NON-BREEDING COMPETITION BETWEEN MIGRANT AMERICAN REDSTARTS (*SETOPHAGA RUTICILLA*) AND RESIDENT ADELAIDE'S WARBLERS (*DENDROICA ADELAIDAE*) IN THE GUÁNICA BIOSPHERE RESERVE, SOUTHWEST PUERTO RICO

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by

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Dr. John Faaborg, Dissertation Supervisor

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The undersigned, appointed by the dean of the Graduate School, have examined the dissertation entitled

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presented by Judith D. Toms, a candidate for the degree of doctor of philosophy, and hereby certify that, in their opinion, it is worthy of acceptance.

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Abstract

Evolutionary processes increase fitness by reducing overt competition among species through morphological character displacement, habitat preference, behavioral adaptations, and divergence in use of resources. However, migrants face a different set of ecological pressures in their breeding, non-breeding and passage/stopover habitats. As a result, they may evolve a compromised set of traits that are not optimal in any of these ecosystems and competition may be more easily detected between migrants and residents than among residents.

I tested the hypothesis that migratory American Redstarts (Redstart; *Setophaga ruticilla*) and resident Adelaide's Warbler (Adelaide's; *Dendroica adelaidae*) compete for food in a dry forest of southwest Puerto Rico. My study was conducted during the non-breeding season, when the only plausible resource that might be in limited supply was food (arthropods). The two species have broadly similar foraging methods, and arthropods are limiting in similar ecosystems on other islands.

In addition, I determined reliable ageing and sexing criteria for Adelaide's, which allowed me to control for age and sex differences. I also described their molt patterns, which indicated the time of year when these criteria could be dependably applied.

Competition will not occur unless food is limiting, so I monitored arthropod biomass through two non-breeding seasons. In the drier of the two years, leaf fall was pronounced in all vegetative layers and total arthropod biomass declined. In contrast, during the wetter year, leaf fall was largely limited to the shrub layer and total arthropod biomass remained fairly constant. Little mortality was observed in either bird species

throughout the non-breeding season. However, the body condition of both species declined during the drier year, while they managed to maintain body condition in the wetter year. Decreased body condition may delay departure of the migratory Redstart, which is correlated with increased mortality during migration and reduced reproductive success. Similarly, decreased body condition in the resident Adelaide's may delay their response to conditions favorable for breeding, limiting their reproductive success.

Even though arthropods are limiting, Redstarts and Adelaide's will not compete unless they forage in the same places using the same methods of attack. When both species were present, they had a very high degree of overlap in both foraging location (type of vegetation, relative location within tree canopies and height from ground) and type of attack (substrate and attack method), both when assessed at the level of the population and at the level of individuals. Thus, they are indeed using the same limiting resources, and should be competing.

The high degree of similarity in foraging niches when both species are present indicates that they do not partition food resources. However, Redstarts might still be preventing Adelaide's from using preferred resources. Therefore, I determined whether Adelaide's shifted their foraging niches when Redstarts left, using Adelaide's without Redstart neighbors as a control for any seasonal changes. Adelaide's did not shift their foraging niche, indicating that depletion competition does not occur.

The two species could also defend territories against the other species. However, detailed territory mapping showed that interspecific overlap of territories was significantly greater than the intraspecific territory overlap of either species. In addition,

Adelaide’s did not shift territories when Redstarts left, indicating that Redstarts were not restricting the space use of Adelaide’s. Thus, interference competition is not present.

I also conducted a behavioral experiment, where I simulated territorial intrusions to determine whether each species was aggressive towards the other species. Aggressive behaviors have high costs, and should be used only if the benefits of aggression outweigh these costs. Both species were significantly more aggressive to the other species than to a non-competitive control, with Adelaide’s being the dominant species.

Adelaide’s and Redstarts do seem to be competing for food, but not through niche partitioning or interspecific territoriality. Instead, the evidence suggests that Redstarts listen to the frequent vocalizations of Adelaide’s, and forage in areas of their territory that reduces the risks of confrontation at any given time: they use temporary competition refuges. Redstarts are not territorial where Adelaide’s densities are high, suggesting that Redstarts may be vagrant in these areas, or avoid them entirely. I conclude that competition does occur between these species, and is mediated through aggressive confrontations and the behavioral flexibility of Redstarts.

Chapter 1: Assessing competition between migrant and resident species.

Abstract

Migratory animals must adapt to multiple ecosystems throughout their annual cycle, each with a different suite of competitors and available food resources. In isolation, each community would induce a different set of adaptations in a migratory species. However, these ecological pressures may conflict, so that migrants may not be able to minimize competition in one or more of these communities. Behavioral adaptations can reduce the resulting interspecific competition through mechanisms such as interspecific territoriality, niche or habitat partitioning, and use of competition refuges. I outline an approach that determines whether competition is occurring between migrant and resident species and the form that it takes. I also argue that studies of competition should be made at the level of individuals whenever possible, rather than at the level of populations or species. Finally, I outline the basis for my hypothesis that resident Adelaide's Warblers (*Dendroica adelaidae*) compete for food with migratory American Redstarts (*Setophaga ruticilla*) during the non-breeding season in the dry forests of southwest Puerto Rico.

Why might migrants and residents actively compete?

A wide range of animal taxa undergo seasonal migrations, including fish, insects, bats, large herbivores, marine mammals and birds. Migration can arise from a variety of ecological pressures, potentially acting at different times of the year; animals migrate to avoid extreme climatic conditions (Fryxell and Sinclair 1988, Fleming and Eby 2003), track seasonally-variable food resources (Fryxell and Sinclair 1988, Alerstam et al. 2003, Fleming and Eby 2003), reduce parasite or predation pressure (Fryxell and Sinclair 1988, Alerstam et al. 2003, Fleming and Eby 2003), or minimize intraspecific and interspecific competition (Cox 1968). Migratory animals move over large distances throughout the year, and thus are members of multiple ecosystems during the annual cycle: at breeding sites, stopover or passage sites during migration, and non-breeding sites. Thus, migrants are exposed to a different set of ecological pressures during different seasons and need to adapt to multiple suites of climate, food resources, predators and competitors (Keast 1980, Rappole and Warner 1980). Strong selective pressures and population limitation can occur at any stage of this yearly cycle (Morse 1980, Martin and Karr 1990, Baillie and Peach 1992, Mönkkönen et al. 1992, Sillett and Holmes 2002, Newton 2004, Norris and Marra 2007, Wilson et al. 2011).

Over evolutionary time scales, these ecological pressures cause a species to become more suitably adapted to its environment through morphological character displacement (Brown and Wilson 1956). However, migratory species may have a limited capacity to diverge from competitors in any one ecosystem, because they also face potentially-conflicting ecological pressures from competitors in other habitats. For example, American Redstarts (*Setophaga ruticilla*) compete with different sets of flycatchers, warblers and other species on their breeding and wintering grounds (Kepler 1977, Bennett 1980, Martin et al. 1996), which may result in conflicting evolutionary pressures on bill morphology (Wilson 1975, Bennett 1980). Conflicting selective pressures force a migrant to evolve a compromised set of morphological traits (Orians and Willson 1964), which may not minimize competition during even one season. Moreover, the act of migration itself also produces strong selective pressures on some aspects of morphology (Morse 1980, Ricklefs 1992, Winkler and Leisler 1992), which may conflict with selective pressures from competitors. Thus, some migrants may not be able to avoid interspecific competition with resident species through morphological adaptations for niche partitioning of resources or habitats.

Over ecological time scales, competition can be reduced using behavioral adaptations. Competition can be reduced by selecting for different habitat types (Kirk and Currall 1994), by defending territories against heterospecific competitors (Reed 1982, Robinson and Terborgh 1995) or by using competition refuges (Durant 1998). At smaller spatial scales, individuals can also avoid competitors (Brown and Wilson 1956, Martin 1986, Durant 1998) or use aggressive behaviors to partition resources (Brown and Wilson 1956, Chipley 1976, Carpenter 1979, Schoener 1983, Martin 1986, Leisler 1988, Kirk and Gosler 1994, Kirk and Houston 1995, Jedlicka et al. 2006). Migrants can also use empty niches (Terborgh and Faaborg 1980, Waide 1981, Leisler 1992, Mönkkönen et al. 1992, Latta and Wunderle 1998) or exploit seasonally available resources or habitats (Mönkkönen et al. 1992, Fleming and Eby 2003). However, even though migrants may sometimes appear to exploit unused resources (empty niches or seasonal resources), they may restrict residents from using these resources; we now recognize that migrants are an integral part of the communities they occupy, rather than visitors forced to use marginal resources (Emlen 1980, Rappole and Warner 1980, Schwartz 1980, Stiles 1980, Rappole and Tipton 1992, Sherry and Holmes 1995).

How can one test if competition is occurring?

Competition between two species will not occur unless they use the same resources, and those resources are limiting in some way (Figure 1). Competition has often been studied at the level of populations or species. However, studies of competition at the level of individuals are more relevant (Martin 1986), because all individuals of a species do not use any given habitat in the same way. For example, male and female Black-throated Blue Warblers (*Dendroica caerulescens*) partition foraging niches by vertical stratification and by habitat (Wunderle 1995). Similarly, intraspecific interference competition occurs among American Redstarts in Jamaica, relegating females to poor quality habitats (Marra 2000, Marra and Holmes 2001, Studds and Marra 2005). Moreover, even within such subsets of the population, individuals may select different subsets of the available resources, resulting in variation in resource use among individuals (Svanbäck and Bolnick 2005). Studies of competition at the population level mask these differences among individuals, and can lead to misleading conclusions. Therefore, a study of competition should measure resource availability, effects of

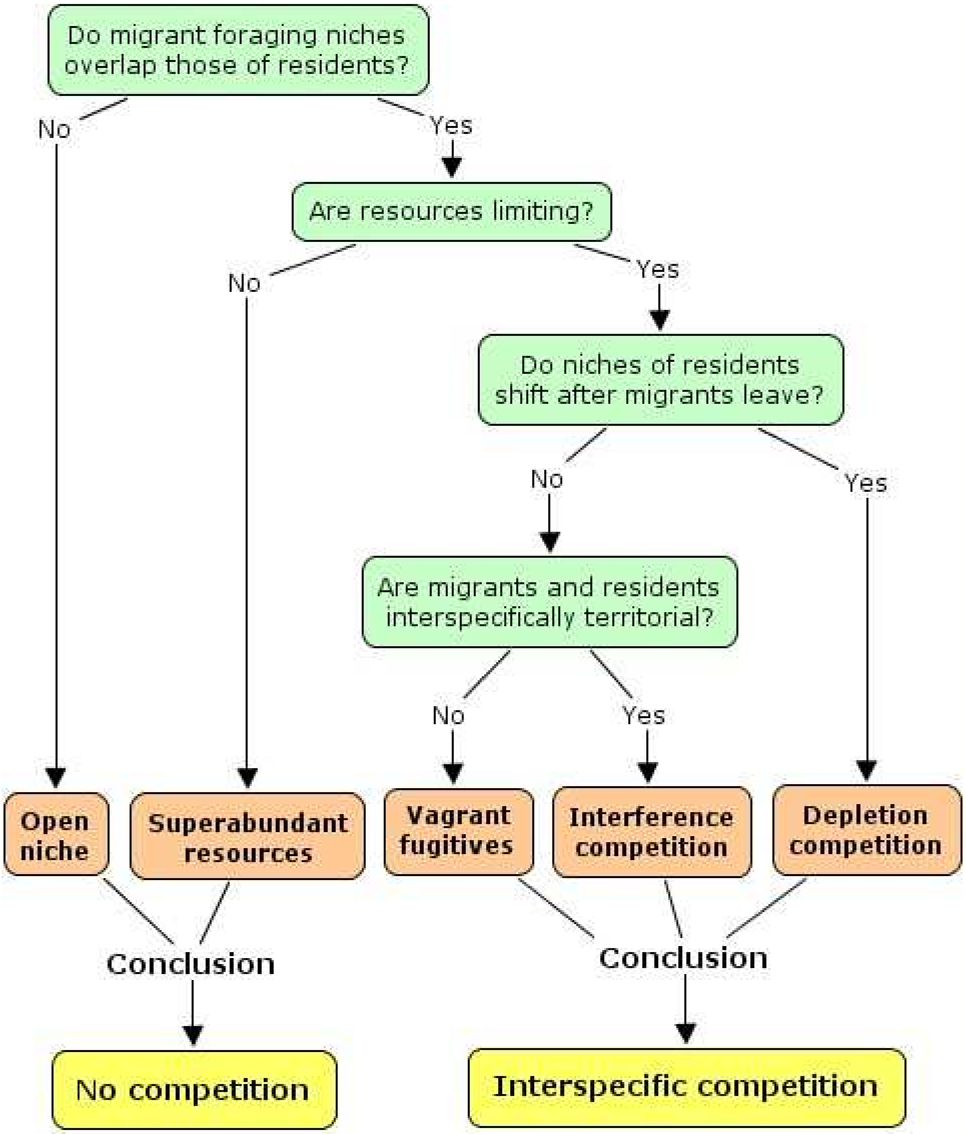

Figure 1. Schematic approach to determining whether residents compete with migrants for resources. If resources are not shared (open niche), or are not limiting (superabundant resources), competition does not occur. If it occurs, competition can take several forms: the subordinate species uses spatiotemporal competition refuges (vagrant fugitives); the two species defend territories against the other species (interference competition); or one or both species shifts its niche in the presence of the other to minimize competition (depletion competition).

resource limitation (i.e. the consequences on fitness), and resource use at the level of individuals whenever possible. Resource limitation need not occur continuously, because limitation during discrete periods can still be important both at the scale of an individual (Wallace 1998, Studds and Marra 2005, 2007) and a population (Waide 1981, Schoener 1983, Jedlicka et al. 2006, Wilson et al. 2011). Moreover, resources can limit the productivity of individuals (and hence limit populations) without causing direct mortality during the non-breeding season; males wintering in low-quality habitat may arrive at the breeding grounds later and in poorer condition (Marra et al. 1998), limiting their ability to gain and defend a good breeding territory (Smith and Moore 2005), while females over-wintering in low-quality habitat produce smaller eggs (Smith and Moore 2005). Moreover, such individuals may have lower fitness during migration (Bearhop et al. 2004), when most mortality may occur (Sillett and Holmes 2002). Thus, even sub-lethal effects on individuals can indicate that resources are limiting.

If resources are shared and limiting, individuals would benefit from reducing direct competition with heterospecifics. Behavioral flexibility can allow individuals to shift their niches to adjust for resource use of heterospecific competitors at any given moment of time (Martin 1986). This niche shift could be masked at the level of a population, since not all individuals face the same suite of potential competitors (Martin 1986), and each individual may shift its niche in a different way (Bolnick et al. 2002). Removal experiments, where one putative competitor is temporarily or permanently removed from an area used by the other species, are the classic approach to assessing whether niche shifts occur in the presence of a putative competitor (Connell 1980, Schoener 1983, Bender et al. 1984). However, removal experiments are not always appropriate, as in studies of rare species, and can be difficult to perform in open systems (Connell 1980). Fortunately, as migrant species move into and out of different communities during their annual cycle, they induce an annual “natural” removal experiment. Although evidence from a natural experiment is not as robust as that from a manipulative experiment, it can provide insight into the mechanisms structuring the community (Bender et al. 1984). Depletion competition between migrant and resident species can be assessed by determining whether the niche of the resident species changes when the migrant is present and absent (Figure 1). However, as the movement of migrants is often associated with seasonal changes or stages of the resident species’ life cycle, this niche shift is best assessed by contrasting niche shifts in individual residents that are or are not in direct contact with individual migrants.

