented larger bills for structural size. In TBVI, overall size was negatively related to $\delta^{15}\text{N}$ in scrub but not forest habitat (habitat X PC1: $F_{1,144}=11.23$, $p=0.0010$), in sympatry but not in allopatry (location X PC1: $F_{1,147}=4.00$, $p=0.047$), and had a stronger negative relationship in first-years than adults (age X PC1: $F_{1,149}=10.20$, $p=0.0017$). Larger bills were positively related to $\delta^{15}\text{N}$ in adults but not first-years (PC2 X age, $F_{1,149}=3.87$, $p=0.051$). In WEVI, $\delta^{15}\text{N}$ was not related to PC1 (all $p=0.72$) or PC2 (all $p=0.23$).

Seasonal effects (2012/13 data): Both species consumed higher trophic levels (larger $\delta^{15}\text{N}$ values) in the winter than the fall, and WEVI consumed higher trophic levels than TBVI (Fig. 2-3). The effects of season on $\delta^{13}\text{C}$ varied with species, sex, habitat and location.

In allopatric TBVI, $\delta^{15}\text{N}$ increased from fall to winter ($F_{1,26}=12.92$, $p=0.0013$) and was higher in scrub than forest habitats but only for first-years (age X habitat, $F_{1,50}=11.54$, $p=0.0013$). $\delta^{13}\text{C}$ was lower in females than males ($F_{1,94}=4.58$, $p=0.035$) and decreased from fall to winter ($F_{1,44}=101.18$, $p<0.0001$).

In sympatric TBVI, $\delta^{15}\text{N}$ increased from fall to winter ($F_{1,29}=12.74$, $p=0.0013$) and was higher in forest than scrub habitat ($F_{1,42}=10.65$, $p=0.0022$). $\delta^{13}\text{C}$ was lower in forest than scrub habitat for adults but not first-years (age X habitat, $F_{1,58}=5.84$, $p=0.019$).

In allopatric WEVI, $\delta^{15}\text{N}$ increased from fall to winter ($F_{1,39}=12.12$, $p=0.0012$) but only in adults (age X season: $F_{1,39}=8.23$, $p=0.0066$) and only in forest habitats (habitat X season:

$F_{1,39}=6.63$, $p=0.041$). $\delta^{13}\text{C}$ was lower in females than males ($F_{1,41}=7.51$, $p=0.0090$) and decreased from fall to winter ($F_{1,41}=14.50$, $p=0.0005$).

In sympatric WEVI, $\delta^{15}\text{N}$ increased from fall to winter ($F_{1,16}=12.53$, $p=0.0027$). $\delta^{13}\text{C}$ also increased from fall to winter ($F_{1,15}=6.72$, $p=0.020$) but only in females (sex X season: $F_{1,15}=6.81$, $p=0.020$).

In sympatry, WEVI and TBVI has similar $\delta^{15}\text{N}$ values in the fall but though both species had higher values in the winter, WEVI had even higher values than TBVI (season X species, $F_{1,98}=22.78$, $p<0.0001$).

Year effects (winter season only): The effect of year on $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ varied with species, habitat and age. In allopatric TBVI, $\delta^{15}\text{N}$ was higher in forest habitats during 2011/12 than 2012/13 (year X habitat, $F_{1,18}=5.06$, $p=0.038$). Males but not females had lower $\delta^{13}\text{C}$ in 2011/12 than 2012/13 (year X sex, $F_{1,43}=4.91$, $p=0.032$).

In allopatric WEVI, adults had higher $\delta^{15}\text{N}$ than first-years ($F_{1,16}=6.32$, $p=0.023$) and individuals in forest had higher $\delta^{15}\text{N}$ than in scrub in 2012/13 but not 2011/12 (year X habitat, $F_{1,16}=5.57$, $p=0.031$). Adults had lower $\delta^{13}\text{C}$ in 2012/13 than 2011/12 ($F_{1,16}=7.92$, $p=0.012$). In sympatric WEVI, no factor affected $\delta^{15}\text{N}$ (all $p>0.16$) or $\delta^{13}\text{C}$ (all $p<0.25$).

$\delta^{15}\text{N}$ variance: I used Levene's test to assess whether isotopic trophic ($\delta^{15}\text{N}$) variance differed by location, habitat and species within each year. Sympatric WEVI had much higher variance in $\delta^{15}\text{N}$ than sympatric TBVI (could only be tested for 2012/12: $F_{1,100}=19.59$, $p<0.0001$). As variance in baseline prey $\delta^{15}\text{N}$ did not vary by location, I directly compared allopatric and sympatric locations within each species to test for differences in population niche width. TBVI $\delta^{15}\text{N}$ variance did not differ by location or season (all $p>0.34$). TBVI had higher $\delta^{15}\text{N}$ variance in scrub than forest habitat in allopatry in 2011/12 only (allopatry 2011/12:

$F_{1,24}=5.54$, $p=0.027$; sympatry 2012/13: $F_{1,64}=1.16$, $p=0.28$; allopatry 2012/13: $F_{1,115}=0.40$, $p=0.53$). Sympatric WEVI had higher $\delta^{15}\text{N}$ variance than allopatric WEVI, but only in 2011/12 (2011/12: $F_{1,37}=8.08$, $p=0.0072$; 2012/13: $F_{1,80}=2.23$, $p=0.12$). Habitat ($p>0.10$) and season ($p>0.62$) had no effect on $\delta^{15}\text{N}$ variance in WEVI.

Stable isotope analysis in R (SIAR): In order to compare diet between sympatry and allopatry, I used a mixing model to account for the differences in average baseline prey isotope values across locations. I restricted the analysis to forest habitat, as that was the predominant habitat type where WEVI established territories, and the isotope data from 2012/13, as I did not collect baseline data from 2011/12. SIAR revealed slight seasonal increases in the proportion of higher trophic level prey consumed (spiders and beetles) and decreases in lower trophic level prey (leafhoppers and fruit) in both species in allopatry and sympatry (Fig. 2-4). While WEVI had very similar proportions of prey items consumed in allopatry and sympatry, allopatric TBVI consumed much more fruit (60-70%) and almost no spiders or beetles compared to sympatric TBVI, resulting in both species in sympatry having similar proportions of prey consumed (Fig. 2-4).

Arthropod and fruit abundance

Beat-sheets captured more sedentary arthropods (Table 2-7) than did sticky traps (Table 2-8). Main patterns were consistent across all methods of invertebrate analysis. In general, invertebrates declined from the fall to the winter, were higher in forest than scrub habitats, and were higher in Mexico and San Salvador than Abaco (details in Table 2-9).

Specifically, beat sheets collected more invertebrates in Mexico than Abaco which had more than San Salvador, and total invertebrate number declined from fall to winter but only in

Mexico and Abaco. There were more beetles in the winter than the fall, in Mexico than Abaco and San Salvador, and in scrub than forest habitat. There were more spiders in the fall than the winter. There were more leafhoppers in Mexico than San Salvador and forest than scrub habitat, though this habitat difference was only present in Abaco.

Sticky traps collected more invertebrates in the fall than the winter and in scrub than forest habitat. Mexico and San Salvador had higher abundance of the three taxa than Abaco. There was a seasonal decrease in the abundance of the three taxa in San Salvador that did not also occur in Abaco or Mexico.

Beat sheets collected higher masses of leafhoppers and spiders in forest than scrub habitats, but more beetles in scrub than forest habitats. Mexico consistently had higher masses of all taxa than Abaco, which had higher masses than San Salvador.

Sticky traps consistently collected higher biomasses (measured in lengths) of invertebrates in the fall than the winter. However, the seasonal decrease was much larger in San Salvador than Abaco or Mexico. Abaco consistently had the lowest biomass of invertebrates.

No transects in scrub habitat had any fruiting *B. simaruba* trees, thus results pertain to forest habitat only. Locations differed in how many trees had fruit ($F_{2,39}=5.14$, $p=0.010$); Abaco had more fruiting trees than both Mexico ($p=0.0028$) and San Salvador ($p=0.027$) but Mexico and San Salvador were not different ($p=0.13$). Locations also differed in the amount of fruit per tree ($F_{2,32}=3.55$, $p=0.041$); Mexico had more fruit per tree than San Salvador ($p=0.019$) and Abaco trended towards more fruit than San Salvador ($p=0.067$) but Mexico was not different from Abaco ($p=0.54$).

All locations and years showed a seasonal decline in rainfall and temperature (Table 2-10). In 2012/13 (the only year I collected food resource and isotope data from all three

locations), Mexico was cooler in the fall than either location in The Bahamas, but in winter there was no difference among locations (season X location, $F_{2,630} = 13.99$, $p < 0.0001$). All locations experienced a seasonal decline in temperature ($F_{1,630} = 205.39$, $p < 0.0001$). Mexico experienced more rain than either location in The Bahamas ($F_{2,630} = 11.43$, $p < 0.0001$), and all locations experience a seasonal decline in rainfall ($F_{1,630} = 13.93$, $p = 0.0002$). Year had no effect on rain in San Salvador ($p = 0.56$) but 2012/13 was warmer than 2011/12 ($F_{1,421} = 38.17$, $p < 0.0001$). In Abaco, rain was higher in the fall of 2010 than any other season in either year (year X season, $F_{1,420} = 6.41$, $p = 0.012$), while 2012/13 was warmer than 2010/11 ($F_{1,420} = 11.18$, $p = 0.0009$). Year had no effect on rain in Mexico ($p = 0.54$), and the fall of 2012/13 tended to be warmer than any other season in either year (year X season, $F_{1,420} = 3.68$, $p = 0.056$).

Discussion

I found both temporal and spatial variation in resource availability. Food resources declined from fall to winter, and forest habitats had more food resources than scrub habitats, consistent with other studies of tropical arthropods (Greenberg, 1992). Rainfall declined from fall to winter as well, and is likely the proximate cause of changes in arthropod abundance. Mexico had more arthropod prey than Abaco, which tended to have more than San Salvador, yet Abaco had the most fruit. Together, this suggests that resource competition should be more intense in the winter than the fall and in scrub than forest habitats, and that individuals in sympatry (Abaco) may be competing for limited resources. Though generalizations are somewhat limited due to a single geographical location used for sympatry and allopatry, the use of multiple sites within each location argues against these trends being a temporary phenomenon.

Ecological character divergence predicts that populations experiencing interspecific competition will respond adaptively to minimize competition. In order for an adaptive response to non-breeding conditions to occur, populations under selection for reducing non-breeding interspecific competition must also breed together, and selection must be stronger in the winter than the summer (Marra et al. 2010). Songs of TBVI on San Salvador have diverged from songs on Abaco indicating cultural evolution, and lower haplotype diversity on San Salvador compared to the northern Bahamas islands indicates some population structuring (Walker, 1998), suggesting TBVI populations are distinct enough to adapt to the local competitive environment on an island (Case & Taper, 2010). There is some support for population divergence on the breeding grounds in WEVI (Slager et al. 2014; but see Zwartjes, 1999) and several other migrant passerines show an east-west split in their migration patterns, with populations that breed in the eastern part of their range overwintering in the Caribbean and populations breeding more westerly overwintering in Central America (Kelly & Hutto, 2005). WEVI track climatic conditions from breeding to non-breeding seasons (Nakazawa et al. 2004), but their degree of migratory connectivity is unknown. My study locations contained no other closely-related vireos, but in other parts of their range, WEVI overwinter with six other closely-related vireo species (Hopp et al. 1995), and so selection for reducing interspecific competition during the winter may be common in this species.