Alternatively, an individual can defend its territory not only against conspecifics, but against heterospecifics as well (interference competition; Figure 1). The choice to defend a territory against a heterospecific might depend not only on the costs of competition, but also by the costs of territorial defense and the likelihood that the heterospecific intrudes into their territory (Brown 1964, Brown and Gordon 1970, Terman 1974, Lyon et al. 1977, Dearborn 1998, Mikami and Kawata 2004). If the conflicts required to defend a territory are very strongly weighted towards one species, then the other species could be excluded from areas where individuals of the first species are present. Conversely, if the conflicts are more equally weighted, individuals of each species might intersperse territories with heterospecifics. Intraspecific aggression and the ability to defend a territory against conspecifics often varies among age and sex groups (Piper and Wiley 1989, Marra et al. 1993, Sherry and Holmes 1996, Marra 2000, Latta et al. 2003, Sergio et al. 2009), and this likely carries over into interspecific interactions (Morse 1976). Thus, the degree of interspecific territoriality observed may vary widely among individual pairs of heterospecifics. Although complete interspecific territorial defense is commonly observed (Reed 1982, Robinson and Terborgh 1995), territorial defense may also occur when territories partially overlap (Catchpole 1978, Leisler 1988). Estimating the space use of individuals can determine whether or not territories overlap, but observational or experimental studies are also needed to determine whether each species defends that territory against intrusions by heterospecifics.

An individual can also reduce competition by avoiding heterospecific competitors at a fine spatiotemporal scale (Brown and Wilson 1956, Schoener 1983, Martin 1986, Durant 1998). As this is analogous to Hutchinson's "fugitive" species (Hutchinson 1951), but at a much smaller spatiotemporal scale, I call this behavioral adaptation a vagrant fugitive strategy (Figure 1). If a subordinate competitor can accurately assess the location of its dominant competitor at any given time, it can locate temporary competition refuges (Durant 1998), and may be able to avoid direct competition. This strategy would be particularly effective if the subordinate species is more mobile than the dominant species (Hutchinson 1959), or is able to avoid detection by the dominant species at least part of the time. Ideally, studies would map locations of individuals of each species in real time, to see if the subordinate species seems to actively avoid the dominant species. While this may be realistic in species where locations can be determined remotely, for example by tracking individuals continuously with GPS collars, it is not feasible for most species that are too small for such technology. In these species, the vagrant fugitive strategy may need to be supported by piecing together evidence for a dominance relationship, documenting space use by both individuals, and observing the behavior of individuals of each species as they move through the territory of the dominant individual. The argument is strengthened by studies showing that competition for a particular resource should occur, and that it does not occur through any of the other modes of competition.

The non-breeding bird communities of the West Indies

The West Indies have a seasonal subtropical or tropical climate, with a pronounced dry season from December through April (Ewel and Whitmore 1973, Murphy et al. 1995). Dry forests are the dominant vegetation (Murphy and Lugo 1986a), although wetter forests also occur on islands with higher relief (Faaborg 1985). Dry forests are structurally simpler than wetter forests, and also have lower vegetation diversity (Murphy and Lugo 1986a). Nevertheless, despite the simpler structure, the number and diversity of resident birds is higher in dry forest than rainforest (Kepler and Kepler 1970). During the Pleistocene, dry forests were even more extensive within and among the West Indian islands and wet forests were restricted to a few areas (Pregill and Olson 1981), which may have limited the pool of species available to recolonize wet forests.

Dry forests have lower average arthropod density than wetter forests (Janzen and Schoener 1968, Allan et al. 1973, Janzen 1973, Poulin et al. 1992), and islands have lower densities than the mainland (Janzen 1973). In addition, arthropod densities decline during the dry season (Janzen 1973, Poulin et al. 1992, Parrish and Sherry 1994, Strong and Sherry 2000, Van Bael et al. 2003), with declines in large soft-bodied arthropods, such as Lepidopteran larvae, being particularly pronounced (Janzen and Schoener 1968, Janzen 1973, Johnson et al. 2006b). The low arthropod densities directly limit the populations of some insectivores (Lovette and Holmes 1995), and have sub-lethal limiting effects on others (Marra et al. 1998, Bearhop et al. 2004, Johnson et al. 2006a, Studds and Marra 2007, Wilson et al. 2011).

The West Indies have been well-studied in the context of competition among birds, with incidence functions, size distributions, and saturation curves supporting the idea that competition constrains these bird communities (Terborgh and Faaborg 1980, Faaborg 1982, Faaborg 1985). The distribution of migrants strongly reflects distance to the mainland and island size (Terborgh and Faaborg 1980, Faaborg 1985). Migrants comprise roughly one-third of the non-breeding avian community when averaged across the Greater Antilles (Wunderle and Waide 1993), although this masks considerable variation among islands. Even within the Greater Antilles, the abundance and species richness of migrants declines with distance from the mainland (Wunderle and Waide 1993). Migrants comprise less than one-sixth of the bird community in Puerto Rico, and no more than 1% of the communities in the Lesser Antilles (Terborgh and Faaborg 1980). Resident species within the same guild, particularly insectivores, are typically separated by size, a mechanism postulated to reduce niche overlap (Faaborg and Terborgh 1980, Case et al. 1983, Faaborg 1985).

Migrant species are almost exclusively wood-warblers (Parulinae; Faaborg and Terborgh 1980, Wunderle and Waide 1993), and most of these species are insectivorous in the non-breeding season. Resident warblers in the West Indies are mostly confined to specific habitats, such as mangroves (Yellow Warbler, *D. petechia*), cloud forests (Elfin-woods Warbler, *D. angelae*) and pine forests (Olive-capped Warbler, *D. pitophila*), or have restricted ranges within an island (e.g. Oriente Warbler *Teretistris fornsi*, Yellow-headed Warbler *T. fernandinae*, White-winged Warbler *Xenoligea montana*; Raffaele et al. 2003). Many studies have suggested that migrants compete with residents (e.g. Terborgh and Faaborg 1980, Faaborg 1982, Faaborg et al. 1984, Wolfe et al. 2009). Permanent-resident songbirds (non-migratory residents) are typically non-breeding during the winter (Dugger et al. 2000), possibly to avoid competition with migrant species (Emlen 1980, Faaborg 1982, Jedlicka et al. 2006). Other studies have documented negative correlations between the abundance of migrant and resident insectivores, so that the total number of insectivores remained nearly constant (Hutto 1980, Faaborg 1982, Faaborg et al. 1984), another pattern consistent with competition between residents and migrants. However, no studies have examined competition among non-breeding avian communities at the level of individuals.

What is the scope of this dissertation?

This dissertation tests the hypothesis that a migrant songbird (American Redstart) is competing for food with a Puerto Rican resident songbird (Adelaide's Warbler; *Dendroica adelaidae*) during the non-breeding season. These insectivorous species both hold territories in the dry forests of Puerto Rico in the non-breeding season, and were known to have broadly similar foraging methods and very similar body sizes (Oberle 2000). Recent studies indicate they are congeners (Lovette and Bermingham 1999, Lovette et al. 2010), such that Puerto Rico is one of very few places in the West Indies where such closely related species are sympatric (Faaborg and Terborgh 1980). Arthropods are only shared resource likely to be limiting (Lovette and Holmes 1995, Marra et al. 1998, Bearhop et al. 2004, Smith and Moore 2005, Johnson et al. 2006a, Studds and Marra 2007, Wilson et al. 2011). A previous study (Dugger et al. 2004) speculated that these species might compete. However, no study has previously tested this hypothesis.

This system seemed amenable to a study of interspecific competition for several reasons. First, competition between migrant and resident species may be more pronounced because the restrictions on character displacement in migrants limit the potential for niche displacement between winter residents (migratory species that hold winter territories) and permanent residents. Second, the sudden influx of winter-resident birds into the established community acts as an annual “natural experiment”, which may lead to shifts of foraging niches or territories in permanent-resident birds. Third, food is the only plausible resource that these species might compete for, and arthropods were likely to be a limited resource during the dry season.

Here, I test the hypothesis that these species compete for food in the Guánica Dry Forest, an UNESCO International Biosphere Reserve and Commonwealth Forest (Figure 2). However, little was known about the life history of these species in Puerto Rican dry forests, and there were large gaps in our overall understanding of the ecology of Adelaide's Warblers. Therefore, I could not form a reasonable hypothesis about which form of interspecific competition was most likely. Instead, I conducted a series of studies that would answer each of the guiding questions in Figure 1, and allow me to determine what form of competition was occurring, if it was indeed present. In addition, I established ageing and sexing criteria for Adelaide's Warblers so I could control for differences in behavior among the age classes and sexes.

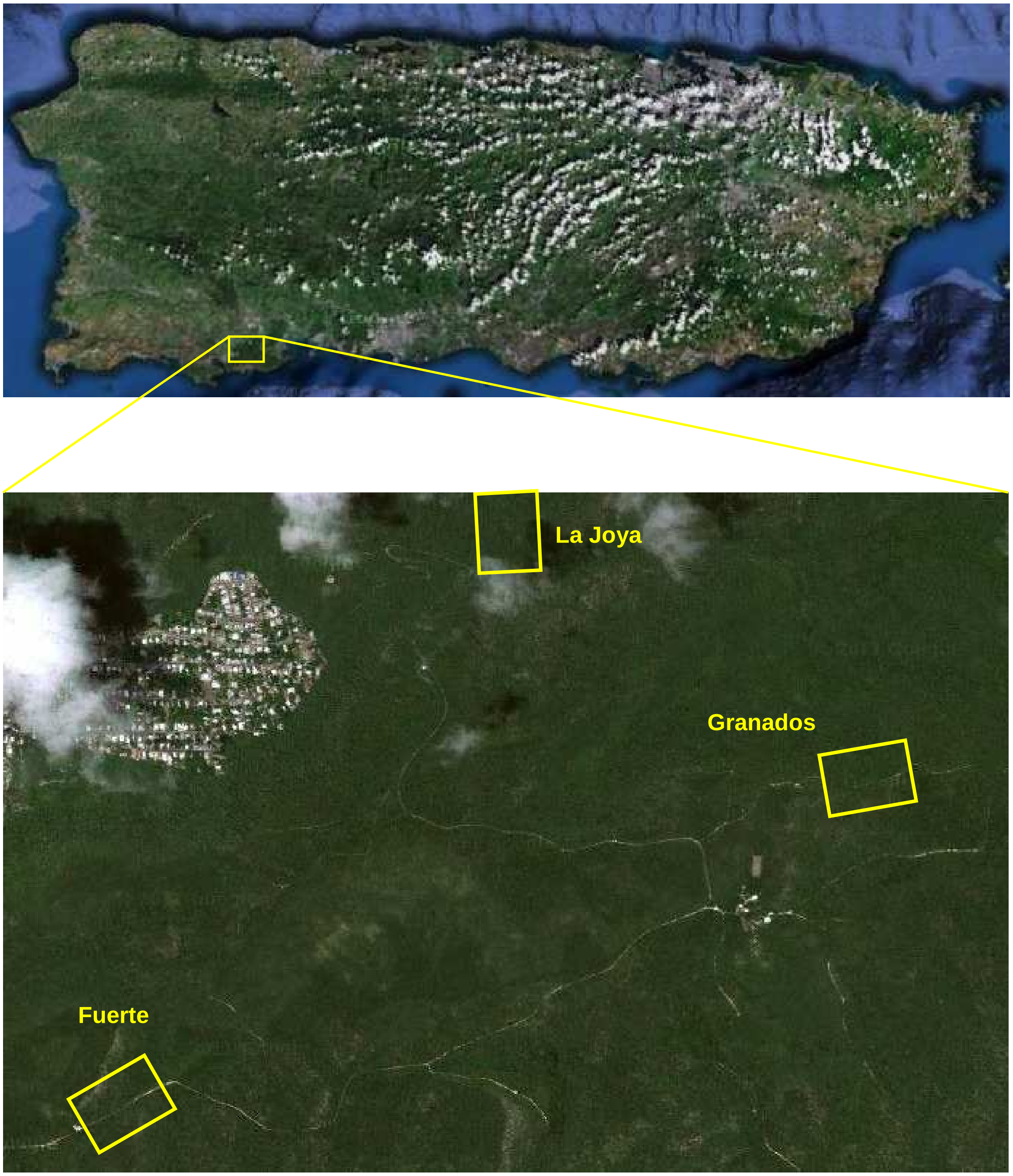

Figure 2. Location of the Guánica Dry Forest within Puerto Rico (top), and the La Joya, Fuerte and Granados study sites within the forest.

Chapter 2: Criteria for ageing and sexing Adelaide's Warbler (*Dendroica adelaidae*) in the field

Abstract

The ability to age and sex birds in the field can be important for many types of ecological studies, but reliable aging and sexing criteria are unknown for many tropical species. I have developed such criteria for Adelaide's Warbler (*Dendroica adelaidae*), an endemic resident of Puerto Rico. In addition, I also described the molt patterns of this species because plumage characteristics are reliable metrics only if the annual molt cycle is known. Adelaide's Warblers have a complex alternate molt strategy like temperate *Dendroica* species, but often suspend the prebasic molt like other tropical species. Primary covert color and the shape of the outer rectrices are very reliable indicators of age. However, no single criterion was a reliable indicator of sex. Instead, sex could be determined by jointly examining the length and thickness of the black lateral crown stripe, wing chord and the amount of white in the rectrices. These criteria, in combination with breeding-specific characters such as brood patches and cloacal protuberances, will allow both age and sex to be determined throughout most of the year.

Introduction

Knowing the age and sex of individuals can be important in elucidating ecological patterns, for example in studies of aggressive behavior (Marra et al. 1993, Marra 2000, Marra and Holmes 2001, Studds and Marra 2005), habitat segregation (Lynch et al. 1985, Morton et al. 1987, Wunderle 1995), vocalizations (Staicer 1991, 1996a, b) and cooperative breeding systems (Green et al. 2002, Cockburn et al. 2008). However, while age- and sex-specific plumage and morphometric characteristics are known for many northern temperate species (Jenni and Winkler 1994, Pyle 1997), they are unknown for most tropical species. While several morphometric characteristics may be diagnostic at any time of the year, for many species plumage characteristics are useful only if their annual molt cycle is known. In particular, the timing and extent of each molt during the annual cycle is often needed to determine when plumage characteristics are reliable indicators of particular age or sex classes.

While the molt patterns of tropical species are often similar to those of temperate species, the timing and duration of molt often differs (Foster 1975, Wolfe et al. 2009, Wolfe et al. 2010). Molt is a costly process, particularly in terms of protein and water requirements: feathers comprise approximately 25% of the total protein in an individual, and feather growth is relatively inefficient, resulting in high total protein and energy costs for a complete molt (Murphy 1996). As a result, most temperate species do not molt and reproduce at the same time (Siikamäki et al. 1994, Murphy 1996). In contrast, 20% of tropical species show overlap between molt and breeding (Foster 1975), and many tropical species show asynchronous or protracted molts (Murphy 1996, Wolfe et al.

2010). Protracted molts that partially coincide with breeding allow breeding seasons to be extended or variably-timed, so individuals can take advantage of temporally unpredictable resources (Foster 1975). Alternatively, individuals may suspend molt in order to breed (Foster 1975), or wait until breeding is complete before initiating molt (Poulin et al. 1992).

Species of dry tropical regions may be more restricted in the seasonal timing of molt than species of the wet tropics. Individuals require 50–200% more water during molt than they require for normal maintenance (Murphy 1996), and water and arthropod taxa rich in water may be in limited supply during the dry season (Janzen and Schoener 1968). Moreover, dry forests have lower arthropod densities than wetter forests (Janzen and Schoener 1968, Allan et al. 1973, Janzen 1973, Poulin et al. 1992), and arthropod densities (particularly large soft-bodied taxa) decline further during the dry season (Janzen and Schoener 1968, Janzen 1973, Poulin et al. 1992, Parrish and Sherry 1994, Strong and Sherry 2000, Van Bael et al. 2003, Johnson et al. 2006b, Studds and Marra 2007). Thus, it may also be more difficult to meet the protein requirements of molt during the dry season. Indeed, in semi-arid and arid Neotropical habitats, prebasic molt is mostly limited to August-October (Poulin et al. 1992).

Adelaide’s Warblers (Adelaide’s; *Dendroica adelaidae*) are endemic to Puerto Rico and Vieques Island, and reach their highest densities in dry forest and scrub (Oberle 2000, Toms 2010). As with many tropical species, very little is known about molt patterns and ageing and sexing criteria in this species (but see Curson et al. 1994). Most other *Dendroica* species are found in temperate regions of North America. *Dendroica* *spp.* usually have a complex alternate molt strategy (Pyle 1997, Howell et al. 2003), with the prebasic molt occurring on the breeding grounds before fall migration and a protracted prealternate molt occurring throughout the winter (Pyle 1997). In most species, age and sex classes can be determined; the shape, color and structural quality of the outer rectrices, primary coverts, back and upper- and under-tail coverts, and the amount of white in the outer rectrices are commonly useful in distinguishing among age and sex classes in this genus (Pyle 1997). Here, I establish some ageing and sexing criteria for Adelaide's, and describe molt patterns to determine when they can be used. I hypothesized that the molt patterns of Adelaide's would be similar to those of other *Dendroica* species, but the timing of molt might differ from temperate species due to the timing of the wet-dry cycle and the breeding season.

Methods

Adelaide's (n = 197) were captured at approximately monthly intervals from October 2008 through September 2009 (excluding August) in the Guánica Dry Forest, southwest Puerto Rico (Figure 2). Sixteen to 24 mist nets (each 12 m long) were placed along trails in upland forest, and run continuously from dawn to dusk for two to four days. Additional individuals were captured with targeted netting (usually passive) along trails and in the forest at irregular intervals from February 2007 through January 2010 as part of another study. After gathering the data described below, a single central rectrix was pulled and each individual was banded and released. Rectrices were stored in paper envelopes at room temperature.

In order to increase the number of samples for months with few captures, and to increase the geographical coverage of the study, museum specimens were also measured (n = 81). Prepared specimens were obtained from the Louisiana State University Museum of Natural Science (specimen numbers 23198, 52884–885, 146246–254, 150281–283, 150285–294) and the Smithsonian Institution (specimen numbers 172383, 172412–414, 231586–590, 231592–599, 232691–694, 232696–699, 232701–702, 238255–259, 238369, 238888–896, 353438, 355791–800, 355802–803, 576778). Sex identification on specimen tags was not used unless the tag indicated that ovaries or testes were found during specimen preparation (n = 27); age of museum specimens was determined following the same criteria used for field samples (see below).

Plumage characteristics and morphometrics

I measured wing chord, tail length, tarsus and bill (culmen length from the nares, bill depth and bill width at the nares; Winker 1998, Arendt et al. 2004). I also described the color and quality of the greater and primary wing coverts, the length of the yellow supercilium and black lateral crown stripe, the shape and quality of the outer rectrices, and the amount of white in each rectrix (Table 1).

I also scored each flight feather (remige or rectrix) as old, new or growing. Growing feathers were scored following EURING standards (EURING 2010): 1, pin feather; 2, feather sheath broken but less than one-third of full length; 3, one-third to two-thirds grown; and 4, feather greater than two-thirds grown, but with some sheath

Table 1. Plumage characteristics examined as potential measures discriminating among age and sex classes of Adelaide's Warblers.

Characteristic	**Quantitative or qualitative scores possible**
Black lateral crown stripe width	Estimated in mm, to the nearest 0.5 mm
Black lateral crown stripe length	Estimated relative to position of the eye (see Figure 4)
Yellow supercilium length	Same as for black lateral crown stripe length
Outer rectrix shape	Tapered (pointed) versus obtuse (rounded; see Figure 3)
Primary covert quality and color	Brownish-gray (formative, of lower quality, more translucent with less dense barbs) versus blackish-grey (basic)
Amount of white in tail	Scored following Pyle (1997; p. 458)
Amount of white in R4	Scored following Curson et al. (1994)

remaining. In addition, I separately scored primary coverts, greater coverts, alula, and body feathers on the crown, back, throat and belly as whole feather groups using the same criteria.

Determining the sex of field captures

I extracted DNA from rectrices in the lab using InstaGene (BioRad; Eggert et al. 2005), and then used two independent methods to determine sex: P2/P8 to amplify part of the CHD1 gene (Griffiths et al. 1998), and F2/R1 to amplify part of the ATP5A1 gene

(Bantock et al. 2008). I used two independent methods to determine sex because any single test can produce misidentification errors (Dawson et al. 2001, Bermudez-Humaran et al. 2002, Jarvi and Farias 2006, Robertson and Gemmell 2006, Casey et al. 2009, Santamaria et al. 2010), and I did not have access to known-sex individuals to estimate the rates of misidentification in this species.

These gene regions were amplified using 15 µl PCR reactions and a Mastercycle ep gradient S thermocycler (Eppendorf). The PCR reaction mix consisted of 1 X AmpliTaq Gold DNA polymerase buffer (Applied Biosystems, Inc.), 0.2 mM each dNTP, 0.5 mM forward and reverse primers, 2.5 mM $MgCl_2$, 0.5 mg BSA, 0.5 u AmpliTaq Gold polymerase, and 8.0 µl of genomic DNA extract. After a 10 min preincubation at 95°C, I ran 45 cycles of 95°C denaturing for 1 min, annealing at primer-specific temperatures for 1 min (P2/P8 48.9°C, F2/R1 52°C), and primer extension at 72°C for 1 min, then followed with a final extension cycle of 10 min at 72°C. I used 4% agarose gels in TBE buffer to separate bands and determine sex.

Identifying molt patterns

Flight feather scores were tabulated as described by Rohwer (2008), except that I also considered molt and wear limits between old and new feathers as potentially useful in determining molt patterns. Only symmetric or near-symmetric (i.e. with the molt/wear limit shifted by a single feather) molt patterns were included. Field observations supported previous studies stating that the primary coverts were retained from juvenile plumage through the first alternate plumage (Curson et al. 1994), and these were used along with other criteria (see Pyle 1997 for descriptions of useful criteria) to initially classify individuals as either hatch-year (HY) / (SY) second-year birds, or after-hatch-year (AHY) / (ASY) after-second-year birds. This allowed me to differentiate molts and plumages in the first molt cycle from plumages in subsequent molt cycles. All molt cycles were described using the terminology of Howell et al. (2003). Because Adelaide's Warbler breeding cycles typically do not cross January 1st (Toms 2010), I chose to use the standard ageing system for temperate species (Pyle 1997), rather than a calendar-independent ageing system (Wolfe et al. 2010). Once molt patterns were described, the age of all individuals was reassessed using this new information.

Identifying useful ageing and sexing criteria

I used discriminant analysis to identify characteristics that were useful in distinguishing between different age (individuals in first plumage cycle versus those in their second or subsequent plumage cycle) and sex classes of Adelaide's Warblers (Table 1). I coded binary variables as 0/1 indicator variables, the most suitable coding for use in discriminant analysis (Huberty 1994, p. 151). I applied Fisher-Lancaster analysis (Huberty 1994, p. 153) to all categorical variables, a procedure that finds numeric values for each level of the categorical variable such that the discriminatory power of that variable is maximized. All other numeric variables were standardized to have zero mean and unit variance, which eliminates potential selection bias due to differences in scaling (Huberty 1994). I used linear discriminant functions because model errors approximated a normal distribution. Models were fit using the mda package (ver. 0.4-2; Leisch et al. 2011) in R (ver. 2.9.1; R Development Core Team 2009).

The variables that appeared most suitable for discriminant analysis were initially determined using linear regressions with age or sex as the response variable. Because age or sex can sometimes be determined in the field (e.g. using juvenile plumage characteristics for age, or cloacal protuberances or brood patches for sex), I conducted simple discriminant analysis separately for age and sex, as well as a joint analysis of the four age-sex classes. Some variables had low weightings in the initial discriminant analyses, and were eliminated when it was determined that including them in the model did not improve error rates (the proportion of individuals that were misclassified using the fitted discriminant function). Final discriminant functions were determined using untransformed variables, for easier use in the field.

Results

Molt patterns

Adelaide's Warblers have a complex alternate molt strategy (Howell et al. 2003), as seen in most *Dendroica* species (Pyle 1997): in the first molt cycle, they initiate a complete prejuvenal molt in the nest, a partial preformative molt around the time of fledging, and go through the partial first prealternate molt in the non-breeding season; in the second and subsequent molt cycles, they initiate a complete prebasic molt following breeding, and go through a partial prealternate molt prior to the next breeding season.

Prejuvenal Molt

Breeding in Adelaide's Warblers is at least partially dependent on rainfall, so nesting can occur any time between January (Staicer 1996b, Toms 2010) and July (Staicer 1991, Nakamura 1995). However, breeding is more commonly observed from March to June (Bowdish 1903, Wetmore 1916, Spaulding 1937). Fledglings are most commonly seen from mid-June to early July (Bowdish 1903, Wetmore 1916), but have been seen as early as late March (Toms 2010). Based on the known breeding season, nestlings and fledglings are also to be expected both earlier and later in the year than indicated by these reports. Thus, the juvenile plumage, while present only for a relatively short period of time, can be expected any time from January through August.

There is little information on the plumage of Adelaide's Warblers in the nest. However, one report indicates that the prejuvenal molt starts before six days of age (Spaulding 1937). The molt is initiated with the spinal tract and the anterior portion of the ventral tract (Spaulding 1937), and pin feathers were apparent in these areas before any juvenile pin feathers were visible on the wings. The feathers of the spinal tract are black, tipped with white; the feathers of the anterior ventral tract were described by Spaulding (1937) as yellow.

The juvenile plumage is retained until the chicks fledge (at approximately 10 days of age; A. Wiewel, pers. comm.). The feathers of the back and upper portions of the head are grey with brownish tips, and the head has a cream-colored supercilium and subocular arc (described as pale primrose yellow or yellowish white by Ridgway 1902). The breast and sides are cream with brownish spots (or pale primrose yellow or yellowish white spotted with grayish dusky; Ridgway 1902). Lower ventral feathers are cream or white (or yellowish white; Ridgway 1902). Rectrices and remiges are brownish-black with brownish or olive-grey edges, and wing bars are narrow and buffy cream (Ridgway 1902, Curson et al. 1994).

Preformative Molt

The preformative molt is partial. The exact timing relative to fledging is not well documented, but it appears to initiate around the time of fledging. Based on fledging dates (see Prejuvenal Molt), the preformative molt could be expected any time from February through September. The juvenal feathers on the breast are quickly replaced by light yellow feathers, even before the flight feathers from the prejuvenal molt have completed growth, and the abdominal feathers are replaced with white. The back feathers are replaced by grey feathers without brownish tips, and the feathers on the mid and lower back are washed with yellowish-olive in some individuals. Body feathers on the head are also replaced, so that the supercilium becomes longer and sometimes partially yellow, and a second, superior, black lateral crown stripe of varying width, length and completeness is acquired. The subocular arc is replaced with white, yellow, or a mixture of white and yellow feathers. All wing coverts except the primary coverts are replaced, so the wing bars are larger and white. However, the alula and flight feathers are retained.

First Prealternate Molt

The first prealternate molt typically includes the body feathers of the breast and abdomen, but does not include any flight feathers (i.e. it is partial). The alula is also replaced in some individuals (34%). Molt was observed from February through May, but may occur at lower rates in December and January, as the throat and breast feathers from 50% of individuals (including both males and females) are comparatively fresh in the spring.

Second and Subsequent Prebasic Molts

The prebasic molt is complete. Most individuals molt in August and September, but some individuals may start as early as May or continue through November. Primaries are typically replaced distally, from P1 to P9. The tertials are replaced proximally (from S7 to S9), as are the secondaries (from S1 to S6). Rectrices are typically molted from R1 to R6. However, one individual was observed with R6 at a later stage of molt than R5 (symmetrically), suggesting that R6 may occasionally be replaced before R5. Wing coverts seem to be replaced before body feathers.

Molt limits in SY birds and feather-wear limits in ASY birds suggest that remex molt is commonly suspended during the prebasic molt. Six individuals showed molt/wear limits in the primaries with the newer feathers on the distal side of the molt/wear limit (with the molt/wear limit between P3 and P7); additionally, one individual showed a molt/wear limit in the secondaries (between S3 and S4), with the newer feathers proximal to the limit. These molt/wear limits were symmetrical, or nearly so (i.e. with the molt/wear limit shifted by a single feather), and were seen from February through May. Remex molt was almost entirely limited to August and September; all other (rare) instances involved a single feather and were likely adventitious molts. Therefore, these molt/wear limits suggest that molt stopped at some stage, and restarted at the next feather at a later date, producing markedly different feather wear on either side of the molt/wear limit. A single individual suspended its prebasic molt during August, where P1 through P6 were worn (on both wings), but P7 through P9 were molting distally (it was also molting S1 through S3 proximately at this time, and had nearly completed or completed molting the other feather groups). This individual was likely resuming molt of the outer primaries suspended since the previous prebasic molt (i.e. from the previous August to November) before initiating the new prebasic molt from P1.

Molt limits in SY birds and feather wear limits in ASY birds are also commonly seen with the feather ages reversed from above (i.e. newer feathers on the proximal side of a molt/wear limit in the primaries, and on the distal side of a molt/wear limit in the secondaries). These limits were seen between P6 and P7 in November (one individual), and S3 to S6 from November through April (five individuals). Although these molt/wear limits are consistent with an arrested molt pattern, given the evidence for restarting of a suspended molt above, they more likely reflect suspension of molt.