Under interspecific exploitative competition, species are predicted to diverge in morphology and/or resource use where they coexist. Many authors have postulated that interspecific competition would select for reduced body size in at least one of the competing species (Hamilton, 1961; Pfennig & Pfennig, 2005). However, I found that both WEVI and TBVI were larger in sympatric than allopatric populations across sex and age classes (Fig. 2-1),

which does not fit the prediction of divergent size in sympatry under ecological character displacement (Brown & Wilson, 1956). Additionally, the ratio of linear measurements for TBVI to WEVI in sympatry is 1.03 – 1.19, much less than the ratio of 1.3 suggested by Hutchinson (1959) as the minimum for stable coexistence. I found that in sympatry, WEVI consumed resources higher on the food chain than TBVI, yet TBVI in sympatry were more similar to WEVI in their diet than were allopatric TBVI. The most obvious explanation for this pattern is that TBVI were selecting their diet based on resource availability. This explanation is not convincing as Abaco (sympatry) had more fruit than San Salvador (allopatry), yet TBVI consumed more fruit in allopatry than sympatry (Fig. 2-4), and there was little consistent differences in arthropod abundance between these locations. Since these species have overlapping territories (Chapter 1), there is no horizontal spatial niche partitioning occurring (Murray, 1971). However, I cannot rule out that the species differ in some other aspect of their niche, such as foraging strata (vertical position) or substrate (leaf type, tree species, bark/stem, etc) (Remsen & Robinson, 1990). TBVI are larger in all dimensions than WEVI, and it is possible that they are partitioning resources based on arthropod size, as longer billed species tend to take larger prey (Grant, 1968), and the breeding currency hypothesis states that residents should take more large soft-bodied prey (Orthoptera, Lepidoptera) while migrants should exploit smaller bodied prey (Coleoptera, Formicidae, Homoptera) (Greenberg, 1995; Johnson et al. 2005). As Orthoptera and Lepidoptera are isotopically similar to Homoptera (Brittain 2009), it is possible that the similar prey proportions in sympatry result from TBVI consuming larger classes and WEVI smaller classes of herbivorous insects. However, the lower body condition seen in sympatric TBVI (Chapter 3) may indicate that this similarity in diet is non-adaptive and has negative consequences for TBVI.

The behaviorally subordinate WEVI (Chapter 1) had a wider niche than the dominant TBVI. Based on the literature, this is consistent with the prediction that subordinate species are also ecological generalists (Morse, 1974). However, WEVI also had equal or larger niche width when sympatric versus allopatric with TBVI. This pattern is opposite to the prediction that the dominant species should restrict the subordinate's access to resources in sympatry (Morse, 1974). Even though TBVI were very aggressive towards WEVI and there was some indication that WEVI temporally avoided TBVI (Chapter 1), the large territories of TBVI (6 times larger than WEVI) mean they may not be able to physically restrict WEVI's access to resources. However, a large niche width is consistent with a species composed of specialists, as a generalist species with no individual specialization would result in isotopic averaging within individuals and thus a smaller niche width (Flaherty & Ben-David, 2010). The theoretical expectation of increased population variance under more intense intraspecific competition (winter season and scrub habitats) was only partially supported (increased variance in TBVI in scrub versus forest habitat in one year only) (Grant & Price, 1981; Roughgarden, 1972; Taper & Case, 1985). Thus neither morphology nor diet conforms to predicted divergence under interspecific exploitative competition. It is possible that selection during the breeding season trumps selection for non-breeding diet and morphology shifts, especially in the ecologically more specialized TBVI, or that intraspecific competition is stronger than interspecific competition in these species.

The more ecologically specialized TBVI also showed stronger evidence of individual specialization. Individuals consumed similar trophic levels in the fall and winter, and from one year to the next. Additionally, the correlation between morphology and diet was stronger under more intense competition (scrub habitats and in sympatry) (Svanback & Bolnick 2007). This is strong evidence that the long-term consistency is caused by morphology and that it is not a

random occurrence. Conversely, the ecologically generalist WEVI showed no relationship between diet and morphology, indicating the population is composed of generalists. This may have consequences if individuals exhibit resource specialization on long time scales, as they may be less able to respond quickly to changes in competitor presence or resource abundance (Bolnick et al. 2003), and is concordant with the strong evidence for negative effects of competition on physiological condition in TBVI (Chapter 3). Additionally, individuals with diets more similar to heterospecifics within the population will be subjected to stronger selective pressures (Bolnick et al. 2003). This suggests that there will be variation in the strength of selection among individuals, which could potentially lead to some individuals experiencing increased costs of coexistence with the heterospecific vireo. Individual specialization is a common phenomenon (reviewed in Araújo et al. 2011) but its causes and consequences have only begun to be explored. To the extent that populations allopatric and sympatric with the heterospecific competitor also breed as separate populations, each population's niche can evolve in response to competition, as both prey preference (Agashe & Bolnick, 2010; Gibbons et al. 2005) and individual differences in niche width (Ackermann & Doebeli, 2004; Taper & Case, 1985) can be heritable.

The seasonal shift in $\delta^{15}\text{N}$, which indicated that more prey at higher trophic levels was included in the diets of both species in the winter than the fall, was unexpected. Spiders, the top trophic level, declined from fall to winter, while beetles increased and leafhoppers showed no seasonal change. However, though I did not find seasonal changes in the abundance of fruit on *B. simaruba* trees, other studies have shown that this fruit does decline in abundance from fall to winter (Valdez-Hernandez et al. 2010). Thus the seasonal shift does not seem to reflect patterns of changing resource abundance. I also found no seasonal shifts in $\delta^{15}\text{N}$ baseline prey values,

arguing against the increase in $\delta^{15}\text{N}$ being due to changing prey baseline values. The fall $\delta^{15}\text{N}$ of WEVI were lower than previously recorded breeding values (Brittain, 2009), indicating that WEVI switch from a moderately insectivorous diet during breeding to a fruit-based diet during migration (Parrish, 1997; Suthers et al. 2000). However their high $\delta^{15}\text{N}$ values in the winter were surprising for several reasons: because it surpassed their breeding values (Brittain, 2009); because WEVI in particular are known to defend *Bursera* trees and accounted for up to 2/3 of seeds dispersed (Graham, 2002; Greenberg, 1992; Greenberg et al. 1995; Ortiz-Pulido & Rico-Gray, 2006); and because WEVI surpassed the average trophic level of TBVI yet migrants in general are predicted to use more fruit than residents (Cox, 1985). For instance, migrant Gray vireos (*V. vicinior*) are thought to be the primary dispersers of *B. microphylla* as their fruit dominate *V. vicinior*'s diet as winter progresses (Bates, 1987). Patterns of seasonal shifts in migratory passerines showed some species increased use of fruit during the winter, while others consumed more insects, yet seasonal changes were not predicted from *a priori* guild classifications (Gagnon & Hobson, 2009). This indicates that winter diet may be affected by more factors than previously considered, such as foraging location in the presence of heterospecifics (Jedlicka et al. 2006), and should be supplemented with detailed observations of actual dietary items. The seasonal shift in diet could indicate more selective use of resources as abundance declines and competition increases. More research into the causes of seasonal dietary shifts is clearly warranted.

Many studies of diet and habitat use in passerines during the non-breeding season have lacked data on baseline prey isotope values. This is the first study to provide location, season and habitat-specific baseline prey isotope values in the Caribbean. Without this information, I could not have accurately compared diet between sympatric and allopatric locations, as all locations

varied in baseline prey values. This means that variation among locations in geochemical processes can drive observed differences in avian isotope values that are unrelated to diet or habitat. $\delta^{15}\text{N}$ values are known to vary due large-scale patterns in soil type, rainfall and temperature (Amundson et al. 2003) in addition to trophic level within a location (Post, 2002). I found that the two islands separated by only 370 km had different prey $\delta^{15}\text{N}$. As many passerines overwinter throughout The Bahamas, any studies that infer diet of wintering birds from avian tissues only will confound trophic differences with island geochemical differences. For instance, Gagnon and Hobson (2009) found that two passerine species had unexpectedly low $\delta^{15}\text{N}$ in tissues that represented their wintering locations. Since neither species feeds on fruit, those low values were likely caused by those individuals wintering in a location with lower average $\delta^{15}\text{N}$. Thus without knowing the prey isotope values, inferences about diet or habitat use are limited (see also Evans et al. 2012).

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Table 2-1: Summary statistics of TBVI morphology. A blank entry in ‘Sex’ refers to individuals that did not have their sex determined. Sample size (N) for bill refers to all three bill measurements.

Location	Sex	Age	Wing			Bill length			Bill depth		Bill width	
			N	mean	SE	N	mean	SE	mean	SE	mean	SE
Sympatry		Adult	12	62.5	0.45	12	8.96	0.09	4.62	0.04	4.4	0.09
Sympatry		First-year	26	60.27	0.26	31	8.74	0.07	4.61	0.03	4.36	0.06
Sympatry	Female	Adult	31	61.71	0.23	34	8.71	0.05	4.6	0.03	4.18	0.04
Sympatry	Female	First-year	11	60.09	0.34	12	8.85	0.05	4.57	0.04	4.3	0.05
Sympatry	Male	Adult	76	63.18	0.17	81	8.83	0.04	4.65	0.01	4.27	0.03
Sympatry	Male	First-year	15	61.4	0.61	17	8.82	0.05	4.64	0.04	4.29	0.04
Allopatry		Adult	13	60	0.54	20	8.78	0.11	4.58	0.03	4.31	0.06
Allopatry		First-year	29	59.86	0.32	36	8.62	0.06	4.51	0.02	4.27	0.03
Allopatry	Female	Adult	24	60.54	0.23	28	8.61	0.06	4.46	0.03	4.11	0.04
Allopatry	Female	First-year	6	58.17	1.14	7	8.53	0.09	4.42	0.08	4.1	0.09
Allopatry	Male	Adult	106	61.47	0.14	132	8.79	0.03	4.61	0.02	4.2	0.02
Allopatry	Male	First-year	12	60.08	0.47	15	8.6	0.1	4.61	0.04	4.28	0.07

Table 2-1 continued: Summary statistics of TBVI morphology. A blank entry in ‘Sex’ refers to individuals that did not have their sex determined. Sample size (N) for bill refers to all three bill measurements.

Tarsus			Mass		
N	mean	SE	N	mean	SE
12	24.54	0.24	12	14.46	0.22
30	24.43	0.16	31	13.65	0.12
34	24.43	0.1	38	13.68	0.11
12	24.28	0.22	14	13.81	0.16
81	24.56	0.06	84	14.4	0.08
17	24.26	0.14	18	14.01	0.18
20	23.95	0.16	20	14.3	0.21
36	24.04	0.12	34	13.84	0.11
28	23.89	0.12	28	13.55	0.11
7	24.09	0.43	6	13.41	0.2
131	23.92	0.06	133	14.38	0.07
14	23.91	0.14	15	14.26	0.14

Table 2-2: Analysis of Thick-billed Vireo morphology by location (allopatry/sympatry), sex, and age (first-year/adult). See text for definitions of measurements. All interactions were initially included but those with $p > 0.06$ were removed in a backward step-wise fashion from the models until only significant interactions and/or main effects remained. The type of morphological measurement is carried down columns until the next entry. All tests except mass included a random term for individual ID. The analysis for mass failed to converge with random ID included.

Measurement	Effect	Num DF	Den DF	F value	p-value
Wing chord	Location	1	185.55	55.7242	<0.0001
	Sex	1	191.01	33.6267	<0.0001
	Age	1	263.54	47.0856	<0.0001
Bill length	Location	1	204.40	2.9684	0.0864
	Sex	1	212.56	3.7127	0.0553
	Age	1	321.99	0.3802	0.5379
Bill depth	Location	1	207.97	8.3918	0.0042
	Sex	1	211.75	21.2084	<0.0001
	Age	1	295.55	4.2224	0.0408
Bill width	Location	1	202.42	5.0583	0.0256
	Sex	1	223.88	8.4597	0.004
	Age	1	291.61	2.0293	0.1554
Tarsus	Location	1	207.75	31.1463	<0.0001
	Sex	1	209.36	0.5035	0.4787
	Age	1	225.77	0.5467	0.4604
Mass	Location	1	335.00	0.1925	0.6611
	Sex	1	335.00	56.8216	<0.0001
	Age	1	335.00	1.8715	0.1722

Table 2-3: Summary statistics of WEVI morphology. A blank entry in ‘Sex’ refers to individuals that did not have their sex determined, and in ‘Age’ refers to an individual that was not aged. Sample size (N) for bill refers to all three bill measurements.

Location	Sex	Age	Wing N	Wing mean	Wing SE	Bill N	Bill length mean	Bill length SE	Bill depth mean	Bill depth SE	Bill width mean	Bill width SE
Sympatry			1	63	-	1	6.62	-	3.85	-	3.86	-
Sympatry		Adult	3	60.67	0.88	3	7.25	0.25	3.75	0.13	3.99	0.26
Sympatry		First-year	35	60	0.34	35	7.38	0.07	3.85	0.03	3.84	0.03
Sympatry	Female	Adult	11	60	0.45	11	7.26	0.07	3.89	0.07	3.89	0.05
Sympatry	Female	First-year	30	59.77	0.34	29	7.36	0.06	3.89	0.03	3.89	0.04
Sympatry	Male	Adult	10	61.4	0.54	10	7.41	0.05	3.95	0.05	3.76	0.1
Sympatry	Male	First-year	29	60.52	0.35	27	7.44	0.07	3.89	0.04	3.89	0.04
Allopatry			1	60	-	1	7.42	-	3.9	-	4.1	-
Allopatry		Adult	3	60.67	1.76	3	7.28	0.3	3.92	0.02	4.09	0.18
Allopatry		First-year	5	59.2	0.66	5	6.97	0.17	3.87	0.1	3.77	0.11
Allopatry	Female	Adult	11	60	0.3	11	7.31	0.09	3.86	0.03	3.79	0.07
Allopatry	Female	First-year	11	59	0.38	11	7.2	0.09	3.8	0.04	3.69	0.06
Allopatry	Male	Adult	29	61.03	0.23	29	7.23	0.07	3.9	0.04	3.81	0.04
Allopatry	Male	First-year	30	59.9	0.32	31	7.17	0.05	3.89	0.02	3.75	0.04

Table 2-3 continued: Summary statistics of WEVI morphology. A blank entry in ‘Sex’ refers to individuals that did not have their sex determined, and in ‘Age’ refers to an individual that was not aged. Sample size (N) for bill refers to all three bill measurements.

Tarsus			Mass		
N	mean	SE	N	mean	SE
1	22.1	-	1	12.5	-
3	21.86	0.54	3	11.14	1.06
35	22.25	0.08	34	12.03	0.19
11	21.52	0.18	11	11.3	0.17
30	21.74	0.12	31	11.35	0.13
10	22.14	0.17	10	11.77	0.25
29	21.81	0.13	30	12.1	0.28
1	22.11	-	0	-	-
3	21.86	0.41	3	11.44	0.43
5	21.87	0.2	5	10.94	0.3
11	21.51	0.24	10	11.24	0.3
11	21.68	0.25	11	11.22	0.27
29	21.68	0.13	28	11.25	0.12
31	21.61	0.17	31	11.33	0.11

Table 2-4: Analysis of White-eyed Vireo morphology by location (allopatry/sympatry), sex, and age (first-year/adult). See text for definitions of measurements. All interactions were initially included but those with $p > 0.06$ were removed in a backward step-wise fashion from the models until only significant interactions and/or main effects remained. The type of morphological measurement is carried down columns until the next entry. All tests included a random term for individual ID.

Measurement	Effect	Num DF	Den DF	F value	p-value
Wing chord	Location	1	155.95	1.3789	0.2421
	Sex	1	144.36	11.6531	0.0008
	Age	1	125.61	11.8559	0.0008
	Age X Location	1	103.45	3.8271	0.0531
Bill length	Location	1	154.70	9.5201	0.0024
	Sex	1	154.90	0.3926	0.5319
	Age	1	144.56	0.0398	0.8421
Bill depth	Location	1	157.67	0.8265	0.3647
	Sex	1	157.55	2.1405	0.1454
	Age	1	156.24	0.9267	0.3372
Bill width	Location	1	149.60	8.2142	0.0048
	Sex	1	153.80	0.009	0.9245
	Age	1	151.73	0.2176	0.6415
Tarsus	Location	1	156.75	0.5212	0.4714
	Sex	1	157.39	1.5482	0.2153
	Age	1	140.29	0.019	0.8906
Mass	Location	1	151.62	6.9044	0.0095
	Sex	1	150.88	4.4845	0.0358
	Age	1	155.31	0.4576	0.4998
	Sex X Location	1	145.02	4.0827	0.0452

Table 2-5: Variation in resource isotope values by location, habitat, and season. Season was not tested for fruit as all fruit were produced during the same period in the summer. N is the number of transects that contributed samples. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values are given as mean \pm SE.

Resource	Location	Habitat	Season	N	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$
Beetle	Abaco	forest	fall	2	2.285 ± 1.275	-26.31 ± 0.38
Beetle	Abaco	forest	winter	2	3.765 ± 0.755	-26.29 ± 0.365
Beetle	Abaco	scrub	fall	1	0.39	-26.25
Beetle	Abaco	scrub	winter	1	1.64	-25.09
Beetle	Mexico	forest	fall	2	3.445 ± 1.365	-27.89 ± 2.44
Beetle	Mexico	forest	winter	2	3.525 ± 1.135	-29.15 ± 0.405
Beetle	Mexico	scrub	fall	1	3.56	-28.34
Beetle	Mexico	scrub	winter	1	3.65	-27.14
Beetle	San Salvador	forest	fall	4	3.922 ± 0.87	-25.055 ± 0.44
Beetle	San Salvador	forest	winter	4	5.03 ± 1.37	-27.28 ± 0.61
Beetle	San Salvador	scrub	fall	2	4.065 ± 1.115	-25.23 ± 0.03
Beetle	San Salvador	scrub	winter	2	3.51 ± 0.08	-25.93 ± 0.41
Fruit	Abaco	forest		2	-0.675 ± 1.315	-28.18 ± 0.93
Fruit	Abaco	scrub		1	-1.68	-27.8
Fruit	Mexico	forest		2	1.59 ± 0.17	-27.39 ± 1.07
Fruit	Mexico	scrub		1	-0.13	-31.5
Fruit	San Salvador	forest		4	1.217 ± 0.55	-26.17 ± 0.53
Fruit	San Salvador	scrub		2	2.53 ± 1.16	-25.93 ± 0.58
Leafhopper	Abaco	forest	fall	2	-1.155 ± 0.135	-29.61 ± 0.83
Leafhopper	Abaco	forest	winter	2	-0.065 ± 0.125	-27.73 ± 0.715
Leafhopper	Abaco	scrub	fall	1	2.73	-28.47
Leafhopper	Abaco	scrub	winter	1	-2.87	-24.94
Leafhopper	Mexico	forest	fall	2	2.11 ± 2.05	-29.015 ± 0.15
Leafhopper	Mexico	forest	winter	2	1.38 ± 1.12	-29.26 ± 0.85
Leafhopper	Mexico	scrub	fall	1	0.81	-29.52
Leafhopper	Mexico	scrub	winter	1	0.93	-26.31
Leafhopper	San Salvador	forest	fall	4	2.097 ± 0.747	-25.705 ± 0.71
Leafhopper	San Salvador	forest	winter	3	2.153 ± 0.69	-26.67 ± 0.975
Leafhopper	San Salvador	scrub	fall	1	-1.22	-26.41
Leafhopper	San Salvador	scrub	winter	2	-0.325 ± 0.555	-27.585 ± 0.19
Spider	Abaco	forest	fall	2	1.72 ± 0.23	-27.845 ± 0.56
Spider	Abaco	forest	winter	2	2.115 ± 0.265	-27.26 ± 0.29
Spider	Abaco	scrub	fall	1	3.34	-23.48
Spider	Abaco	scrub	winter	1	2.82	-25.49

Spider	Mexico	forest	fall	2	4.41 ± 0.33	-27.69 ± 0.015
Spider	Mexico	forest	winter	2	4.355 ± 0.535	-26.82 ± 0.22
Spider	Mexico	scrub	fall	1	4.94	-25.29
Spider	Mexico	scrub	winter	1	5.9	-25.41
Spider	San Salvador	forest	fall	4	5.265 ± 0.320	-25.02 ± -.269
Spider	San Salvador	forest	winter	4	6.017 ± 0.641	-25.86 ± 0.147
Spider	San Salvador	scrub	fall	2	5.065 ± 0.605	-25.03 ± 0.36
Spider	San Salvador	scrub	winter	2	3.715 ± 0.465	-26.31 ± 0.465

Table 2-6: Correlation-based principle components analysis of Thick-billed Vireo (TBVI) and White-eyed Vireo (WEVI) measurements conducted within each species. Only PC1 and PC2 had eigenvalues greater than 1 and so were retained for further analysis. Measurements that contributed to variation on that axis (± 0.3) are bolded.

Measurement	TBVI		WEVI	
	PC1	PC2	PC1	PC2
Wing chord	0.43927	-0.40676	0.26423	-0.85027
Bill length	0.34780	0.59532	0.38358	0.14552
Bill depth	0.53024	0.14750	0.55245	0.17662
Bill width	0.46035	0.33173	0.41011	0.43359
Tarsus	0.43932	-0.59021	0.55646	-0.19147
Eigenvalue	1.7681	1.0181	1.7769	1.0071
Percent variation	35.361	20.363	35.537	20.142

Table 2-7: Total counts (number of individuals) of the four most abundant taxa of invertebrates collected using beat sheets. n = number of transects. The ‘other’ category refers to all other invertebrates collected, and includes the following taxonomic groups: Classes Gastropoda, Chilopoda, Diplopoda, Entognatha (Subclass Collembola); Arachnida (Suborder Ixodida, Order Trombidiformes, and Order Pseudoscorpionida); and Orders Hymenoptera (Suborder Apocrita), Hemiptera (Suborders Sternorrhyncha, Heteroptera, and Auchenorrhyncha), Orthoptera, Isopoda, Psocoptera, Lepidoptera, Blattodea, Thysanura, Thysanoptera, Diptera, Neuroptera, Mantodea, Trichoptera, and Phasmatodea.

Location	Habitat	Season	n	Coleoptera	Araneae	Cicadellidae	Formicidae	Other
Abaco	forest	fall	11	10	85	39	52	81
Abaco	forest	winter	11	6	57	42	24	66
Abaco	scrub	fall	13	25	60	6	102	73
Abaco	scrub	winter	13	24	47	12	41	46
Mexico	forest	fall	18	63	147	38	62	182
Mexico	forest	winter	18	86	132	51	56	73
Mexico	scrub	fall	4	11	55	7	15	48
Mexico	scrub	winter	4	35	21	10	11	21
San Salvador	forest	fall	15	22	93	19	35	43
San Salvador	forest	winter	15	31	100	14	29	58
San Salvador	scrub	fall	9	29	37	7	20	20
San Salvador	scrub	winter	9	48	42	10	26	26

Table 2-8: Total counts (number of individuals) of the five most abundant taxa of invertebrates collected using sticky traps. n = number of transects. The ‘other’ category refers to all other invertebrates collected, and includes the following taxonomic groups: Class Malacostraca (Order Amphipoda); Class Arachnida (Suborder Ixodida); and Orders Hymenoptera (Suborder Apocrita), Hemiptera (Suborders Sternorrhyncha, Heteroptera, and Auchenorrhyncha), Orthoptera, Embioptera, Psocoptera, Lepidoptera, Blattodea, Plecoptera, Thysanoptera, Neuroptera, and Trichoptera.