Rectrix molt might also be suspended in a few individuals. During April and May, three individuals exhibited molt/wear limits with replacement feathers distal to retained inner feathers (two limits at R1 to R2, one at R4 to R5). This pattern likely results from the completion of a suspended molt, rather than partial replacement of rectrices during a prealternate molt; it is highly unlikely that the rectrices would be replaced from R6 to R1 during a prealternate molt and from R1 to R6 during prebasic molts.

Second and Subsequent Prealternate Molts

The second and subsequent prealternate molts (i.e. prealternate molts in third-year or older birds) are partial, as they do not appear to include any flight feathers. However, prebasic molts that were suspended may restart simultaneously with this prealternate molt in some individuals. Molt is seen from December through May. As in the first prealternate molt, the breast and abdominal feathers are replaced.

Ageing and sexing criteria

Age class was very strongly predicted (error rate 0.07, n = 88) using the combination of primary covert color (brownish-gray for individuals in the first plumage cycle, blackish-gray for individuals in their second or subsequent plumage cycle) and shape of the outermost rectrix (Figure 3). These characteristics were almost always reliable indicators of age.

Sex was strongly predicted with two discriminant functions: the first (error rate 0.14, n = 126) uses the length and width of the black lateral crown stripe (mean width 1.5 mm in males, 0.8 mm in females; mean length back of eye in males, just past mid-eye in females; Figure 4) and the unflattened wing chord (mean 52 mm in males, 48 mm in

Figure 3. Shape of juvenile (tapered or pointed, left) and adult (blunt or rounded, right) rectrices. Note that the amount of white in the rectrices is very similar in these two males, despite the difference in age.

females), whereas the second (error rate 0.12, n = 113) used the length of the black lateral crown stripe, unflattened wing chord and the amount of white in the rectrices (averaging more white in males). Both discriminant functions (Figure 5 and Figure 6) can be used to determine sex. However, although these variables were reliable in combination, there is considerable overlap between sexes for all these measurements when viewed individually.

When combined, age and sex classes were reliably distinguished (error rate 0.15, n = 88) using a combination of the primary covert color, shape of outermost rectrix, unflattened wing chord and width of the black lateral crown stripe. This model was very similar to a simple combination of the separate discriminant functions for age and sex, and provided no additional power to separate age and sex classes.

Figure 4. Examples of the black lateral crown stripe length in first-year females (top row), adult females (second row), first-year males (third row) and adult males (fourth row). Males have longer and thicker black lateral crown stripes.

Score black lateral crown stripe (LCS) length as follows:

Each mm in front of eye, subtract 0.25 from 0 (the score for the front of eye)

Front of eye = 0

Mid-eye = 0.5

Back of eye = 1

Each mm past the back of eye, add 0.25 to 1 (the score for back of eye)

Calculate the discriminant function:

0.38*(LCS width in mm) + 0.90*(LCS length score) + 0.50*(wing chord in mm) – 26.70

Males have values greater than -0.70 (median 0.63), whereas females have values less than -0.73 (median -1.52). Values near -0.70 should be used to assign sex only with caution and in conjunction with other criteria.

Figure 5. The first discriminant function used to determine the sex of Adelaide's Warblers.

Score the white in the tail from 1 to 6 following scores A to F in Pyle (1997; p. 458)

See Figure 5 for LCS length score.

Calculate the discriminant function:

1.24*(LCS length score) + 0.50*(wing chord in mm) + 0.21*(Pyle score) – 27.01

Males have values greater than -0.78 (median 0.52), whereas females have values less than -0.84 (median -1.53). Values from -0.78 to -0.84 should not be used to assign sex, and values near these limits should be used to assign sex only with caution and in conjunction with other criteria.

Figure 6. The second discriminant function used to determine the sex of Adelaide's Warblers.

Discussion

Overall, the molt strategy of Adelaide's Warblers followed that of other *Dendroica* species (Pyle 1997), as hypothesized; they had a complex alternate molt strategy (Howell et al. 2003), with a complete prebasic molt in the fall wet season, and a prealternate molt during the dry season. Prealternate molts are rare in tropical species (Wolfe et al. 2009), which suggests that phylogeny is more important than environment in determining basic patterns of molt. The *Dendroica* genus is predominantly found in temperate regions of North America, and Adelaide’s Warbler and other West Indian *Dendroica* species almost certainly diverged from temperate species (Bond 1963). Thus it is not surprising that Adelaide’s Warblers have a molt pattern typical of temperate species.

In addition, the timing of these molts is very similar to temperate *Dendroica*. In contrast, prebasic molts occur throughout the year in many tropical species (Wolfe et al. 2009). During the year of my study, the timing of the prealternate molt (December through May) overlapped the bulk of the breeding season (February through July). However, no molting individuals were caught with cloacal protuberances or brood patches, suggesting that the overlap may only occur in the population, rather than in individuals. The breeding season typically does not start until March, when the rainy season begins. However, in 2009 breeding started earlier than usual due to early rains. Thus, the molt strategy of Adelaide’s Warblers also shows some similarities with those of other tropical species that suspend, arrest or protract molt when a flush of temporally unpredictable resources becomes available for breeding (Foster 1975).

Previous studies suggested that the timing of molt in tropical resident species was constrained by competition with migrants, as most species molted flight feathers when migrants were absent (Wolfe et al. 2009). However, this did not hold in all species or ecosystems (Ward 1969). In my system, the prebasic molt of Adelaide’s Warblers occurs in the presence of migrants, which begin to appear in or before September. However, September and October are relatively wet in Guánica, so that competition for arthropods is unlikely to limit the food available for an individual. Thus, my study does not contradict Wolfe et al.'s hypothesis (2009).

Adelaide's Warblers often suspend the prebasic molt, as indicated by molt and wear limits in flight feathers. One individual even appeared to suspend molt for almost a full year, resuming the suspended remex molt at the beginning of the next prebasic molt. Suspended prebasic molts may also restart simultaneously with the following prealternate molt. In Guánica, the dry season typically begins in late November or early December, and the availability of water and arthropods decreases through to March or April (Chapter 3). Competition with winter resident warblers may also limit the food available for individuals, exacerbating this effect. Winter resident warblers and Adelaide's Warblers show declines in body condition during this time (Chapter 3), indicating that food is limiting. Molt is known to negatively affect body condition in other species (Ward 1969, Gosler 1991), and individuals may take a long time to recover condition when food is scarce (Ward 1969). Because flight feathers are much more costly to molt than body feathers, Adelaide's Warblers may molt them only during the wet season when resources are not limiting, while still renewing some of their "cheaper" body feathers during the dry season in a protracted prealternate molt.

Individuals in their first molt cycle can be reliably distinguished from individuals in their second or greater molt cycle using primary covert color and shape of the outer rectrices. These criteria are robust until the second prebasic molt begins in May. After May, any individual showing adult primary coverts (blackish-grey) and rectrices (obtuse) should be aged as AHY, unless molt or wear limits are present where both groups of feathers can be clearly identified as adult. From May through November, feather wear of individuals with juvenile primary coverts (brownish-grey) or rectrices (tapered) should be examined carefully to determine whether it should be classified as HY or SY; the juvenile feathers of SY individuals should show more wear than those of HY individuals.

In some cases, males may be distinguished from females by their thicker and longer black lateral crown stripe, longer wings and a larger amount of white in the rectrices. However, there is considerable overlap between sexes for these and other morphometric variables (Arendt et al. 2004, Toms 2010, this study), and none are reliably diagnostic on their own. Knowing the age of an individual may be useful in determining the sex, as remiges are usually shorter in juveniles than in adults (Pyle 1997). However, these sexing criteria did not depend on age, and the discriminant function can be used to distinguish between sexes at any time of year. Male Adelaide’s Warblers do not develop a brood patch (pers. obs.), so brood patches and cloacal protuberances are also useful criteria during the breeding season. Curson et al. (1994) suggested that the amount of white in R4 (the fourth rectrix on either side of the uropygial gland) can be used to distinguish among age and sex classes. However, I found broad overlap in the amount of white in the outer rectrices among sexes, suggesting that it is not a reliable character. Further study on this point is warranted, because tail patterns are useful in most *Dendroica* species (Pyle 1997).

The ageing and sexing criteria determined here should prove useful in future ecological studies of this species, as genetic methods will no longer be required to determine the sex of non-breeding individuals. Molt patterns indicate that these criteria, in combination with breeding-specific characters such as brood patches and cloacal protuberances, will allow both age and sex to be determined throughout most of the year. Future studies may find other plumage characteristics that are useful, but it appears unlikely that a single character will be sufficient to determine sex in this species.

Chapter 3: The dry-season phenology of a Caribbean dry forest: implications for the availability of arthropod prey to insectivorous birds.

Abstract

The phenology of a resource affects its availability to consumers and thus determines whether that resource may be limiting a species' population growth. In tropical ecosystems, rainfall strongly influences the phenology of many ecosystem processes. Here, I measure the phenology of arthropods during two winters in a dry forest of southwest Puerto Rico, and determine whether arthropods may be a limiting resource for insectivorous birds. In the drier of the two years, leaf fall was significant in all vegetation layers, significant declines were seen in arthropod biomass, body condition of Adelaide's Warblers (*Dendroica adelaidae*) declined significantly, and body condition of American Redstarts (*Setophaga ruticilla*) declined non-significantly. In contrast, during the wetter of the two years, leaf fall was largely restricted to the shrub layer and arthropod biomass and body condition of both species remained fairly constant. Although no differences were seen in over-winter survival of the insectivores, sub-lethal carryover effects likely affect the reproductive success of both species. This study indicates that arthropods are a limiting resource in dry winters.

Introduction

Variation in the abundance and availability of necessary resources among habitat types, seasons and regions has long been of interest to animal ecologists, as this variation is thought to strongly affect many ecological processes such as reproductive success (Kemp and Keith 1970, Smith and Moore 2005, Newton 2006, Zanette et al. 2006, Brouwer et al. 2009, Karell et al. 2009, Reudink et al. 2009, Veen et al. 2010), survival rates (Baillie and Peach 1992, Johnson et al. 2006a, Newton 2006, Calvert et al. 2009, Karell et al. 2009), population growth rates (Baillie and Peach 1992, Sibly and Hone 2002, Sherry et al. 2005, Newton 2006, Calvert et al. 2009), habitat selection (Wunderle 1995, Johnson and Sherry 2001) and intraspecific and interspecific competition (MacArthur 1958, Marra 2000, Strong and Sherry 2000, Marra and Holmes 2001, Studds and Marra 2005, Newton 2006, Veen et al. 2010). Spatiotemporal variation in resource availability can result from differences in environmental conditions (bottom-up processes), differences in predation on or competition for the resource (top-down processes) or, more likely, a combination of both bottom-up and top-down processes (Sinclair and Krebs 2002). The relative strength of bottom-up processes is likely to be weaker at higher trophic levels, as the effects of short-term environmental changes are buffered through the lower trophic levels (Both et al. 2009). However, environmental changes of longer duration, such as seasonal effects, may lead to cascading effects through several trophic levels. Such changes occurring on an annual basis are termed phenological changes.

The phenology of a given resource through an annual cycle determines its availability to consumers, and thus the potential for competition to occur within and among species. Competition will not occur between two species unless they use the same resources, and those resources are limiting in some way. However, in many ecosystems we do not know how resources are distributed in time or space and whether they are potentially limiting population growth of consumers. Although direct mortality is one source of population limitation, resources can be limiting even if they produce only sub-lethal effects. For example, the quality of habitat used by an individual in the non-breeding season may affect the risk of mortality during migration (Bearhop et al. 2004), time of arrival at the breeding site (Marra et al. 1998), quality of the breeding territory obtained (Smith and Moore 2005), and ultimately reproductive success (Smith and Moore 2005, Reudink et al. 2009). Even short periods of resource limitation can have significant effects on individuals and populations (Waide 1981, Schoener 1983, Wallace 1998, Studds and Marra 2005, Jedlicka et al. 2006, Studds and Marra 2007, Wilson et al. 2011).

Rainfall and temperature patterns are often important drivers of resource phenology. In temperate regions, temperature is often the most important determinant. Cold winter temperatures induce leaf fall in deciduous plant species, and few arthropods are subsequently available (Wolda 1988). As a result, many herbivores and insectivores migrate to warmer climates where these resources are available. In tropical regions, where temperatures are relatively stable throughout the year, rainfall patterns are the more important determinant of ecosystem phenology. In the West Indies, rainfall exceeds evapotranspiration only for August through October, with a pronounced dry season from December through April (Ewel and Whitmore 1973, Murphy et al. 1995). During this dry season, deciduous foliage is lost (Murphy et al. 1995) and arthropod densities are reduced (Janzen 1973, Poulin et al. 1992, Parrish and Sherry 1994, Strong and Sherry 2000, Van Bael et al. 2003, Studds and Marra 2007). Declines in large soft-bodied arthropods, such as Lepidopteran larvae, are particularly pronounced (Janzen and Schoener 1968, Janzen 1973, Johnson et al. 2006b). Thus, insectivorous predators may find it increasingly difficult to obtain adequate food as the dry season progresses.

Other evidence suggests that West Indian insectivores might actually be limited by arthropod availability during the dry season. Islands typically have lower arthropod densities than the mainland (Janzen 1973), and the dry forests typical of the West Indies have lower average arthropod density than wetter forests (Janzen and Schoener 1968, Allan et al. 1973, Janzen 1973, Poulin et al. 1992). Moreover, the influx of winter resident birds, which are largely insectivorous, into the community just before the onset of the dry season greatly increases the number of individuals competing for arthropods during this time of relative scarcity (Terborgh and Faaborg 1980, Wunderle and Waide 1993). Strong intraspecific competition for arthropod resources is known to occur in some of these winter residents (Marra 2000, Marra and Holmes 2001, Studds and Marra 2005), and is thought to limit their populations (Lovette and Holmes 1995, Marra et al. 1998, Bearhop et al. 2004, Johnson et al. 2006a, Reudink et al. 2009, Wilson et al. 2011). However, we do not know if this resource shortage also induces competition among permanent resident species, or between permanent resident and winter resident species.

Here, I measure the phenological pattern of the arthropod community, and associated measures of vegetation, rainfall and body condition of insectivores during two dry seasons. In particular, I was interested in determining whether arthropod biomass might be limiting for insectivores, as part of a larger study of competition between Adelaide's Warbler (Adelaide's; *Dendroica adelaidae*) and American Redstart (Redstart; *Setophaga ruticilla*).

Methods

This study took place in the upland forest of the Guánica Dry Forest in southwest Puerto Rico (Figure 2), an International Biosphere Reserve recognized for the quality of its dry forest. The forest is dominated by semi-deciduous vegetation, typically less than 5 m in height, with occasional larger emergent trees in favorable microsites. In most areas the upland forest has thin soils underlain with limestone, and water run-off is common during large rainfall events (Lugo et al. 1978).

Arthropod sampling and vegetation surveys were conducted monthly during the dry seasons (November to March) of 2007–2009, excluding February 2008. In addition, total rainfall for these months was obtained from a weather station within the Biosphere Reserve (M. Canals Mora, unpubl. data). Arthropod and vegetation sampling were conducted along eight netlines (each approximately 200 m long) used in a long-term study of bird populations at Guánica (Faaborg et al. 2004). Sampling was not conducted along the La Hoya netline of Faaborg et al. (2004) due to persistent vandalism.