Location	Habitat	Season	n	Coleoptera	Diptera	Hymenoptera	Cicadellidae	Araneae	Other
Abaco	forest	fall	22	14	121	34	30	3	9
Abaco	forest	winter	22	9	99	71	43	1	52
Abaco	scrub	fall	22	24	252	93	19	0	11
Abaco	scrub	winter	22	14	141	109	13	2	33
Mexico	forest	fall	36	89	254	56	147	12	45
Mexico	forest	winter	36	111	93	77	67	13	31
Mexico	scrub	fall	8	31	50	10	43	0	2
Mexico	scrub	winter	8	32	27	14	16	4	0
San Sal	forest	fall	40	99	362	158	320	19	57
San Sal	forest	winter	40	52	105	116	76	13	40
San Sal	scrub	fall	24	93	489	145	68	14	23
San Sal	scrub	winter	24	23	208	144	55	5	39

Table 2-9: Analysis of relative invertebrate abundance assessed using beat sheets and sticky traps. Measurement refers to either mass of invertebrates collected using beat sheets, or length of invertebrates measured on sticky traps; number refers to the count of individuals collected using either method. Summary refers to the group analyzed, where ‘total’ is all invertebrates captured, ‘three groups’ is the sum of Cicadellidae, Coleoptera, and Araneae, and the three separate taxa are all individuals collected within that taxa. Season contrasts fall and winter, location contrasts Abaco (The Bahamas), San Salvador (The Bahamas), and Los Tuxtlas (Mexico), and habitat contrasts forest and scrub. Too few Araneae were captured using sticky traps for analysis. Non-significant interactions ($p>0.06$) were removed in a backward step-wise fashion from the models until only significant interactions remained. Main effects always remained in each model, as assessing their effects was the primary goal. Method, measurement and summary are carried down columns until the next entry.

Method	Measurement	Summary	Effect	Num DF	Den DF	F value	p-value
Beat sheet	Mass	Total	Season	1	123	0.04	0.8388
			Location	2	123	14.35	<0.0001
			Habitat	1	123	0.72	0.3965
			Season X Location	2	123	1.37	0.2592
			Season X Habitat	1	123	2.72	0.1015
			Location X Habitat	2	123	0.25	0.7762
			Season X Location X Habitat	2	123	3.62	0.0297
		Three groups	Season	1	128	0.19	0.6637
			Location	2	128	13.26	<0.0001
			Habitat	1	128	0.75	0.3866
		Cicadellidae	Season	1	128	3.12	0.0796
			Location	2	128	8.63	0.0003
			Habitat	1	128	5.67	0.0187
		Coleoptera	Season	1	128	2	0.1602
			Location	2	128	14.07	<0.0001
			Habitat	1	128	11.52	0.0009
		Araneae	Season	1	128	1.05	0.3063
			Location	2	128	20.75	<0.0001
Habitat	1		128	4.5	0.0358		

Beat sheet	Number	Total	Season	1	126	8.25	0.0048
			Location	2	126	6.47	0.0021
			Habitat	1	126	0.42	0.5196
			Season X Location	2	126	8.6	0.0003
		Three groups	Season	1	128	0	0.9483
			Location	2	128	3.82	0.0245
			Habitat	1	128	0.33	0.5645
		Cicadellidae	Season	1	128	1.42	0.2355
			Location	1	128	11.79	0.0008
			Habitat	2	128	5.67	0.0044
			Location X Habitat	2	128	7.4	0.0009
		Coleoptera	Season	1	128	7.58	0.0068
			Location	2	128	13.21	<0.0001
			Habitat	1	128	10.75	0.0013
		Araneae	Season	1	123	8.71	0.0038
			Location	2	123	3.38	0.0373
			Habitat	1	123	2.7	0.1031
			Season X Location	2	123	4.65	0.0113
			Season X Habitat	1	123	1.58	0.2108
			Location X Habitat	2	123	1.36	0.2597
Season X Location X Habitat	2		123	3.38	0.0373		
Total	Season		1	138	14.77	0.0002	
Sticky trap	Length	Total	Location	2	138	5.01	0.0079
			Habitat	1	138	0	0.964
			Season X Location	2	138	8.25	0.0004
			Three groups	Season	1	138	13.71
		Location	2	138	8.69	0.0003	
		Habitat	1	138	3.47	0.0645	
		Season X Location	2	138	4.93	0.0086	

Sticky Trap	Number	Cicadellidae	Season	1	138	4.48	0.0361	
			Location	2	138	5.18	0.0068	
			Habitat	1	138	4.55	0.0347	
			Season X Location	2	138	3.97	0.021	
		Coleoptera	Season	1	138	8.77	0.0036	
			Location	2	138	15.04	<0.0001	
			Habitat	1	138	0.54	0.4649	
			Season X Location	2	138	6.58	0.0019	
		Total	Season	1	138	9.56	0.0024	
			Location	2	138	2.83	0.0624	
			Habitat	1	138	9.37	0.0002	
			Season X Location	2	138	0.37	0.5467	
		Three groups	Season	1	138	15.69	0.0001	
			Location	2	138	9.03	0.0002	
			Habitat	1	138	1.78	0.1844	
			Season X Location	2	138	7.77	0.0006	
		Cicadellidae	Season	1	135	10.07	0.0019	
			Location	2	135	4.67	0.0109	
			Habitat	1	135	1.73	0.1901	
			Season X Location	2	135	1.86	0.1599	
			Season X Habitat	1	135	0.07	0.7946	
			Location X Habitat	2	135	0.69	0.5043	
		Coleoptera	Season X Location X Habitat	2	135	3.42	0.0357	
			Season	1	138	3.61	0.0596	
			Location	2	138	8.53	0.0003	
			Habitat	1	138	1.13	0.2889	
				Season X Location	2	138	4.32	0.0151

Table 2-10: Historic rainfall and temperature data collected from an online source for each location and season when I also collected morphology/diet information (fall: Sept-Nov; winter: Jan-Mar). Data are mean \pm standard deviation, in mm (rainfall) and $^{\circ}$ C (temperature).

Year	Location	Rainfall (mm)		Temperature ($^{\circ}$ C)	
		fall	winter	fall	winter
2010/11	Abaco	7.29 \pm 11.16	1.09 \pm 2.99	27.50 \pm 2.56	22.24 \pm 1.78
2011/12	San Salvador	5.46 \pm 10.55	1.10 \pm 2.53	27.06 \pm 1.58	23.08 \pm 1.42
2011/12	Mexico	5.42 \pm 8.63	3.45 \pm 7.54	23.72 \pm 2.18	22.48 \pm 2.93
2012/13	Abaco	2.23 \pm 5.77	0.55 \pm 1.32	28.20 \pm 3.03	23.02 \pm 2.20
2012/13	San Salvador	3.88 \pm 14.63	1.32 \pm 2.72	28.81 \pm 2.63	24.08 \pm 1.99
2012/13	Mexico	7.91 \pm 11.11	3.30 \pm 5.77	25.06 \pm 2.18	23.12 \pm 3.44

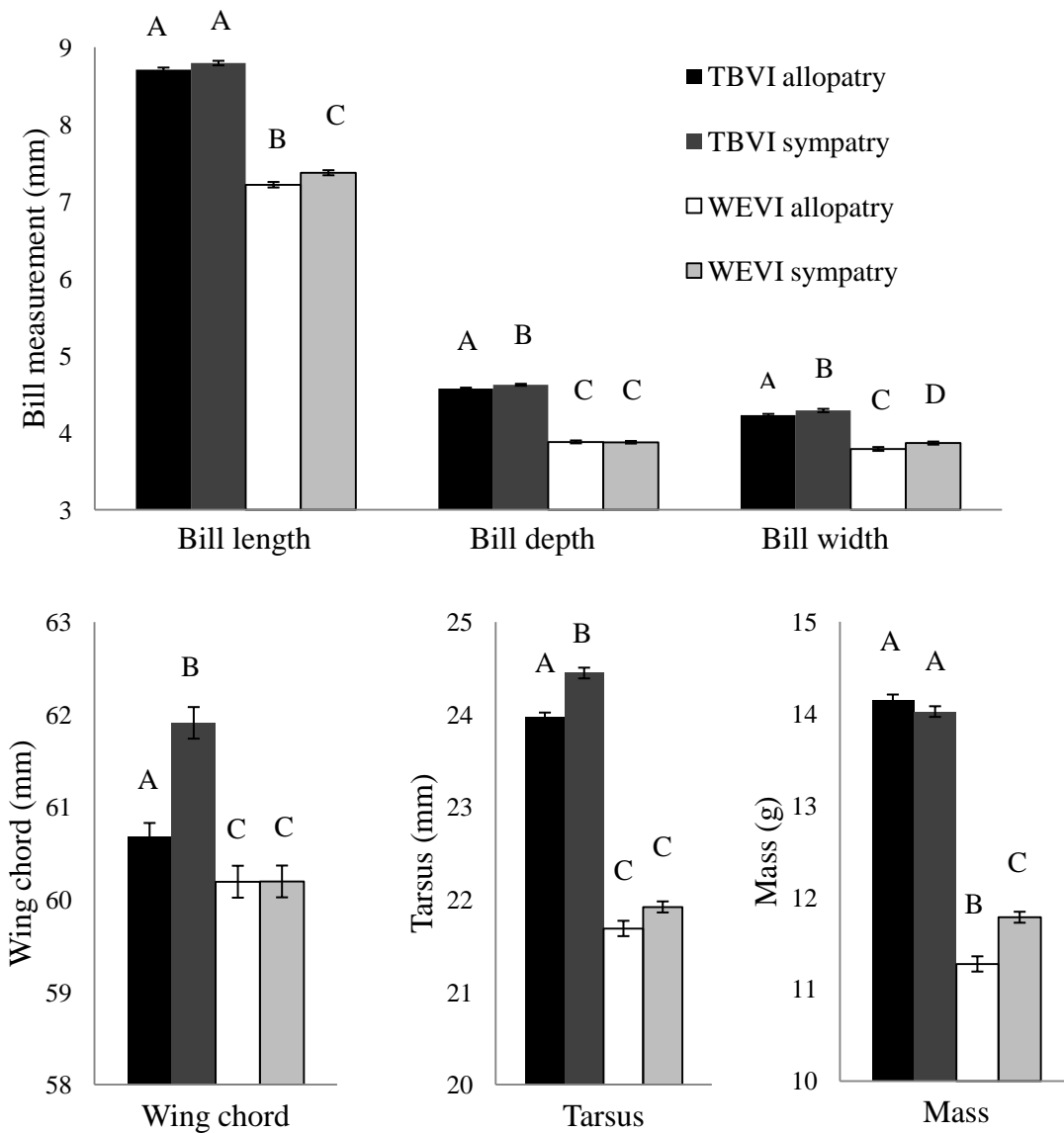


Figure 2-1: Morphology of Thick-billed Vireos (TBVI) and White-eyed Vireo (WEVI) in locations allopatric from each other, and a location sympatric with each other. Data are shown mean \pm SE. Note that the y-axis in each graph starts at an arbitrary number to highlight the differences between locations. Each graph has the same color coding (see legend). Levels not connected by the same letter are significantly different from each other within each measurement.