Arthropod and vegetation sampling was conducted at 0, 100 and 200 m along these netlines.

Vegetation plots were located 10 m perpendicularly into the forest from the edge of a trail, with the direction from the trail selected randomly. Plots were 5 m in diameter, and flagged to ensure consistent measurements from month to month. Within each plot, the percent cover of each structural layer (litter, shrubs, saplings and canopy layer) was estimated. The change in each of these response variables was assessed separately over each winter using mixed effect models, with month as a fixed effect and location as a random effect.

Arthropods were sampled using aerial traps analogous to standard window flight-interception traps (modified from Carrel 2002). These traps consisted of two 1-gallon water jugs, each cut to form a window trap, suspended upside-down from a wooden plank (Figure 7). Each trap was filled with soapy water, and suspended in the lower canopy of a tree using ropes. Traps were run for four consecutive days per month; arthropods were stored in isopropyl alcohol and later identified and measured in lab.

Although Redstarts and Adelaide's can be considered generalist insectivores, previous studies have shown that Hemiptera, Coleoptera, Lepidoptera, Hymenoptera and Diptera make up the majority of their diets (from 83% to 100%; Wetmore 1916, Lefebvre et al. 1992, Sherry and Holmes 1997, Toms 2010). Studies of related species suggest that arthropods smaller than 3 mm in length likely comprise a very small proportion of their diets (Raley and Anderson 1990, Hagar et al. 2007). Therefore, only arthropods 3 mm or larger in the five orders listed above were included in estimates of arthropod biomass.

Figure 7. Aerial traps used for arthropod sampling. Each gallon container has two windows, aligned so that one window faces each direction. Traps are suspended in the lower canopy of trees using a rope system.

Since Lepidopteran adults and larvae differ markedly in behavior and seasonal availability, I recorded them separately (Cooper et al. 1990). Similarly, non-flying ants (Formicidae) were separated from other Hymenoptera because they markedly differ in behavior, and may be of lower energetic value to birds (Zach and Falls 1978, Bell 1990).

Biomass of arthropods is a more relevant measure of food availability than abundance of different groups, because small and large arthropods provide vastly different amounts of energy to predators (Saint-Germain et al. 2007). Published length-weight regressions can be used to estimate the biomass of individual arthropods, and the biomass of all individuals within each group of interest can be summed to give an estimate of total biomass (Saint-Germain et al. 2007). Length-weight regressions are available from several study sites (Table 2), so I used a bivariate meta-analysis (van Houwelingen et al. 2002, Paul et al. 2006) to estimate a single best-fit regression equation for each order (or group within order, as appropriate; Table 2). This meta-analysis weights the contribution of each study to the overall equation inversely to its precision and sample size (i.e. studies with large sample size and high precision receive more weight), and accounts for any covariance present between the intercept and slope regression coefficients. The total biomass for each group, as well as total arthropod biomass, was determined at each location for each sampling session. The change in biomass over the winter was assessed for each group using analysis of variance models with month as a fixed effect. Larval Lepidoptera were caught only rarely, possibly because the aerial trap was not effective at sampling this group. Therefore, they were not analyzed separately, but were included in the calculations of total biomass. The traps appeared to be effective for all other arthropod groups used in this study. In addition, two samples captured mating swarms of an unidentified beetle species. As the Coleopteran biomass in these samples was 700% and 1370% greater than the next largest sample biomass of Coleopterans, they were excluded from statistical analyses.

Morphometrics of birds were available for the same periods through three netting projects: a long-term banding study (Faaborg et al. 2004), a year-long banding study (Toms et al. unpubl.), and this study. Most netting was passive, and occurred along trails. However, a few Adelaide’s Warblers and American Redstarts were caught using targeted

Table 2. Length-weight regression equations used in a meta-analysis to estimate a single best equation for each group of arthropods (in bold font). All equations are of the form $\ln W = \ln \beta_0 + \ln \beta_1 L$, where W is dry weight in mg and L is length in mm. The precision of regression coefficients in Beaver and Baldwin (1975) and Schoener (1980) was reported with 95% confidence intervals; these were converted to standard errors under the assumption that a standard linear regression was used to fit the model (i.e. the model assumed normal errors), so that a 95% confidence interval equals ± 1.96·SE.

Group	**n**	**β_0**	**SE(β_0)**	**β_1**	**SE(β_1)**	**Ecosystem**	**Reference**
Hemiptera[1]	12	0.048	0.449	2.354	0.247	Temperate mesic forest	Hódar (1996)
	21	0.034	0.530	2.688	0.253	Temperate mesic forest	Hódar (1996)
	23	0.042	0.294	2.311	0.219	Tropical forests	Johnson and Strong (2000)
	52	0.086	0.143	1.876	0.119	Tropical forests	Johnson and Strong (2000)
	93	0.039	0.062	2.566	0.045	Temperate shrub-steppe	Rogers et al. (1977)
	70	0.008	0.313	3.075	0.147	Temperate mixed forest	Sample et al. (1993)
	106	0.059	0.273	2.225	0.158	Temperate mixed forest	Sample et al. (1993)

Group	n	β_0	SE(β_0)	β_1	SE(β_1)	Ecosystem	Reference
Hemiptera cont.	14	0.006	0.090	3.130	0.372	Temperate mixed forest	Schoener (1980)
	42	0.035	0.224	2.480	0.286	Tropical dry forest	Schoener (1980)
	16	0.027	0.214	2.280	0.388	Tropical rainforest	Schoener (1980)
	36	0.024	0.112	2.310	0.235	Temperate mixed forest	Schoener (1980)
	84	0.023	0.065	2.650	0.138	Tropical dry forest	Schoener (1980)
	62	0.030	0.067	2.230	0.184	Tropical rainforest	Schoener (1980)
		0.030	**0.031**	**2.458**	**0.097**		
Coleoptera	147	0.112	0.088	3.148	0.141	Temperate mesic forest	Beaver and Baldwin (1975)
	156	0.041	0.195	2.640	0.080	Temperate mesic forest	Hódar (1996)
	51	0.057	0.226	2.166	0.158	Tropical forests	Johnson and Strong (2000)
	151	0.031	0.105	2.790	0.050	Temperate shrub-steppe	Rogers et al. (1977)
	330	0.039	0.175	2.492	0.081	Temperate mixed forest	Sample et al. (1993)
	47	0.082	0.082	1.990	0.138	Temperate mixed forest	Schoener (1980)
	150	0.117	0.052	2.110	0.087	Tropical dry forest	Schoener (1980)

Group	**n**	**β_0**	**SE(β_0)**	**β_1**	**SE(β_1)**	**Ecosystem**	**Reference**
Coleoptera cont.	171	0.126	0.048	1.910	0.097	Tropical rainforest	Schoener (1980)
		0.083	**0.030**	**2.408**	**0.141**		
Lepidoptera (Larva)	16	0.011	0.534	2.571	0.180	Temperate mesic forest	Hódar (1996)
	28	0.006	0.319	2.809	0.146	Temperate shrub-steppe	Rogers et al. (1977)
	196	0.554	0.257	2.959	0.085	Temperate mixed forest	Sample et al. (1993)
		0.235	**0.224**	**2.829**	**0.091**		
Lepidoptera (Adult)	124	0.001	0.053	2.661	0.082	Temperate mesic forest	Beaver and Baldwin (1975)
	20	0.010	0.455	2.969	0.170	Temperate mesic forest	Hódar (1996)
	22	0.018	0.133	2.903	0.080	Temperate shrub-steppe	Rogers et al. (1977)
	384	0.006	0.157	3.122	0.064	Temperate mixed forest	Sample et al. (1993)
	18	0.014	0.187	2.550	0.571	Temperate mixed forest	Schoener (1980)
	29	0.026	0.094	2.500	0.153	Tropical dry forest	Schoener (1980)
	7	0.078	0.140	1.320	0.684	Tropical rainforest	Schoener (1980)
		0.013	**0.039**	**2.805**	**0.101**		

Group	n	β_0	SE(β_0)	β_1	SE(β_1)	Ecosystem	Reference
Diptera	145	-0.011	0.483	2.703	0.081	Temperate mesic forest	Beaver and Baldwin (1975)
	36	0.031	0.264	2.392	0.158	Temperate mesic forest	Hódar (1996)
	75	0.085	0.196	1.881	0.146	Tropical forests	Johnson and Strong (2000)
	84	0.037	0.115	2.366	0.078	Temperate shrub-steppe	Rogers et al. (1977)
	257	0.041	0.184	2.213	0.085	Temperate mixed forest	Sample et al. (1993)
	171	0.022	0.056	2.420	0.097	Temperate mixed forest	Schoener (1980)
	107	0.074	0.069	1.640	0.122	Tropical dry forest	Schoener (1980)
	124	0.068	0.051	1.590	0.117	Tropical rainforest	Schoener (1980)
		0.041	**0.032**	**2.157**	**0.134**		
Formicidae	11	0.010	0.524	2.763	0.294	Temperate mesic forest	Hódar (1996)
	10	0.003	1.056	3.610	0.511	Temperate mesic forest	Hódar (1996)
	21	0.024	0.298	2.103	0.238	Tropical forests	Johnson and Strong (2000)
	34	0.018	0.171	2.572	0.097	Temperate shrub-steppe	Rogers et al. (1977)
	45	0.009	0.350	2.919	0.171	Temperate mixed forest	Sample et al. (1993)

Group	n	β_0	SE(β_0)	β_1	SE(β_1)	Ecosystem	Reference
Formicidae cont.	13	0.034	0.155	2.190	0.342	Temperate mixed forest	Schoener (1980)
	25	0.012	0.114	2.720	0.260	Tropical dry forest	Schoener (1980)
	20	0.021	0.127	2.310	0.224	Tropical rainforest	Schoener (1980)
		0.019	**0.065**	**2.586**	**0.105**		
Other Hymenoptera	24	0.164	0.286	1.900	0.154	Temperate mesic forest	Hódar (1996)
	50	0.037	0.241	2.102	0.132	Tropical forests	Johnson and Strong (2000)
	82	0.016	0.072	2.550	0.107	Temperate mixed forest	Schoener (1980)
	174	0.043	0.051	2.070	0.092	Tropical dry forest	Schoener (1980)
	122	0.022	0.057	2.290	0.138	Tropical rainforest	Schoener (1980)
		0.034	**0.034**	**2.192**	**0.100**		

[1/] Here, Hemiptera includes both former orders Hemiptera and Homoptera, which were considered separate groups in some of these studies. For these studies, both equations were included in the meta-analysis of length-weight regressions.

netting with song playbacks and decoys, using netlanes placed in the forest. During banding, I measured unflattened wing chord, tarsus length and mass. These were used to derive an index of body condition: mass corrected for body size (Marra and Holmes 2001). In addition, pectoral muscle volume was scored from 0–3 and fat was scored from 0–5 following Latta (2003). The change in each of these measures of body condition through the winter was estimated separately for each year and species using linear regression models.

The meta-analysis was conducted using Proc Mixed in SAS (ver. 9.2). All other models were fit using R (ver. 2.9.1; R Development Core Team 2009).

Results

In both dry seasons examined in this study, rainfall declined precipitously after October, with rainfall in November below the long-term average (Figure 8). However, in 2008–2009 the dry season was partially relieved with a substantive rainfall event in January.

The decline in rainfall was associated with changes in vegetation. In 2007–2008, percent cover of litter increased significantly over the winter ($F_{1,47} = 22.99$, $p \ll 0.001$), while the percent cover of shrubs, saplings and the canopy layer decreased significantly (shrubs: $F_{1,47} = 54.68$, $p \ll 0.001$; saplings: $F_{1,47} = 59.97$, $p \ll 0.001$; canopy $F_{1,47} = 51.08$, $p \ll 0.001$). In 2008–2009, these changes were less pronounced: percent cover of shrubs significantly declined ($F_{1,71} = 6.83$, $p = 0.011$), but the increase in percent cover of litter

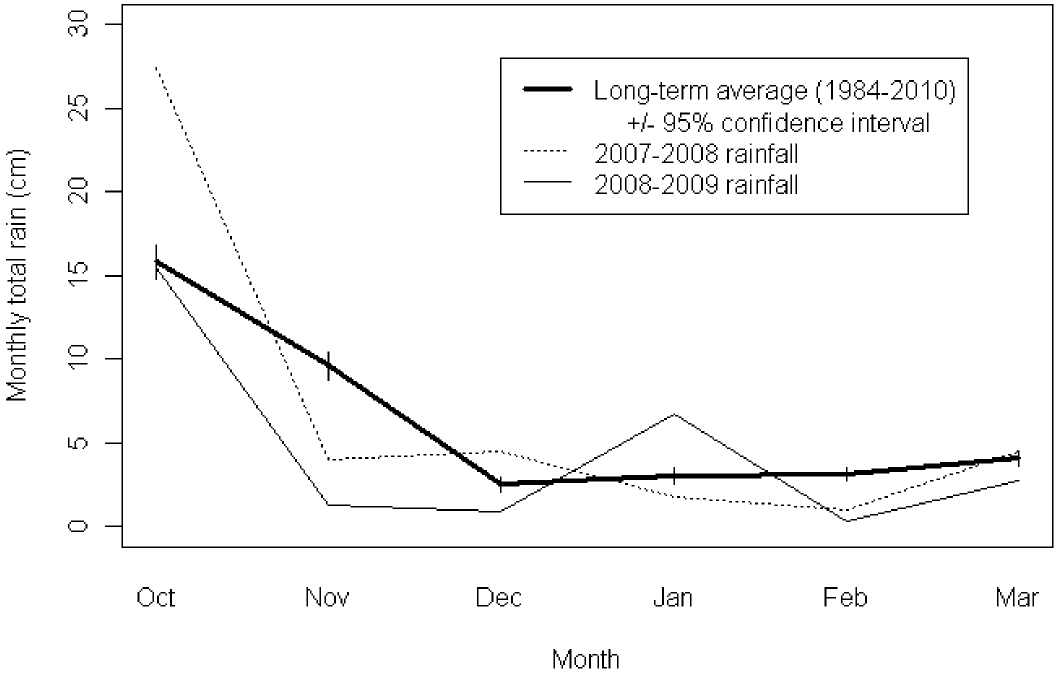

Figure 8. Monthly rainfall in study years compared to long-term average monthly rainfall.

($F_{1,71}$ = 0.04, p = 0.847) and decrease in percent cover of saplings and canopy trees were not significant (saplings: $F_{1,71}$ = 0.72, p = 0.398; canopy: $F_{1,71}$ = 1.41, p = 0.238).