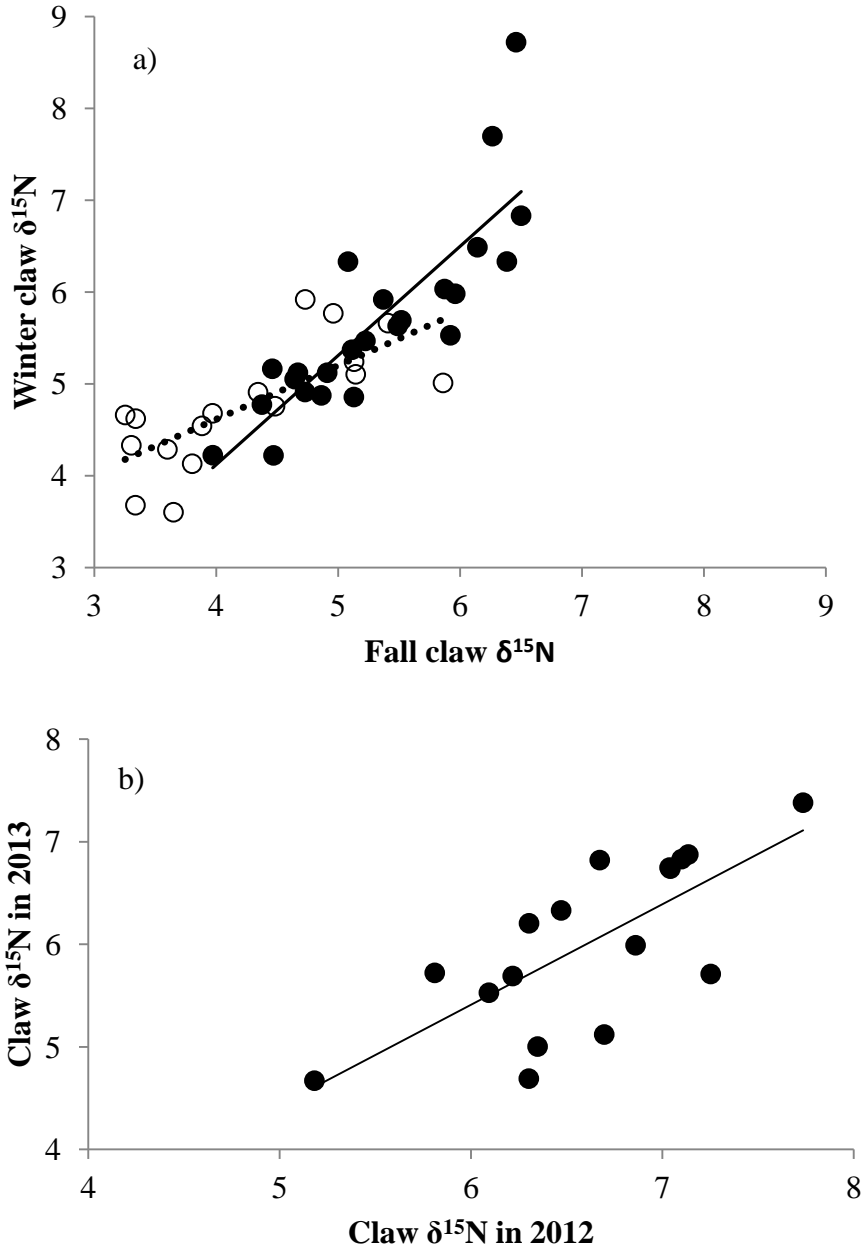


Figure 2-2: Individual consistency in Thick-billed Vireo recaptures. Filled circles and solid line is a population allopatriy from White-eyed Vireos; open circles and dashed line is a population sympatriy with White-eyed Vireos. a) Data collected in the fall and winter of 2012/13. The time from fall to winter samples was approximately 3 months. The regression for allopatriy ($R^2=0.71$, $p<0.0001$) and sympatriy ($R^2=0.54$, $p=0.0008$) was significant. One individual that was removed from the sympatriy seasonal comparison is not shown. b) Data collected in the winter of 2012 and 2013 in allopatriy. The regression is significant ($R^2=0.42$, $p=0.0027$).

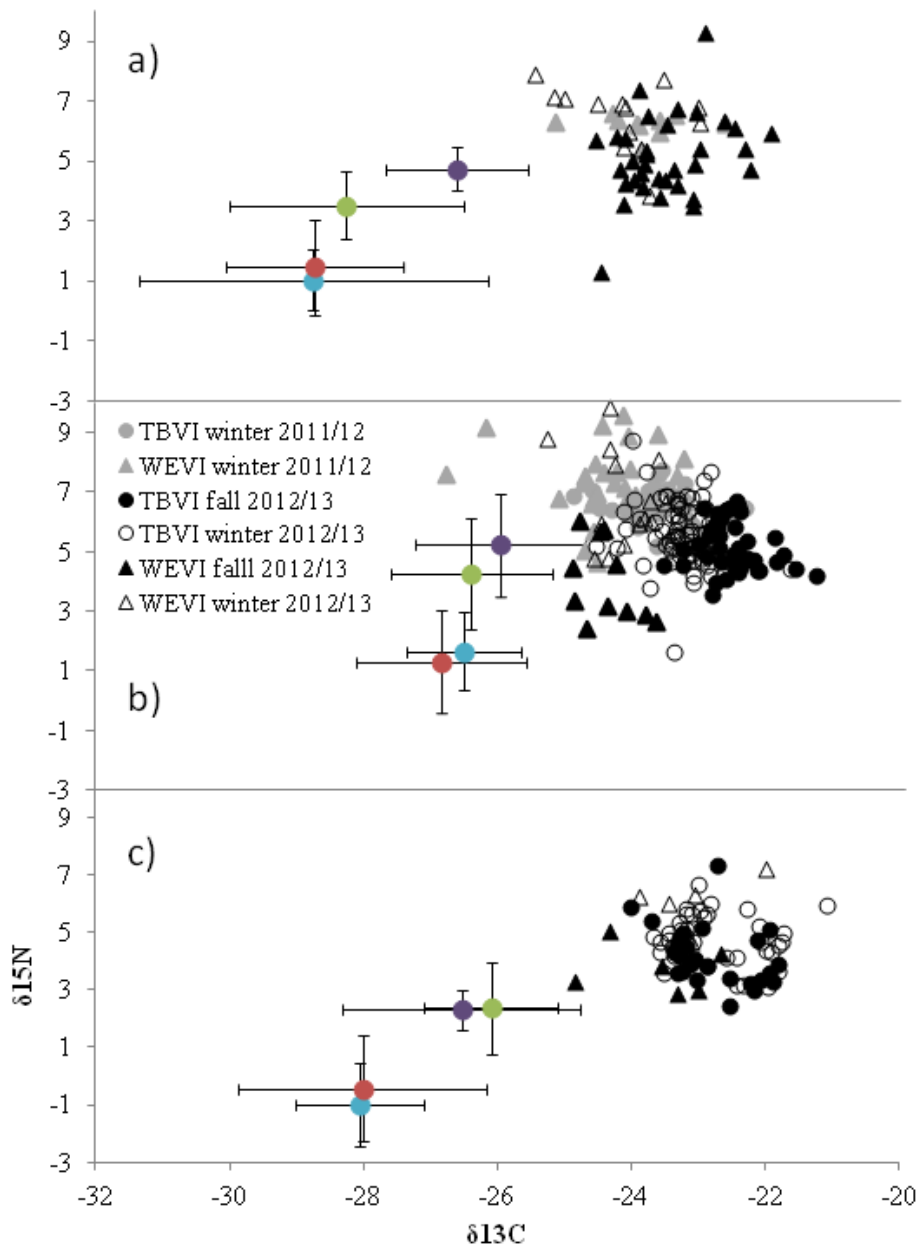


Figure 2-3: $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of prey and vireo claw tissue. Prey values are shown as mean \pm SD, and are color coded as follows: blue: *Bursera simaruba* fruit; red: leafhopper; green: beetle; purple: spider. Note that no trophic enrichment factor has been applied (raw values shown). Legend in panel b) applies to all three panels. All graphs are scaled the same to show differences in isotope values among locations. a) Mexico (allopatric WEVI). b) San Salvador (allopatric TBVI; some WEVI also caught). c) Abaco (sympatric).

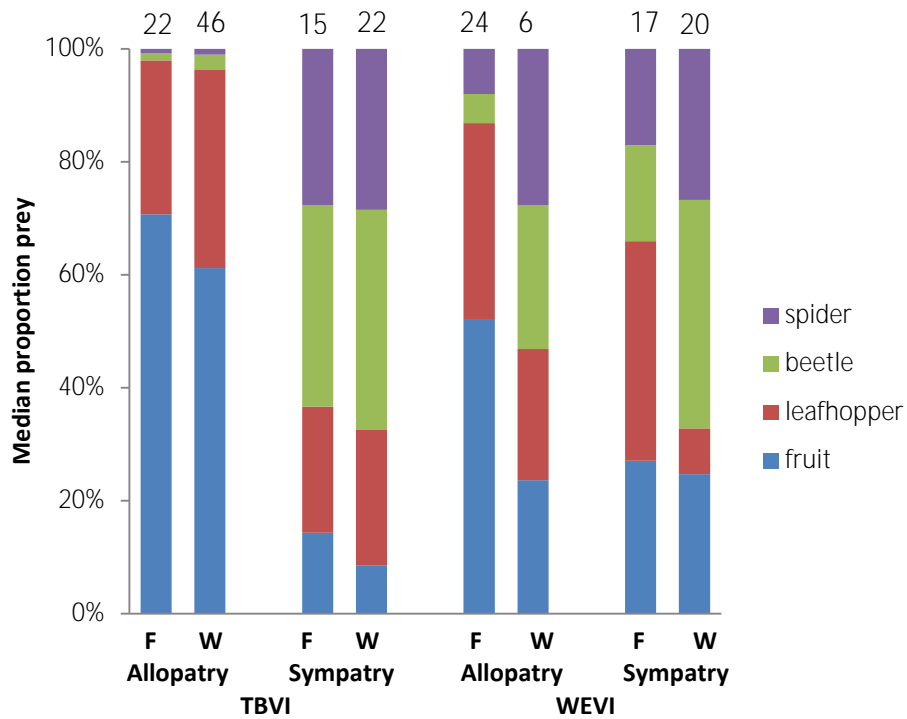


Figure 2-4: Median proportion of four prey categories to the diet of Thick-billed Vireos (TBVI) and White-eyed Vireos (WEVI) in a population allopatric from each other and in a population sympatric with each other, from forest habitat in the fall (F) and winter (W). Prey proportions were calculated from the SIAR mixing model. Numbers above bars refer to sample size of vireos for that category.

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Chapter 3. Effects of habitat quality on corticosterone levels and body condition in resident Thick-billed Vireos (*Vireo crassirostris*) and migrant White-eyed Vireos (*Vireo griseus*) during the non-breeding season

Abstract

Variation in both the availability of resources and the type of social interactions within environments is predicted to result in differences in condition among individuals occupying those habitats. However, little is known about the effects of this variation during the non-breeding season. The resident Thick-billed Vireo (*Vireo crassirostris*) and migrant White-eyed Vireo (*V. griseus*) are ecologically similar sister taxa that only coexist during the non-breeding season. I tested whether variation in habitat quality resulted in physiological effects in these two species by utilizing a seasonal decline in resource abundance within habitats, and a spatial contrast in resource abundance between forest and scrub habitat types. I also compared locations allopatric and sympatric with the heterospecific vireo to test for effects of interspecific social interactions. To assess physiological condition, I used three metrics: body condition (size-corrected mass) which is predicted to decrease in response to lower food abundance; and baseline and acute corticosterone which is a stress-induced hormone that is predicted to increase in response to lower food abundance and/or increased behavioral interactions. I found that lower resource abundance at both temporal and spatial scales negatively affected body condition in both species, and that heterospecific competitor presence increased corticosterone levels in resident males but not females. Since resident males but not females engage in territory defense, this suggests that corticosterone increased in response to social interactions with heterospecifics. Thus both the availability of food and interactions with heterospecifics can affect the quality of

the habitat an individual occupies, which can have negative consequences that may carry-over to other parts of the annual cycle.