In 2007–2008, total arthropod (> 3 mm) biomass declined after November, and dropped again between January and March ($F_{3,127}$ = 2.47, p = 0.065; Figure 9). This decline was driven by declines in two arthropod groups: the biomass of non-ant Hymenoptera was significantly higher in November than it was later in the winter ($F_{3,128}$ = 6.31, p « 0.001),and the biomass of Diptera was higher in November and December than it was later in the winter ($F_{3,128}$ = 2.48, p = 0.064). The biomass of Hemiptera, Coleoptera, adult Lepidoptera and ants remained approximately constant

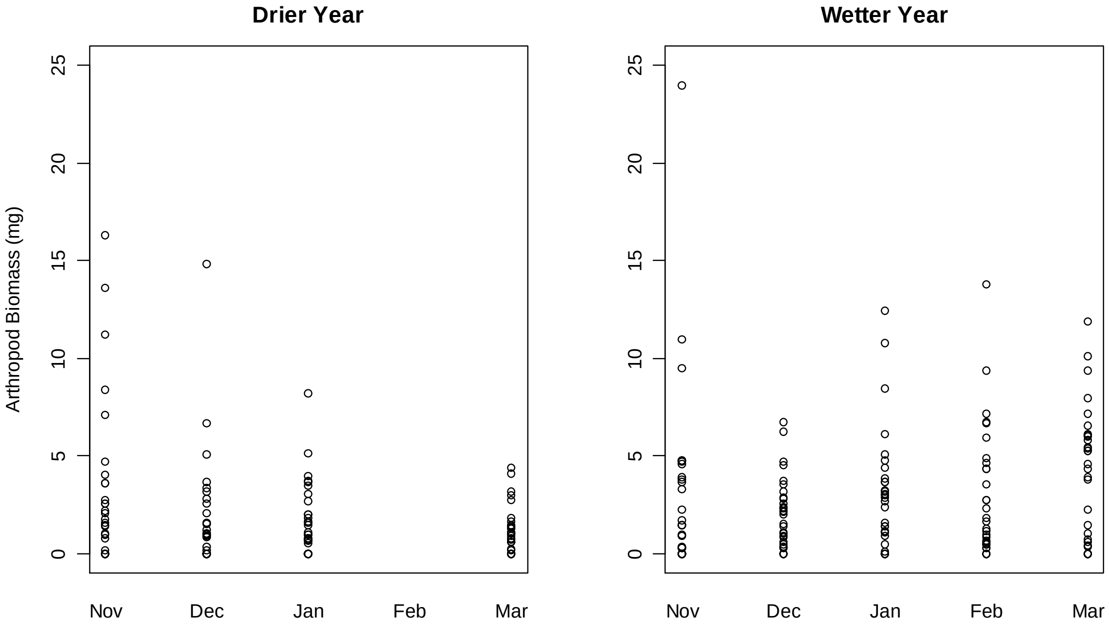

Figure 9. Total arthropod biomass for the 2007-2008 (drier year) and 2008-2009 (wetter year) field seasons.

throughout the winter (Hemiptera: $F_{3,128} = 1.10$, $p = 0.350$; Coleoptera: $F_{3,127} = 0.62$, $p = 0.603$; adult Lepidoptera: $F_{3,128} = 1.37$, $p = 0.255$; ants: $F_{3,128} = 0.89$, $p = 0.447$). In contrast, during 2008–2009 total arthropod biomass remained roughly constant throughout the winter ($F_{4,159} = 1.15$, $p = 0.334$), with a slight decline in December and a slight increase in March (Figure 9). When examining individual arthropod groups, the biomass of Hemiptera and ants remained constant (Hemiptera: $F_{4,160} = 0.97$, $p = 0.427$; ants: $F_{4,160} = 0.51$, $p = 0.728$), but significant changes in biomass were seen in the other groups. The biomass of Hymenoptera was lower in November and December than later in the winter ($F_{4,160} = 6.15$, $p \ll 0.001$), and the biomass of Coleoptera was higher in February than in the other months ($F_{4,160} = 2.33$, $p = 0.058$). In contrast, the biomass of Diptera declined throughout the winter ($F_{4,160} = 2.40$, $p = 0.052$). Adult Lepidoptera were

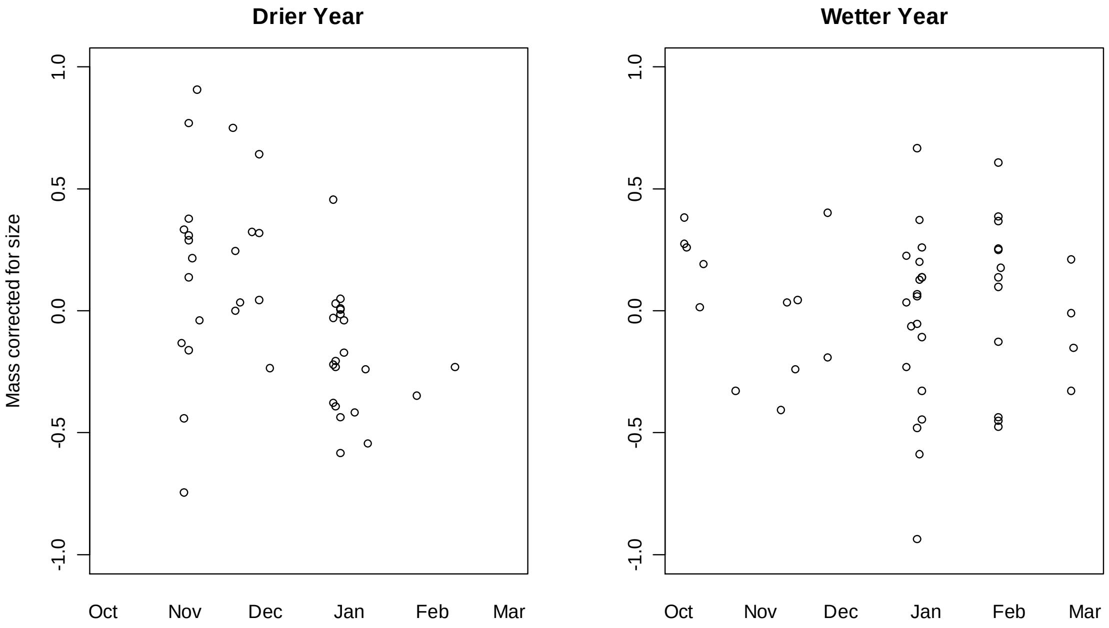

Figure 10. Body condition of Adelaide's (mass corrected for body size) for the 2007-2008 (drier year) and 2008-2009 (wetter year) field seasons.

most common in November and March, and least common in January and February ($F_{4,160} = 4.89$, p « 0.001).

Body condition of both bird species also followed rainfall and vegetation patterns. Pectoral muscle volume and mass corrected for body size both declined significantly in Adelaide's Warblers during 2007–2008 (pectoral muscle: $F_{1,45} = 17.39$, p « 0.001; mass: $F_{1,39} = 26.69$, p « 0.001; Figure 10), while both declined non-significantly in American Redstarts (pectoral muscle: $F_{1,8} = 0.18$, p = 0.682; mass: $F_{1,6} = 2.32$, p = 0.178; Figure 11). In 2008–2009, pectoral muscle volume and mass corrected for body size declined only slightly in Adelaide's Warblers (pectoral muscle: $F_{1,51} = 0.87$, p = 0.356; mass: $F_{1,44} = 0.27$, p = 0.608; Figure 10), while those of American Redstarts increased slightly (pectoral muscle: $F_{1,17} = 2.20$, p = 0.156; mass: $F_{1,13} = 0.07$, p = 0.794; Figure 11). Fat

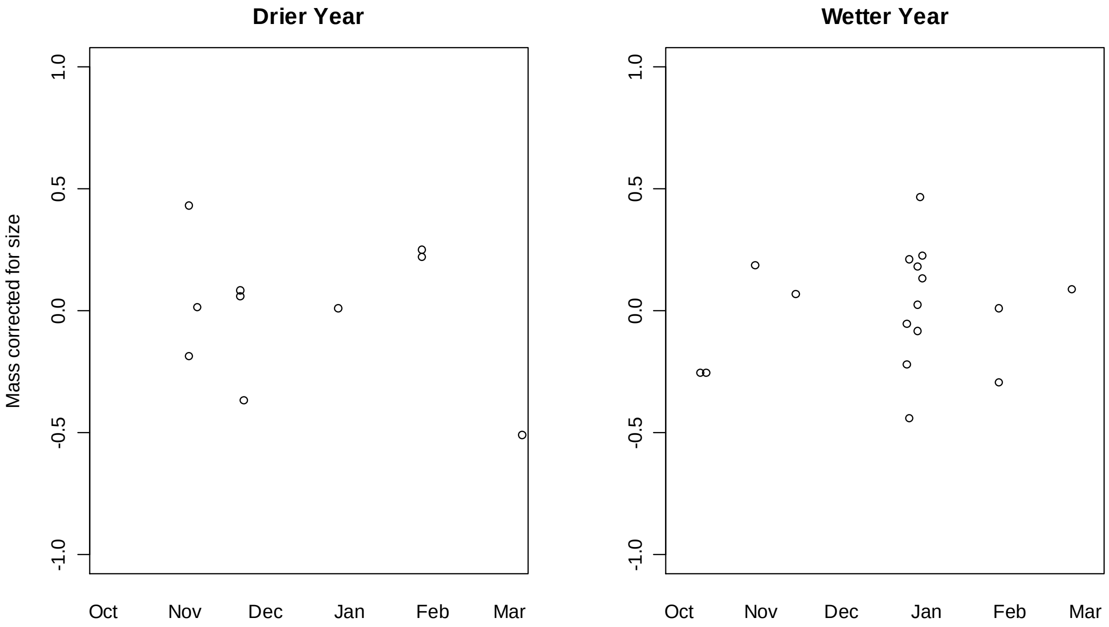

Figure 11. Body condition of Redstarts (mass corrected for body size) for the 2007-2008 (drier year) and 2008-2009 (wetter year) field seasons.

scores remained constant throughout the winter in all cases (p ≥ 0.389 for all tests), with individuals of both species remaining relatively lean in both 2007–2008 (means of both species between no fat and a trace of fat) and 2008–2009 (means of both species between a trace of fat and a little fat).

Discussion

Rainfall does seem to be a key factor influencing the arthropod community of Guánica Dry Forest. While the overall rainfall patterns of 2007–2008 and 2008–2009 were similar, the heavier than normal rainfall in January 2009 lead to some pronounced changes in the phenology of the plant and arthropod communities. In the drier year, significant leaf fall occurred in all structural layers (shrub, sapling and canopy layers), leading to significant declines in vegetative cover and total arthropod biomass. Wasps and flies showed the most pronounced declines, suggesting they may be particularly sensitive to dry conditions or lack of vegetative cover. In contrast, during the wetter year only the shrub layer experienced significant leaf fall, and the total biomass of arthropods remained fairly constant throughout the dry season. Overall, the phenology of the plant and arthropod communities of Guánica seem to be similar to those of other Caribbean dry forests (Janzen and Schoener 1968, Janzen 1973, Poulin et al. 1992, Parrish and Sherry 1994, Murphy et al. 1995, Strong and Sherry 2000, Van Bael et al. 2003, Johnson et al. 2006b, Studds and Marra 2007).

Low arthropod biomass does not necessarily limit insectivore populations. However, the observed declines in body condition in the two insectivores examined suggest that arthropods are sometimes limiting in this system. Both species declined in body condition during the drier year, while they managed to maintain body condition throughout the wetter year. These declines occurred even though individuals of both species spent more time foraging when the forest was dry, and began to forage more frequently in the lower structural layers (pers. obs.), where arthropod prey may decline to a lesser degree (Poulin et al. 1992, Strong 2000). Other studies in Cuba and Jamaica have also shown that body condition of winter-resident birds is lower in years when the winter is dry and arthropod densities are relatively low (Wallace 1998, Studds and Marra 2007).

Body condition did not decline so drastically as to cause significant direct mortality through starvation, although one Adelaide's with a broken tarsus disappeared during the dry season of 2006–2007 (pers. obs.). However, the decline may well have produced sub-lethal limiting effects on individuals, and body condition has been found to be a good predictor of annual survival in other studies (Johnson et al. 2006a). Adelaide's Warblers in poor condition probably have to delay breeding until they are able to regain good condition (Drent and Daan 1980, Schoech 1996). This limits their ability to take advantage of environmental conditions suitable for breeding when they arise, for example by breeding earlier than usual if the dry season ends unusually early (Toms 2010). In addition, individuals in good condition may be able to raise multiple broods if they start to breed as early as possible (Staicer 1991). Similarly, American Redstarts probably have to delay migration until they can regain good body condition and acquire sufficient fat stores. As a result, individuals that lose body condition through the winter are likely to arrive on the breeding grounds later and in poorer condition than individuals that were able to maintain their body condition (Marra et al. 1998), leading to reduced reproductive success (Smith and Moore 2005, Reudink et al. 2009).

The body condition of Adelaide's Warblers declined more strongly than that of American Redstarts. Playback experiments have shown that Adelaide's Warblers are behaviorally dominant over Redstarts (Chapter 6), so it is unlikely that Redstarts are preventing Adelaide's from foraging in preferred areas. Instead, this may be due to subtle differences in habitat selection: Adelaide's Warblers are more common than Redstarts in the drier habitats of Guánica (pers. obs.), where food limitation might be most pronounced. In addition, Adelaide's Warblers must remain on their territory year-round, while American Redstarts are able to switch from a territorial to vagrant strategy if resources in a particular area become in short supply. This behavioral flexibility may buffer American Redstarts against seasonal changes in food supply.

In conclusion, the phenology of the Guánica Dry Forest in the dry season seems to be driven by rainfall. As the dry season progresses, the deciduous vegetation begins to drop leaves, and the biomass of arthropods shows a parallel decrease. In turn, the reduced availability of arthropod prey appears to eventually overcome the compensatory foraging strategies of insectivores, leading to reduced body condition. However, if the dry season is broken by one or more substantive rainfall events, leaf loss is drastically reduced, arthropod biomass remains relatively constant, and insectivores are able to maintain their body condition. Models suggest that Puerto Rico will experience warmer and drier dry seasons under projected patterns of climate change (Singh 1997), suggesting that insectivore populations may be more severely limited by arthropod resources in the future.

Chapter 4: Adelaide's Warblers (*Dendroica adelaidae*) and American Redstarts (*Setophaga ruticilla*) have similar foraging niches during the non-breeding season

Abstract

Two species will not compete unless they both depend on a shared limiting resource. In the dry tropical forests typical of the West Indies, food is the only resource likely to be limiting for insectivores, and is known to affect the body condition of two insectivores that are sympatric in southwest Puerto Rico, the migratory American Redstart (Redstart; *Setophaga ruticilla*) and the resident Adelaide's Warbler (Adelaide's; *Dendroica adelaidae*). I examined the foraging niches of these species to determine whether they might be competing for arthropods. The foraging location of both species (type of vegetation, relative location within tree canopies and height above ground) were very similar (BA = 0.951, where BA = 0 indicates no overlap and BA = 1 indicates identical niches), both at the level of the population and at the level of individuals. Attack type (substrate and method of attack) was also very similar at both levels (BA = 0.861), and Adelaide's bills share some flycatcher-like features with Redstarts. Adelaide's did not shift their foraging niche when Redstarts left, indicating that Redstarts were not restricting the foraging niche of Adelaide's. Competition between these species is probable, at least in years when arthropods are a limiting resource.

Introduction

The concept of ecological niches was developed early in the last century, and has been one of the central ideas in competition theory ever since. The first descriptions of the ecological niche by Grinnell (1917) and Elton (1927) were fairly similar (Udvardy 1959), but in modern usage Grinnellian and Eltonian niches refer to different aspects of niches: Grinnellian niches focus on environmental (non-consumable) resources at large spatial scales, while Eltonian niches focus on species interactions at small spatial scales (Leibold 1995, Soberón 2007). In recent years, the Grinnellian niche has been prominent in the ecological literature, due to the increasing number of biogeographic studies focusing on invasive species and potential range shifts of species in response to climate change (Colwell and Rangel 2009, Holt 2009, Soberón and Nakamura 2009, Wake et al. 2009). Eltonian niches are more relevant when examining competition among sympatric populations or species, but are examined less frequently because intensive field studies are usually required to collect the data needed.

Competition theory states that two species cannot coexist if they have identical niches (Grinnell 1917, Gause 1934), and many studies have examined sympatric species within the same guild in order to determine how their niches differ. Most such studies have simply described an average niche for the species, ignoring any variation in niches that may exist among individuals (Morse 1974, Schoener 1974, Connell 1983, Schoener 1983). However, there is reason to believe that individual variation may be important, because individuals may behave differently due to age class, sex, dominance, predator risk, learned behaviors, or intensity of intraspecific or interspecific competition (Martin

1986, Werner and Sherry 1987, Wunderle 1995, Marra 2000, Marra and Holmes 2001, Bolnick et al. 2002, Studds and Marra 2005, Svanbäck and Bolnick 2005). As a result, some individuals may experience interspecific competition even if the species' average niches differ, or may not experience competition even if the average niches are almost identical.

No matter whether niche overlap occurs for the entire species or merely for some individuals, evolutionary pressures should act to reduce the overlap in niches through morphological or behavioral character displacement (Brown and Wilson 1956). However, in some circumstances character displacement due to competition can be constrained due to conflicting selective pressures on morphology. Migratory species are one group that faces such constraints. Migration induces strong selective pressures on the physiology, morphology and behavior of a species to increase the efficiency of long-distance travel (Morse 1980, Ricklefs 1992, Winkler and Leisler 1992). In addition, migrants may also be constrained from diverging with a particular species because they need to be adapted to multiple ecosystems during their annual cycle (Orians and Willson 1964, Wilson 1975, Bennett 1980). For example, an adaptation that would reduce competition with a species in the non-breeding season might increase competition with another species on their breeding grounds. As a result, a migratory species might not be able to avoid competition in any of the ecosystems it uses during the annual cycle.

In this study, I examine the potential for competition between two insectivorous bird species, one a migrant (American Redstart, *Setophaga ruticilla*) and one a resident (Adelaide's Warbler, *Dendroica adelaidae*), during the non-breeding season. These species are sympatric in the subtropical dry forests of southwest Puerto Rico, are of very similar size and have broadly similar foraging methods (Oberle 2000). In this ecosystem, a pronounced dry season occurs from December through April (Ewel and Whitmore 1973, Murphy et al. 1995). Arthropods are known to be a limiting resource in the late dry season, at least during some years (Chapter 3), and a previous study suggested that these species might compete (Dugger et al. 2004). However, this hypothesis has not been tested previously.

These species will not compete for food unless they have similar foraging niches, in terms of location, the method of attack and the types of prey taken. However, previous diet studies have shown that both species are generalist insectivores (Wetmore 1916, Lefebvre et al. 1992, Sherry and Holmes 1997, Toms 2010) and are unlikely to select different prey if they forage in the same places with the same techniques (MacArthur 1958). Therefore, the diet of these species was not examined directly. However, bill morphology was examined, as it may affect a species' ability to capture prey.

It is also possible that Adelaide's Warblers (Adelaide's) and American Redstarts (Redstarts) compete even if they do not share the same foraging technique when both are present. Instead, if Redstarts were dominant competitors, they might force Adelaide's to shift their niche during the non-breeding season (Case and Gilpin 1974). However, Redstarts depart at about the same time as Adelaide's begin breeding (Toms 2010), and it is plausible that Adelaide's might also shift their niche due to breeding requirements or other seasonal effects. Therefore, I determined whether Adelaide's with and without Redstart neighbors shifted their niche in different ways due to competitive release. This individual-based approach allows me to control for changes related to the onset of the breeding season, which would not be possible with a species-level approach. If these species have very similar niches when present in the same community, or if Adelaide's with Redstart neighbors have different niches than those without Redstart neighbors, then it is likely that these species compete for limited food resources.

Methods

Three study sites within the upland forest of Guánica Dry Forest were used in this study, each centered on a trail (Figure 2). All had a mixture of ridge-top dry scrub, deciduous and semi-evergreen vegetation, the main forest types characteristic of the upland forest (Lugo et al. 1978). The La Joya site was monitored for the winters of 2006–2010 (i.e. four winters), the Fuerte site for the winters of 2007–2010, and the Granados site only for the winter of 2008–2009. At each study site, Adelaide's and Redstarts were captured in mist-nets and banded with unique color-band combinations. Most Adelaide's pairs monitored included at least one color-banded bird, but a few additional unbanded pairs were included if they could be easily distinguished from color-banded neighbors. Due to low densities and difficulty in capturing Redstarts, several unbanded female Redstarts were included in this study. Observations from these individuals were included only if they could be identified as a particular resident individual by finding them in an area used only by a single unbanded Redstart of that age-sex class, or by establishing their location relative to other known Redstarts using counter-chips (see Chapter 5 for additional details).

Foraging observations were obtained by locating focal individuals at the site, and then following them for as long as possible as they moved through the site. Although individuals were often initially wary of observers, they became habituated to our presence within a few days, sometimes moving to within 1–2 m of us while foraging. Each time the individual changed position or attempted to attack prey, an observer recorded the type of vegetation they were foraging in: large tree, medium tree, small tree, shrub, ground, or snag. Their relative location within tree canopies was further classified by dividing the horizontal and vertical dimensions of the tree into thirds (e.g. upper outer third). In addition, all attempts at capturing prey were classified by the type of foraging method used (glean, probe, hang, jump, hover, sally and chase; Remsen and Robinson 1990), and by substrate (leaf, bark, bromeliad, air, or other). Miscellaneous (other) substrates used by Adelaide's were flowers, seed pods, leaf litter, dead leaves and a termite mound. Miscellaneous substrates used by Redstarts were leaf litter and a spider web. Height from the ground was also estimated. Since height was the only continuous variable assessed in this study, it was divided into height classes to simplify the statistical analyses. Height data were examined to find natural breaks using histograms, and were split into four classes: 0–2 m, 2–4 m, 4–6 m, and > 6m, where the upper end of a height class is included in the category, but the lower end is not (except that 0 was included in the lowest height class).

Foraging niches have usually been compared at the level of populations. However, this may obscure important differences among individuals. In order to determine whether there was significant variation among individuals in either species, I calculated the similarity between each individuals' foraging niche and the population average for that species (Bolnick et al. 2002), assessing Adelaide's separately for the time periods when Redstarts were present and absent. I looked at two aspects of the foraging niche separately, foraging location (vegetation class, relative horizontal and vertical location within a tree canopy, and height) and attack type (method and substrate of attempted attack), because attack type could not always be determined. As a measure of similarity among foraging niches, I used Bhattacharyya's affinity (BA; Bhattacharyya 1943, Fieberg and Kochanny 2005). BA ranges from zero (niches have no similarity) to one (identical niches).

Initially, I compared these two aspects of the foraging niches of Adelaide's and Redstarts by calculating the similarity between the average niches of each population. In this analysis, all observations for that species were combined into one frequency table. BA was then calculated to estimate the similarity between the Redstart and Adelaide's tables. However, I also wanted to account for potential differences among individuals. Thus, I calculated similar tables for each individual, calculated the pairwise similarity of foraging niches for all individual Adelaide's and Redstarts, and used a Mantel test to determine whether the niches differed (Patterson 1986).

I also compared the foraging niches of Adelaide's when Redstarts were present with their foraging niches after the Redstarts had departed. If Redstarts restricted the foraging niche of Adelaide's, then Adelaide's should shift their foraging niche when released from interspecific competition. In order to control for potential shifts in foraging niches due to the onset of the breeding season, I determined whether foraging niche shifts differed between Adelaide's with and without Redstart neighbors. I assessed this at the population level by determining the overlap between the population averages of these groups of Adelaide's, for both foraging location and attack type, in the same manner as the population-level analyses for species comparisons. In addition, I assessed this shift at the level of individuals by determining the overlap of an individual Adelaide's territory when Redstarts were present and absent. I then used a Mann-Whitney test to determine whether this overlap differed among Adelaide's that did or did not have Redstart neighbors.

Bill morphology of West Indian migrant and resident *Dendroica spp.* was obtained from Arendt et al. (2004), along with data for American Redstart. Analysis of variance was used to determine if the bill width-to-depth ratio of Adelaide's was significantly different from Redstarts and from the other *Dendroica* species.

The Mantel test was conducted using the APE package for R (ver. 2.4-1; Paradis et al. 2004). All other statistical tests were conducted in R (ver. 2.9.1; R Development Core Team 2009).

Results

Variation among individuals in foraging location and attack type was fairly low for both species (Table 3). There was no significant difference in the degree of individual variation across groups for foraging location ($\chi^2_2 = 3.009$, $p = 0.222$), but there was for attack type ($\chi^2_2 = 7.757$, $p = 0.021$). Post-hoc Mann-Whitney tests revealed that there

Table 3. Individual variation in foraging location (height, type of vegetation and location within vegetation) and attack type (substrate and method of attack). BA scores are a measure of similarity between individual foraging niche and the population average niche for that group, where a score of zero would indicate no similarity and a score of one would indicate 100% similarity.

	BA score for location		**BA score for attack type**	
Group	**Mean**	**SE**	**Mean**	**SE**
Redstarts	0.762	0.037	0.934	0.020
Adelaide’s when Redstarts are present	0.721	0.015	0.868	0.011
Adelaide’s when Redstarts are not present	0.752	0.016	0.878	0.015

was significantly more variation among Adelaide’s attack types than there was for the attack types of Redstarts. Nevertheless, overlap was very high for all groups and these differences may not be biologically significant.

At the population level, foraging locations of Redstarts and Adelaide’s were very similar (BA = 0.951; Figure 12), as were attack types (BA = 0.861; Figure 13). Both aspects of the foraging niche were also very similar when assessed at the level of individuals (foraging location Z = 265.89, p = 0.753; attack type Z = 283.75, p = 1.000).

Adelaide’s did not shift their foraging location (BA = 0.947; Figure 14) or attack type (BA = 0.981; Figure 15) after Redstarts left, when assessed at the level of the population. There was also no difference in attack type when assessed at the level of

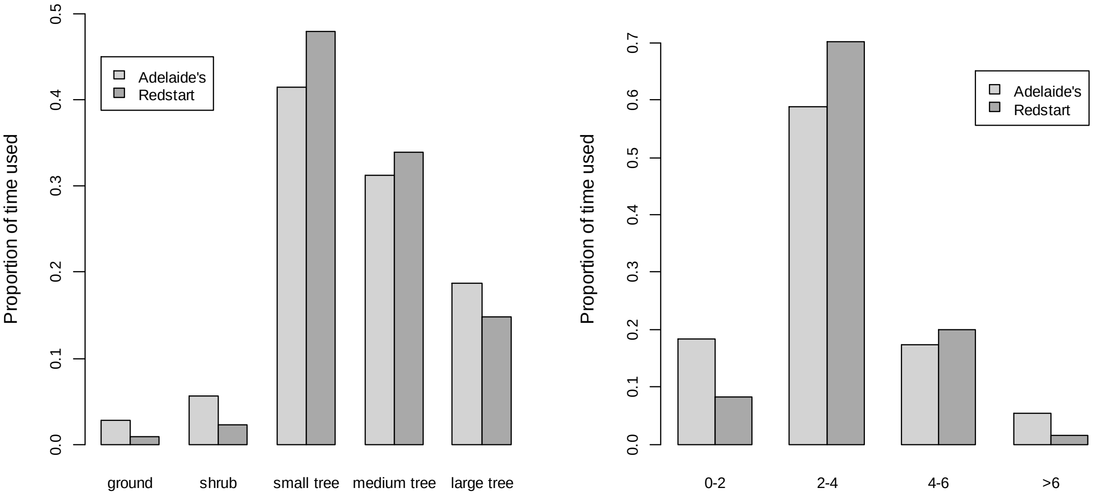

Figure 12. Two of the four univariate components of foraging location for Adelaide's and Redstarts, at the level of populations. Relative vertical and horizontal locations within tree canopies are the other components of foraging location.

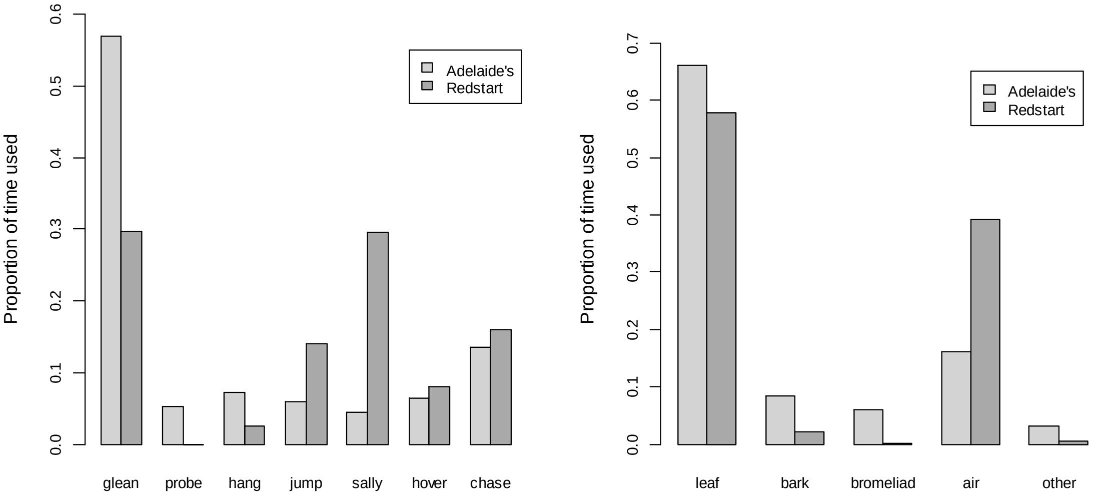

Figure 13. The two univariate components of attack type for Adelaide's and Redstarts, at the level of populations.