Introduction

Habitat quality can be affected by many factors, including predation pressure (Rodriguez et al. 2001), resource abundance (Lambrechts et al. 2004), and competition (Forsman et al. 2008), which can vary in space and time (Johnson, 2007). In territorial animals, spatial variation in these factors leads to some individuals occupying poor quality habitats (higher predation, lower resource availability, and/or increased competition), and temporal variation in these same factors may lead to all habitats being of reduced quality during certain times of the year.

Individuals are predicted to experience negative effects when they occupy these sub-optimal habitats. In extreme cases these negative effects are immediately lethal, but more commonly they affect some metric, such as physiological condition, related to fitness (Cresswell, 2008; Romero, 2004).

To document habitat-related sub-lethal fitness effects, direct measures of physiological condition are preferable to using resighting or recapture rates of marked individuals, as differences across habitats detected with the latter two techniques may reflect emigration instead of mortality. Glucoid hormones affect physiological condition through their influence on energy balance (Breuner et al. 2008; Dallman & Bhatnagar, 2011). Corticosterone, the major glucocorticoid in birds, increases the rate of gluconeogenesis, which allows glucose to be metabolized from skeletal muscle instead of carbohydrates (Harvey et al. 1984; Holmes & Phillips, 1976). Corticosterone is released into the bloodstream in response to environmental stress (Wingfield et al., 1994, 1998). For example, food restriction (Lynn et al. 2003; Pravosudov

et al. 2001), predators (Cockrem & Silverin, 2002; Silverin, 1998), harsh weather (Wingfield, 1984) and conspecific territorial intrusions (Gill et al. 2008; Landys et al. 2007; Silverin, 1998) have all been shown to increase circulating corticosterone. Corticosterone also leads to increased activity and food intake (Wingfield & Silverin 1986; Sapolsky 1987; Angelier et al. 2007; Lohmus et al. 2006), behaviors which favor self-maintenance in order to survive short-term environmental perturbations. However, chronically elevated corticosterone can have negative consequences, as it can suppress the immune system (Siegel, 1980), catabolize skeletal muscle if an individual cannot meet its energy demand leading to a loss of body condition (Cherel et al., 1988; Malheiros et al. 2003), and inhibit reproduction (Romero, 2004). Body condition by itself may also be affected by habitat quality, especially by food restriction (Brown & Sherry 2006; Cucco & Malacarne 1997). Thus both levels of corticosterone and body condition can reflect the social or physical quality of the habitat an individual occupies.

Many species of migrant birds are territorial during the non-breeding season (Rappole & Warner, 1980) and thus upon arrival on the wintering grounds select a habitat to occupy for six months or more. While in some species, sex and/or age classes are distributed non-randomly across latitude or habitats due to intrinsic preferences and intraspecific competition, variation in overwintering location in other migrants is not linked to such mechanisms (Ketterson & Nolan 1983; Komar et al. 2005; Cristol et al. 1999; Hutto 1985; Murphy et al. 2001). Regardless of what determines where individuals overwinter, the result is that some individuals maintain territories in lower quality locations, which may result in negative physiological consequences for those individuals. Additionally, as the non-breeding season progresses, rainfall declines throughout much of the tropics (Chen & Taylor, 2002), and arthropod abundance is correlated with rainfall (Studds & Marra, 2011). One of the most commonly studied determinants of spatial

and temporal variation in habitat quality for small passerines is insect abundance. For instance, during the non-breeding season wet mangrove habitats have more insects than dry scrub habitats (Parrish & Sherry, 1994; Studds & Marra, 2005, 2011; Studds & Marra, 2007). This results in American redstarts (*Setophaga ruticilla*) engaging in intraspecific interference competition for higher quality wet habitats (Marra et al. 1993), reaching higher overall densities and having proportionally more socially dominant males in wet compared to dry habitats (Sherry & Holmes, 1996), losing body condition from the fall to winter in dry habitats (Marra & Holberton, 1998; Sherry & Holmes, 1996; Studds & Marra, 2005), and increasing corticosterone levels from the fall to the winter in dry habitats (Marra & Holberton, 1998). While a few other studies have documented either seasonal or habitat-related physiological effects due to resource competition in overwintering migrants (Brown & Sherry 2006; Strong & Sherry 2000; Norris & Marra 2007), the few that have tested for these same patterns in residents found contrasting results (seasonal decrease in body condition (Toms, 2011); no change in body condition (Brown & Sherry 2006)), and none have tested whether the presence of a heterospecific can also influence physiological condition. In general, very little is known about the effects of non-breeding competition for food, especially across habitat types, in tropical birds (Latta & Baltz, 1997) and how individuals respond to stress when reproduction is not occurring (Patterson et al. 2014). Here I test for the physiological effects of variation in habitat quality by utilizing two contrasts that reflect resource abundance: a seasonal change within habitats, and a spatial contrast between forest and scrub habitat types; and comparing locations allopatric and sympatric with the heterospecific vireo to test for effects of interspecific social interactions.

The migratory White-eyed Vireo (WEVI: *Vireo griseus*) and resident Thick-billed Vireo (TBVI: *V. crassirostris*) are sister taxa that diverged 110,000 ybp (Walker, 1998). These two

species only coexist during the non-breeding season and only in parts of their range, creating natural variation in heterospecific presence. The northern migratory population of WEVI (subspecies *V. g. noveboracensis*) breeds in the south-eastern United States and winters in some parts of the Caribbean and Central America (Hopp et al. 1995), and are declining throughout their breeding range (Sauer & Droege, 1992). TBVI are resident in the Caribbean, and the Bahamas subspecies (*V. c. crassirostris*) occurs on all the islands and cays of the Bahamas (Walker, 1998). TBVI pairs maintain territories year-round, with the male active in defense (Peiman, 2013) while male and female WEVI establish separate winter territories (Greenberg et al. 1993; Chapter 1). TBVI are behaviorally dominant to WEVI, and TBVI sympatric with WEVI are more aggressive to simulated territorial intrusions than TBVI in allopatry (Chapter 1). Both species consume similar diets of arthropods and fruit (Greenberg et al. 1995; Hopp et al. 1995; Chapter 2). They also both use diverse habitat types in allopatry, but WEVI are more restricted to forest habitats when sympatric with TBVI, and there WEVI territories overlapped TBVI territories by 70% (Chapter 1) while still foraging in the same strata (0-6m: Bradley, 1994; Greenberg et al. 1993; Kirkconnell & Garrido, 1991; Rappole & Warner, 1980). Thus, these two species behaviorally interact and compete for similar food resources during the non-breeding season. Additionally, there is spatial and temporal variation in habitat quality: forest habitats contain more fruit and arthropod prey and so are higher quality than scrub habitats, and arthropod abundance decreases from fall to winter (Chapter 2).

In order to assess the effects of competition, I used three metrics to determine whether individuals were in poor physiological condition: body condition (size-corrected mass), baseline corticosterone levels, and acute corticosterone levels. If condition depends on resource abundance, then individuals in forest habitats will have better physiological condition than

individuals in scrub habitats (Marra & Holberton, 1998), and individuals will have lower condition in the winter than the fall as food resources decline seasonally. If interactions with a heterospecific are stressful, sympatric individuals will have lower condition than allopatric individuals. Additionally, if individuals with elevated corticosterone are unable to meet their energetic demands, corticosterone should be negatively correlated with body condition (Astheimer et al. 2000; Schoech et al. 1997; Schoech et al. 1999; Smith et al. 1994).

Methods

I collected data on corticosterone and body condition during the fall (Sept-Nov 2012) and winter (Jan-Mar 2013) to test for seasonal effects, and used three locations to test for the effects of heterospecific presence: allopatric TBVI (San Salvador Island, The Bahamas), sympatry (Abaco Island, The Bahamas) and allopatric WEVI (Los Tuxtlas, Mexico). WEVI overwinter in variable numbers throughout the range of TBVI, and thus TBVI are not completely allopatric from WEVI. However, since WEVI density is variable among islands, I used an island with a low density of WEVI (San Salvador) instead of a completely allopatric location for TBVI, as has been done in previous studies of competition when the range of one species is completely within the other (Goldberg & Lande 2006; Kirschel et al. 2009; Pfennig & Murphy 2002; Tynkkynen et al. 2004; Anderson & Grether 2010) (for brevity, San Salvador will be referred to as an allopatric TBVI locations). Any WEVI captured on San Salvador Island were considered sympatric, as they would encounter many TBVI but TBVI would mainly encounter other TBVI. I used body condition data from additional sympatric individuals caught in fall 2010 and winter 2011 and from allopatric individuals caught in fall 2011 and winter 2012. To test for spatial variation in habitat quality, within each location I used 2-3 forest and scrub habitats. Forest habitats consisted

of coppice (broad-leaved evergreen forest) in The Bahamas and rainforest in Mexico; scrub habitats consisted of human-disturbed habitat or coastal scrub in The Bahamas and secondary growth (acahual) in Mexico.

To assess corticosterone, it is standard to measure levels immediately after capture to establish a baseline, and then to re-bleed each individual after holding them for 30 minutes to establish an acute response (Holberton et al. 1996; Marra & Holberton, 1998; Wingfield et al. 1994). I captured birds using target mist-netting and conspecific playbacks, which due to the immediate extraction of the individual from the mist-net, results in a more accurate baseline corticosterone than passive netting (Angelier et al. 2009). I collected 50-100 μ l of blood from the brachial vein within 5 minutes of capture. Individuals were then color-banded, aged (Peiman, 2013; Pyle, 1997), and measured (mass, wing chord, tarsus length), and then placed in an opaque cloth bag until the 30 minute mark when I collected a second blood sample (the acute response). Individuals were sexed by observing males singing (only males of both species sing) or genetically in the lab (see Chapter 1 for details). Whole blood was stored on ice for <6 hours and then centrifuged (Zipocrit hematocrit centrifuge, 11,000 rpm for 10 minutes), and the plasma removed and stored at -20°C in the field and then at -80°C until it was assayed for corticosterone using an enzyme immunoassay kit (Cayman Chemical number 500655). I performed the enzyme immunoassay in B. Schlinger's lab at UCLA following the Cayman kit's instructions. Each sample was analyzed in duplicate, and the mean value was used in analyses. Samples below the detection limit of the assay (n=4 baseline samples) were assigned the value of the lowest standard for that assay. The mean within-assay coefficient of variation of duplicate pooled samples was 11%, and the between-assay coefficient of variation was 17.6%.

Species were analyzed separately as the covariates of sex and age were applied differently in each species. I used linear mixed models to test whether baseline and acute corticosterone were affected by competitor presence (location: sympatry/allopatry), season (fall/winter), habitat (forest/scrub), and their interactions. I also used linear mixed models to test whether body condition was affected by the same variables, plus year. Corticosterone values were log transformed to improve normality. Individual ID was included as a random effect to account for repeated measures of some birds across seasons in both models. As only male TBVI defend territories and so experience different energetic costs than females, sexes were analyzed separately for corticosterone. Both male and female WEVI defend territories, and so sex was included as a covariate in all models. All TBVI analyzed for corticosterone in both habitats were adults (first-year birds rarely maintain territories and so do not experience the costs of behavioral interactions over territory defense), and so age (first-year or adult) was not tested in TBVI corticosterone. For TBVI body condition, age was analyzed separately as first-years were rarely territory holders and thus moved among habitats, while adults were almost always territory holders (Peiman, 2013). WEVI of both ages classes defend territories and so age was included in all WEVI analyses. To assess body condition, an index was obtained by performing a correlation-based principle components analysis (PCA) within each species using tarsus length (measured from the notch at the intertarsal joint to the point created by bending the toes 90° to the tarsus) and unflattened wing chord, and then using the residuals of a regression of PC1 against body mass as my structurally size-corrected measure of condition (Schulte-Hostedde et al. 2005). For WEVI, individuals with fat score >5 (n=8) were excluded as these individuals were caught early in the fall with high body masses and were assumed to have just arrived from migration (Helms & Drury, 1960), and thus body condition was likely not related to local

conditions. While most birds were caught between 06:30 and 13:00, a few were caught in the afternoon and evening. Since body mass can vary due to daily rhythms (Dunn, 2000), capture time was included as a covariate in those models. I also calculated correlation coefficients between each of the two measures of corticosterone and body condition to test for a relationship between those variables. As changes in body condition could be due to loss of water instead of reduced food intake, I tested whether dehydration affected body condition by correlating the change in hematocrit levels (percent packed red blood cell volume of the total sample collected at baseline) against the change in body condition from individuals captured in both the fall and the winter (Marra & Holberton, 1998). Baseline and acute corticosterone was log transformed to improve normality. Non-significant interactions were removed from each model until only significant interactions or main effects remained. All analyses were conducted in JMP Pro v11.2. Tukey's HSD and an ordered difference report was used to conduct pairwise comparisons when those terms were significant.

Results

Baseline corticosterone

Male TBVI had higher baseline corticosterone in sympatry than allopatry ($F_{1,47}=7.57$, $p=0.0084$), especially in the winter (location X season: $F_{1,4}=15.0$, $p=0.021$; Tukey HSD contrast of sympatry in the winter vs allopatry in the fall $p=0.020$ and winter $p=0.0017$) but this seasonal change was primarily driven by an increase in sympatric forest habitat only (three-way interaction, $F_{1,4}=26.13$, $p=0.0086$; Tukey HSD contrast of sympatric forest habitat in the fall vs winter $p=0.01$; all other contrasts not significant; Fig. 3-1). Female TBVI showed a different pattern of baseline corticosterone: it decreased from fall to winter in sympatry but did not change

in allopatry (location X season, $F_{1,6}=18.51$, $p=0.0051$; Tukey HSD contrast of sympatry fall vs winter: $p=0.053$; all other contrasts not significant; Fig. 3-2). In WEVI, no factors (sex, age, location, habitat, season, or their interactions) affected baseline corticosterone (all $p>0.17$).

Acute corticosterone

Male TBVI had higher acute corticosterone in the winter than the fall ($F_{1,20}=12.53$, $p=0.0021$). In female TBVI, acute corticosterone was not affected by any factor ($n=38$, all $p>0.087$). First-year WEVI had higher acute corticosterone in allopatry than sympatry, while there was no location effect in adults (age X location: $F_{1,39}=6.05$, $p=0.018$).

Body condition and corticosterone

Male TBVI showed a tendency to decline in body condition with increasing baseline corticosterone ($n=57$, $R^2=0.06$, $p=0.061$) and significantly declined in body condition with increasing acute corticosterone ($n=54$, $R^2=0.20$, $p=0.0006$; Fig. 3-3). In TBVI, female body condition was not related to baseline ($n=41$, $p=0.72$) or acute ($n=38$, $p=0.34$) corticosterone. There was no relationship between change in body condition and change in hematocrit in recaptured TBVI ($n=12$, $p=0.10$). In WEVI, body condition was not related to baseline ($n=43$, $p=0.80$) or acute ($n=41$, $p=0.24$) corticosterone.

Body condition – population effects

Sex was not included as a covariate for the model of first-year condition, as I did not determine the sex of most young birds. First-years had lower condition in the winter than the fall

($F_{1,29}=4.80$, $p=0.0366$), and were in the poorest condition in sympatric forest habitat (location X habitat: $F_{1,9}=8.99$, $p=0.0039$).

Adult TBVI body condition was affected mainly by factors interacting with the presence of heterospecifics. Like first-years, adults were in the poorest condition in sympatric forest habitat compared to scrub sympatric habitat and both habitats in allopatry (location X habitat: $F_{1,161}=4.82$, $p=0.029$; Fig. 3-4). Allopatric individuals had lower condition in the winter than the fall, while sympatric individuals were in poorer condition than allopatric individuals in both seasons (location X season: $F_{1,102}=26.05$, $p<0.0001$; Fig 3-5). Allopatric individuals were in better condition during 2011/12 than during 2012/13, while sympatric individuals were in equally poor condition during 2010/11 and 2012/13 (location X year: $F_{2,124}=10.31$, $p<0.0001$). Males were in better condition than females ($F_{1,158}=23.42$, $p<0.0001$).

Body condition in WEVI was affected by multiple factors (Table 3-1). Importantly, allopatric individuals had higher condition in the winter than the fall, while condition of sympatric individuals did not change between seasons (allopatry, fall vs winter: $p=0.0003$; sympatry, fall vs winter: $p=0.99$) although this pattern was driven by a seasonal effect in females only (allopatric females in fall vs winter: $p=0.0012$; allopatric males in fall vs winter: $p=0.97$). Individuals in coppice habitat had higher condition in the winter than the fall while the condition of those in scrub habitats did not change (forest in fall vs winter: $p=0.0002$; scrub in fall vs winter; $p=0.99$) although this pattern was also driven by a seasonal effect in females only (females in forest, fall vs winter: $p=0.0001$; males in forest, fall vs winter: $p=1.0$). Adults had higher condition in the winter than the fall, while first-years did not show a change in condition (adults in fall vs winter: $p=0.0056$; first-years in fall vs winter: $p=0.83$). In sympatry individuals in scrub habitat had higher body condition than those in forest habitat but the opposite pattern

occurred in allopatry (sympatric scrub vs forest: $p=0.0043$; allopatric scrub vs forest: $p=0.0008$) but the allopatric pattern was driven by females only (females in allopatric scrub vs forest: $p<0.0001$; males in allopatric scrub vs forest: $p=0.99$).

Discussion

Though over-wintering migrants can experience strong intraspecific competition (Marra et al 1998; Marra & Holmes, 2001; Strong & Sherry, 2000), there are few studies on non-breeding interspecific interactions in general and on migrant-resident interactions in particular (Greenberg, 1986). Many authors have pointed out the dearth of studies on interspecific competition (e.g. Faaborg et al. 2010; Latta, 2012) and though evidence is now accumulating in the Afro-Palearctic system that migrants and resident competitively interact (Bensusan et al. 2011; Salewski et al. 2002), the Neotropic-Nearctic system still lacks studies testing for similar interactions (but see Toms, 2011). Interspecific interactions may cause stress to migrant populations overwintering with ecologically similar residents, and so compound documented intraspecific carry-over effects in some locations. This possibility is largely untested and if ubiquitous may be an additional factor in the decline of some species already constrained by winter food limitation (Sherry et al. 2005). Physiological effects in non-breeding tropical residents are even less studied, and high density of migrants may be stressful through increased aggressive and exploitative interactions. Here I used a migrant and resident vireo to test for the physiological effects of variation in habitat quality by utilizing a seasonal change within habitats and a spatial contrast between forest and scrub habitat types, and for the first time also contrast physiological effects between locations allopatric and sympatric with the heterospecific vireo competitor.

Both resource availability and physical interactions may affect levels of stress and body condition. By testing for these associations in a species where both sexes use the same resources but only the males engage in territory defense, I was able to tease apart the effects of direct and indirect interactions. Male TBVI in sympatry had higher baseline corticosterone than in allopatry, while in female TBVI baseline corticosterone decreased from fall to winter in sympatry but did not change in allopatry. It is unlikely that this sex-specific difference in baseline profiles between the islands was caused by differences in resource availability, as both sexes were exposed to the same level of resource abundance within each island. Instead, the elevated corticosterone levels in sympatric males were likely caused by direct physical interactions, as males were more aggressive towards simulated intruders in sympatry than allopatry (see Chapter 1). Stonechats (*Saxicola torquata axillaris*) showed a similar pattern, as only male defend territories, and in territories with predators present, male stonechats had higher baseline corticosterone than males without predators while females showed no difference (Scheuerlein et al. 2001). The seasonal increase in baseline and acute corticosterone shown by male but not female TBVI also implies the role of behavioral interactions, as male TBVI were more aggressive in the winter compared to the fall (see Chapter 1), while resource decline should have affected both sexes. Importantly, WEVI only established territories in forest habitat, and this was the only place where the seasonal increase in the baseline corticosterone of male TBVI occurred. The socially dominant TBVI engages in direct physical interactions with the subordinate WEVI (Chapter 1), and it may be that the increased energetic cost to male TBVI exceeds the available resources especially in the face of seasonal resource declines (Goymann & Wingfield, 2004). This is supported by the negative relationship between body condition and acute corticosterone in male TBVI, which suggests that individuals were unable to consume

enough resources to counteract the increased energetic demand of stress-induced higher corticosterone (Astheimer et al. 2000; Schoech et al. 1997, 1999; Smith et al. 1994). The lack of an effect on baseline corticosterone in the subordinate WEVI was unexpected, as subordinate individuals often experience increased stress (Blanchard et al. 2001; DeVries et al. 2003). However, subordinate individuals may reduce physiological effects by avoiding dominant individuals temporally and spatially (Creel et al. 2013). WEVI avoid TBVI spatially as some individuals use small habitat fragments, and temporally by responding less to trials and spending less time near TBVI mounts (Chapter 1). Though manipulative experiments are necessary to make definitive conclusions about the role of behavior in elevating corticosterone, the presence of consistent patterns are suggestive of causal links.

Body condition followed similar patterns in TBVI, except that for this metric sexes and even non-territorial first-year birds had similar responses. Both sex and age classes had the lowest body condition in sympatric forest habitat, which is the only location where they coexisted with territorial WEVI and therefore there were both conspecifics and heterospecifics consuming resources. TBVI lost condition from the fall to the winter, paralleling declines in resource abundance and rainfall (Chapter 2) and showing a similar pattern to resource-related declines in condition in the resident Adelaide's warbler (*Dendroica adelaidae*) in Puerto Rico (Toms, 2011). The parallel responses between sexes and age classes in TBVI suggest that overall resource abundance, not behavioral interactions, caused changes in body condition. Surprisingly, adult WEVI (but not first-years) were able to gain condition from the fall to the winter, as were females (but not males) in forest habitats and in allopatry, which contrasts with numerous other studies showing a seasonal decline in body condition in migrants (Johnson et al. 2006; Marra & Holberton, 1998; Sherry & Holmes, 1996; Strong & Sherry, 2000; Studds & Marra, 2005). It is

possible that these age differences were caused by young birds in their first winter being less effective than adults at foraging (Desrochers, 1992; Vanderhoff & Eason, 2008). Forest habitats and allopatry had more resources available (Chapter 2), which may explain how individuals in these locations were able to gain condition, but it is unclear why these effects were seen in females but not males. The increase in body condition under only a subset of ecological conditions may lead to later departure for spring migration in first-years in general and especially those individuals overwintering in scrub habitats and in locations sympatric with heterospecifics, possibly leading to lower reproductive success the following summer (Marra et al. 1998; Smith et al. 2010). Thus food abundance is implicated in seasonal and habitat-related differences in body condition for both species.

Carry-over effects result from events that happen in one part of the annual cycle that have effects in another part of the cycle (Harrison et al. 2011). The observed higher corticosterone in sympatric male TBVI during the winter may lead to reduced survival (Koren et al. 2012) and/or a delay in reproductive behavior (Salvante & Williams, 2003) and a decrease in reproductive success (Wingfield & Silverin 1986) the following spring. Most studies of the seasonality of corticosterone profiles compare data within breeding stages or between non-breeding and breeding stages and often use extreme environments (Romero, 2002). The more subtle environmental differences documented here during the non-breeding season suggest that if this increase is truly due to interspecific competitive interactions, then the effects of migrants on residents have been underestimated. Experiments on free-living species are needed to test the ubiquity of these stresses and their effects on fitness (Wingfield, 2013), as have been done for intraspecific competition in migrants (see reviews by Harrison et al. 2011; Norris, 2005; Norris & Marra, 2007). Considering the diversity of migrant-resident species pairs that interact over

decreasing food resources during the non-breeding season, the lack of studies documenting similar competitive effects in residents likely reflects a sampling bias and not the absence of an effect. Additionally, climate change models predict drying and thus likely decreased arthropod availability in parts of the non-breeding range (Neelin et al. 2006), suggesting that the intensity of competition may increase in the future (Ahola et al. 2007). Sub-lethal non-breeding effects similar to those documented here may underlie variation in subsequent reproductive success and survival for both migrants and residents (Norris & Marra, 2007), and are a worthy avenue for future investigation.

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Table 3-1: Linear mixed effects models of body condition in White-eyed Vireos (WEVI). Rows with significant p-values are bolded.

Factor	Num DF	Den DF	F value	p-value
Habitat	1	120.0755	0.0908	0.7637
Sex	1	117.8817	0.4176	0.5194
Habitat X Sex	1	119.5263	6.4701	0.0122
Age	1	109.3849	0.6639	0.4169
Sex X Age	1	104.9988	0.4513	0.5032
Season	1	67.03229	8.6139	0.0046
Habitat X Season	1	115.2577	4.3528	0.0392
Sex X Season	1	72.01772	1.9171	0.1705
Habitat X Sex X Season	1	113.3076	10.7	0.0014
Age X Season	1	83.51698	6.0849	0.0157
Location	1	120.2956	3.7805	0.0542
Habitat X Location	1	119.0764	24.747	<0.0001
Sex X Location	1	119.6735	2.3721	0.1262
Habitat X Sex X Location	1	119.315	10.5781	0.0015
Season X Location	1	120.8338	8.0435	0.0054
Sex X Season X Location	1	120.9466	9.9593	0.002
Year	1	62.22474	0.0043	0.9478
Sex X Year	1	68.11877	1.8867	0.1741
Age X year	1	110.673	0.4637	0.4973
Sex X Age X year	1	114.0578	5.4956	0.0208
Time capture	1	50.58178	25.9162	<0.0001

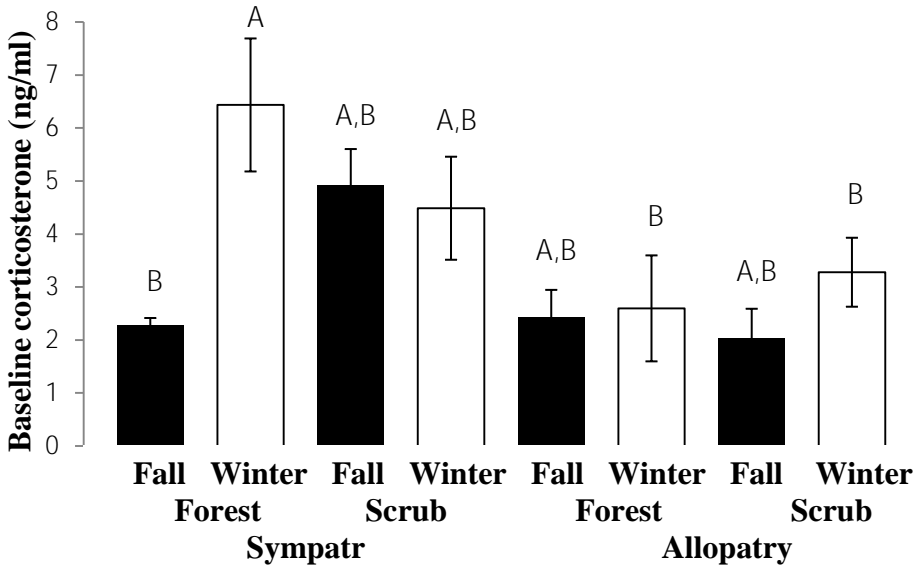


Figure 3-1: Baseline corticosterone in male Thick-billed Vireos (TBVI) during the fall and winter within forest and scrub habitats in locations sympatric and allopatric with White-eyed Vireos (WEVI). Bars are mean \pm SE. Levels not connected by the same letter are significantly different (based on least squared means; see text for details).

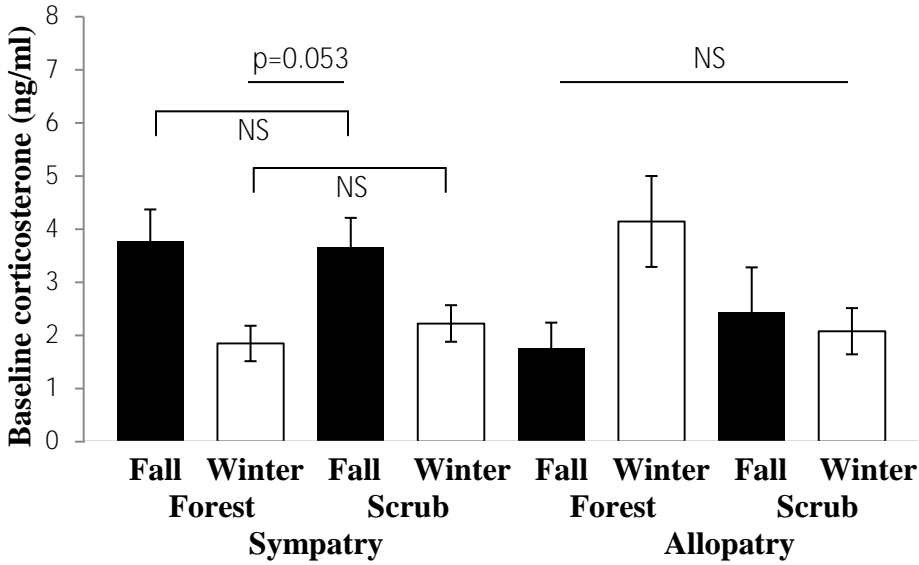


Figure 3-2: Baseline corticosterone in female Thick-billed Vireos (TBVI) during the fall and winter within forest and scrub habitats in locations sympatric and allopatric with White-eyed Vireos (WEVI). Bars are mean \pm SE. Baseline corticosterone decreased from fall to winter in sympatry but did not change in allopatry (see text for details); NS = not significant.

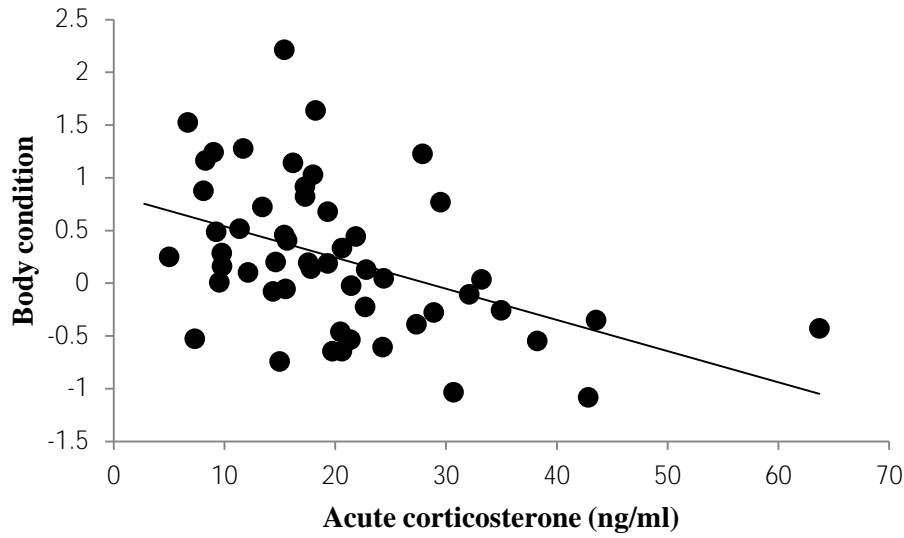


Figure 3-3: Negative relationship between acute corticosterone and body condition in adult male Thick-billed Vireos (TBVI; $n=54$, $R^2=0.20$, $p=0.0006$). The body condition index was obtained by performing a correlation-based principle components analysis using tarsus length and unflattened wing chord, and then using the residuals of a regression of the first principle component against body mass.

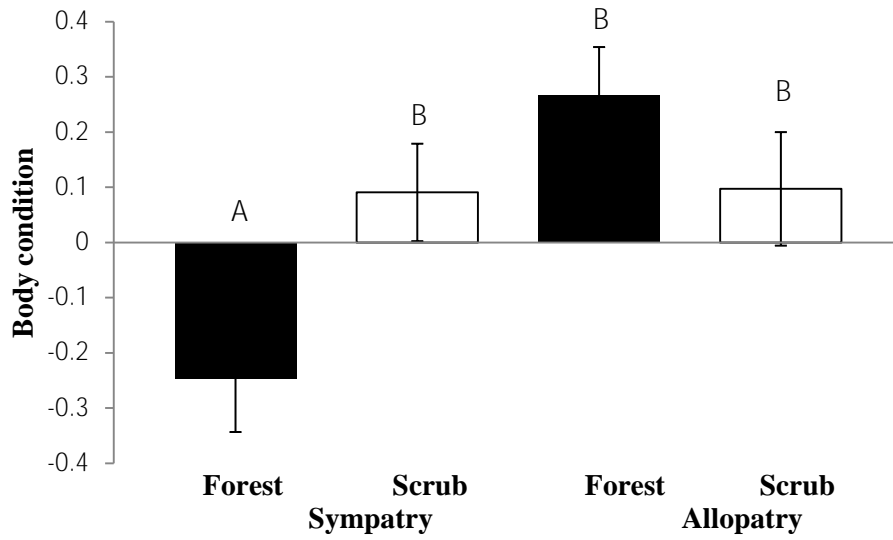


Figure 3-4: Body condition in adult Thick-billed Vireos (TBVI) within forest and scrub habitats in locations sympatric and allopatric with White-eyed Vireos (WEVI). Both years are included and sexes are combined. Bars are mean \pm SE. Levels not connected by the same letter are significantly different (see text for details).

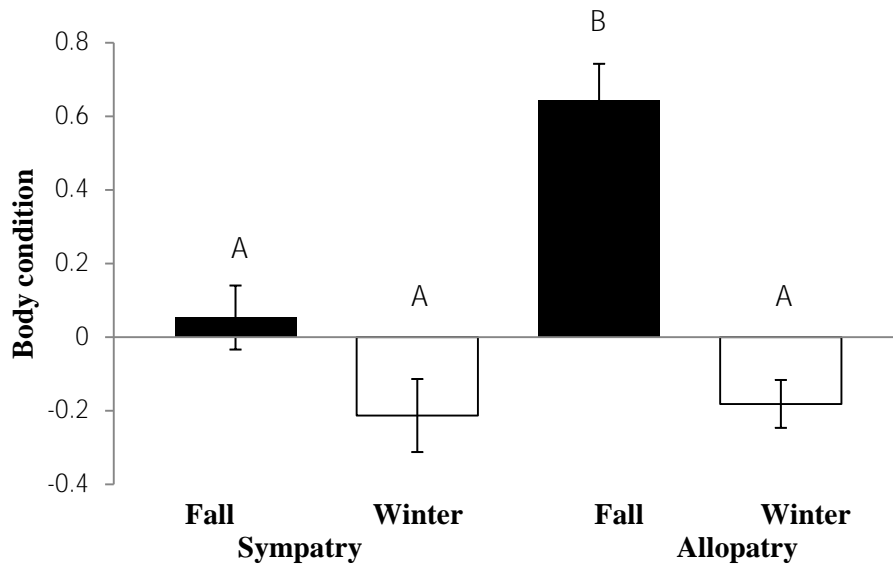


Figure 3-5: Body condition in adult Thick-billed Vireos (TBVI) during the fall in locations sympatric and allopatric with White-eyed Vireos (WEVI). Both years are included and sexes are combined. Bars are mean \pm SE. Levels not connected by the same letter are significantly different (see text for details).

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