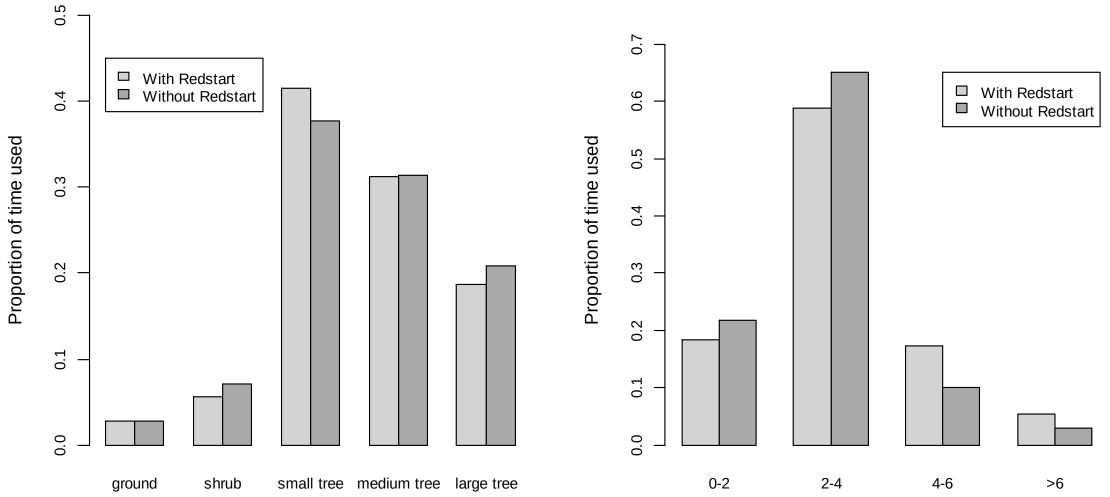

Figure 14. Two of the four univariate components of foraging location for Adelaide’s, assessed at the level of the population both when Redstarts were present and when they were absent. Relative vertical and horizontal locations within tree canopies are the other components of foraging location.

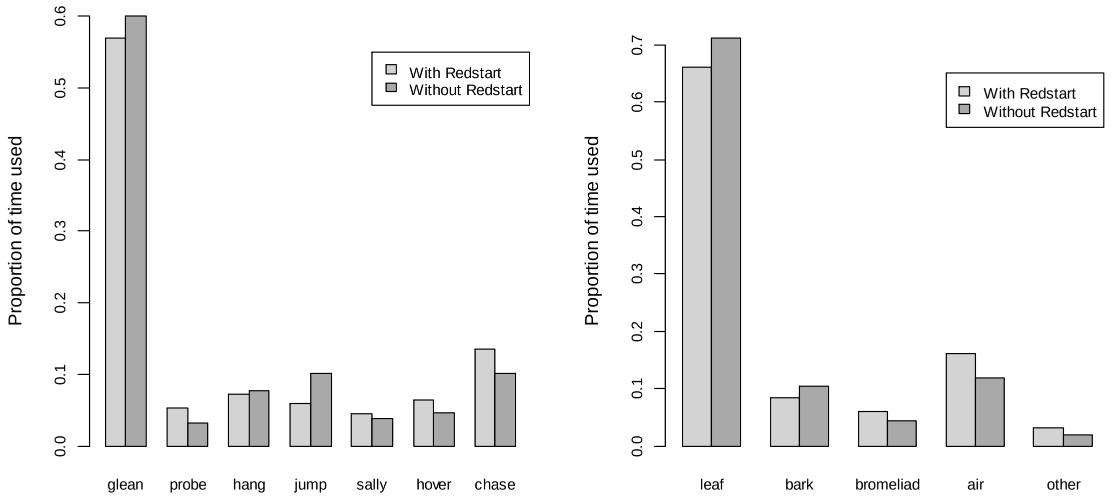

Figure 15. The two univariate components of attack type for Adelaide’s, assessed at the level of the population both when Redstarts were present and when they were absent.

individuals (W = 77, p = 0.979), but there was a difference in foraging location (W = 35, p = 0.060). When each component of foraging location was assessed separately, only foraging height appeared to differ (height W = 36, p = 0.069; vegetation class W = 65, p = 0.976; vertical position W = 55, p = 0.525; horizontal position W = 74, p = 0.651). However, mean overlap scores for height were still high for both groups (without Redstart neighbors mean BA = 0.936, with Redstart neighbors mean BA = 0.876), and the overlap in height at the species level was extremely high (BA = 0.992). Therefore, the near-significance of differences in foraging location among these groups likely results from a complex combination of component variables (height, vegetation class, and relative vertical and horizontal position within tree canopies), and could be a sampling artifact.

Bill morphology did differ significantly among species (Table 4; $F_{13,395} = 49.81$, $p \ll 0.001$). Post-hoc t-tests indicated that Redstart bills were significantly wider than those of Adelaide's. However, Adelaide's bills were significantly wider than all other *Dendroica* with a sample size greater than eight individuals, except for the St. Lucia Warbler (*D. delicata*).

Discussion

MacArthur (1958) argued that the foraging niches of two species would differ only if they foraged in different locations, at different times, in different manners, or have different preferences for food types. Redstarts and Adelaide's both forage throughout the day, with similar temporal patterns (pers. obs.). In this study, I have shown that the

Table 4. Bill morphology of Adelaide's Warblers and American Redstarts, as compared to other migrant and resident *Dendroica* of the West Indies (species ordered by depth to width ratio). Data from Arendt et al. (2004).

Species	**n**	**Depth at nares (mm)**	**Width at nares (mm)**	**Depth:width Ratio**
S. ruticilla	100	2.74	4.05	1.49
D. adelaidae	126	2.70	3.07	1.14
D. delicata	9	2.87	3.28	1.14
D. caerulescens	37	2.88	3.13	1.09
D. petechia	49	3.13	3.36	1.08
D. plumbea	1	3.23	3.42	1.06
D. tigrina	19	2.76	2.89	1.05
D. angelae	7	2.84	2.99	1.05
D. subita	3	2.85	2.95	1.04
D. discolor	51	2.83	2.94	1.03
D. magnolia	1	3.18	3.23	1.02
D. coronata	3	3.11	2.99	0.96
D. palmarum	2	3.05	2.75	0.91
D. virens	1	3.40	2.90	0.85

foraging niches of Redstarts and Adelaide's are very similar both in terms of foraging location and type of attack, and that they both have bills with flycatcher-like traits. Moreover, several studies have shown that dietary differences arise from search mode, rather than bill morphology or differential prey selection (MacArthur 1958, Robinson and Holmes 1982, Radford and Du Plessis 2003), so these generalist predators are also likely to consume similar prey. Elsewhere, I have also shown that arthropod density declines under dry conditions, and that this decline is associated with a reduction in body condition of both species (Chapter 3). Thus, this study indicates that the foraging niches of these species are very similar, and competition for food is probable in years when arthropods are a limiting resource.

On the breeding grounds Redstarts have been described as a member of the flycatching guild, as they use more aerial techniques (sallies and chases) than most other gleaning wood-warblers (Sherry 1979, Robinson and Holmes 1982). The proportion of aerial attacks is even higher in winter than in summer (Lovette and Holmes 1995), so it may be surprising that Adelaide's have such high similarity in attack method. However, Adelaide's are also very active foragers and frequently use aerial maneuvers (Wetmore 1916, Kepler 1977, Post 1978, Toms 2010). Moreover, Adelaide's also have a flycatcher-like bill. Both species have rictal bristles which aid in capturing prey in the air, and the bill width-to-depth ratio of Adelaide's is more similar to that of Redstarts than to all other *Dendroica* in the West Indies, except for the St. Lucia Warbler. Adelaide's form a super-species complex with the St. Lucia Warbler and the Barbuda Warbler (*D. subita*), and these three species were formerly considered a single, polytypic species (Lovette et al. 1998). Thus, it is not surprising that the St. Lucia Warbler also has a flycatcher-like bill.

Both Redstarts and Adelaide’s have moderate overlap with Puerto Rican Todies (*Todus mexicanus*) in attack type (Kepler 1977). However, Todies typically forage in the forest understory or low trees (height ≤ 3 m; pers. obs.), while Adelaide’s and Redstarts forage over a broader range of heights. The other potential competitors in Guánica are relatively uncommon, often of markedly larger size and are more specialized in either flycatching (e.g. Puerto Rican Pewee *Contopus portoricensis*, Puerto Rican Flycatcher *Myiarchus antillarum*) or gleaning (e.g. Puerto Rican Vireo *Vireo latimeri*, Northern Parula *Parula americana*).

During the breeding season, Redstarts and Least Flycatchers (*Empidonax minimus*) compete for food, with moderate-high overlaps in foraging niche (0.49–0.84) and morphology (0.97; Sherry 1979). Overlap in attack type was slightly higher than overlap in foraging location in this study, while there was more overlap in vertical height distribution than in attack type in Sherry’s study (1979). However, overlaps in both aspects of foraging niche were higher in this study (0.86–0.95), which implies that Redstarts face more intense competition with Adelaide’s than they do with Least Flycatchers.

Even though niche overlaps are high during the non-breeding season, Redstarts could be restricting Adelaide’s use of preferred foraging locations, either by interference or depletion competition. If this were so, we would expect to see a shift in or expansion of Adelaide’s foraging niche after Redstarts left, as seen in other observational and experimental studies (Morse 1974, Alatalo et al. 1985). However, in this study Redstarts appeared to have little effect on the foraging niche of Adelaide’s. This corresponds with the results of a complementary study on interspecific aggression between these species (Chapter 6). That study found Adelaide's to be dominant, and a subordinate species such as the Redstart would not be expected to restrict the foraging niche of a dominant aggressor.

There are several advantages to assessing foraging niches at the level of individuals, as I did here, rather than averaging over a population or species. First, using individuals as the sampling unit is not only more consistent with most other approaches in ecological analysis, but is also a better representation of the true distribution of niches within the species. A broad foraging niche at the level of a species could result either from each individual having a broad niche, or because each individual has a different, narrow foraging niche. Second, comparing the average niches of species could be misleading, because each individual of that species may have different opportunities for foraging, as well as a different set of intraspecific and interspecific competitors. Thus, one individual might face strong competition and be forced to shift its niche away from its preferred niche, while others may face little competition but need to shift their niche in a different way in order to optimize their energetic intake. Third, assessing niches at the level of individuals allows the researcher to determine whether differences in niche breadth or position are correlated with potential explanatory variables, such as sex, age or dominance. Fourth, without individual niches, it would have been impossible to determine whether Adelaide's foraging niches shifted in response to seasonal release from competition with Redstarts. Thus, whenever possible, researchers should collect data on resource use from known individuals.

In this study, foraging niches of individual Adelaide's and Redstarts were very similar to the mean niche of the species. Thus, the results of individual-level and population-level analyses were not qualitatively different. The foraging niches of Adelaide's were slightly more variable than those of Redstarts. This may result from differences in the foraging niches of males and females (Holmes et al. 1978, Radford and Du Plessis 2003). Most Redstarts observed (80%) were females, so any differences between sexes would have to be very large in order to be detected. In contrast, similar numbers of male and female Adelaide's were observed, which increases the likelihood that any differences between the sexes would impact the distribution of foraging niches.

Adelaide's and Redstarts show an unusually high degree of similarity in foraging niches for such closely related species (they will soon be classified as congeners; Lovette and Bermingham 1999, Lovette et al. 2010). In other studies I have shown that food is limiting in this system (Chapter 3) and that they are not interspecifically territorial (Chapter 5). How then can they coexist, when competition theory suggests that one of them should be excluded (Grinnell 1917, Gause 1934)? The migratory behavior of Redstarts may be part of the answer. On an evolutionary scale, Redstarts' fundamental foraging niche may have been constrained by their migratory behavior and the necessity of adapting to multiple ecosystems, each with different competitors (Chapter 1). Adelaide's may not have shifted their niche because Redstarts occur at relatively low densities (Terborgh and Faaborg 1980; Chapter 5), so that the ecological pressures from conspecific competitors are much stronger than those from heterospecific competitors. Such trade-offs can promote stable coexistence between competitors (Chesson 1991).

Periodic reductions in competitive pressure, as occurs here when Redstarts are absent for the breeding season, can also allow competitors to coexist (Willson et al. 2010). Since over-wintering mortality rates are low (Sillett and Holmes 2002), the effects of competition during the non-breeding season are likely manifested during migration or the breeding season. Thus, as long as individuals are sufficiently well-adapted to survive the non-breeding season, evolution of behavioral and morphological traits may be most strongly influenced by competitive pressures outside of the non-breeding season.

Adelaide's are constrained by intraspecific competition to defend their territory year-round, while Redstarts can be more flexible in their behavioral strategies. Although these species are not interspecifically territorial (Chapter 5), they are interspecifically aggressive (Chapter 6). Due to strong intraspecific competition, Adelaide's frequently vocalize as they move through their territory, even while foraging (Toms 2010). In contrast, the subordinate Redstarts are typically silent, and may use a strategy of identifying the location of territorial Adelaide's through their vocalizations, and then foraging in areas of their territory that minimize the risk of confrontation at that moment. Use of these fine-scale spatiotemporal competition refuges would allow Redstarts to coexist with the dominant Adelaide's.

Chapter 5: Are American Redstarts and Adelaide's Warblers interspecifically territorial in the non-breeding season?

Abstract

If competition occurs among species, it may be adaptive to defend territories against heterospecifics as well as against conspecifics. Territorial defense is costly, so interspecific territoriality is strong evidence of interspecific competition for defensible resources. Adelaide's Warblers (Adelaide's; *Dendroica adelaidae*) and American Redstarts (Redstarts; *Setophaga ruticilla*) are sympatric in the dry forests of southwest Puerto Rico during the non-breeding season and compete for arthropods. I assessed the space use of these species to determine whether this competition was mediated by interspecific territoriality. Territories of these species overlapped significantly more than did conspecific territories, and the resident Adelaide's did not change their space use after the migratory Redstarts left. Redstarts may not be able to defend territories in areas of high Adelaide's density, and may switch to a vagrant strategy in these areas. In areas of lower Adelaide's density, Redstarts may be able to hold territories overlapping Adelaide's territories by using temporary competition refuges that allow them to avoid direct confrontations.

Introduction

Most birds defend territories against conspecifics during the breeding season and many species, both migratory and non-migratory, are also intraspecifically territorial in the non-breeding season (Greenberg 1986). During the breeding season, territorial defense prevents other individuals from using potentially limiting resources such as food resources and nest sites within the defended area (Tinbergen 1957, Brown 1964, Brown and Gordon 1970, Cody 1974, Robinson 1981) and also reduces the likelihood of extra-pair mating (Sheldon 1994, Kempenaers et al. 1995, Johnsen et al. 1998). During the non-breeding season, breeding-specific resources such as nest sites are not needed, so territorial behavior may be limited to the defense of consumable resources such as food.

Competition for resources is expected to be strongest within a species, but where morphologically-similar species coexist interspecific competition may also be important. When interspecific competition occurs, individuals might defend their territory against both conspecific and heterospecific intruders. Territorial defense can be costly in terms of energy used, time lost for other activities, risk of injury and increased risk of predation (Tinbergen 1957, Brown 1964, Orians and Willson 1964). Therefore, interspecific territorial defense should occur only if the benefits of defense outweigh these costs (Brown 1964, Murray 1971). An individual is more likely to defend against heterospecifics if intruders consume many limiting resources due to high niche overlap, if intrusions are frequent in the absence of territorial defense, and if the costs of defending against intruders are low (Brown 1964, Brown and Gordon 1970, Terman 1974, Lyon et al. 1977, Dearborn 1998, Mikami and Kawata 2004).

The costs of territorial defense may be low if the defender is larger or more aggressive than the intruder (Greenberg et al. 1996, Dearborn 1998). If the defender almost always wins conflicts, heterospecifics may be completely excluded from an area if the superior species occurs at high density (Orians and Willson 1964, Hildén 1965, Cody 1974, Reed 1982, Robinson and Terborgh 1995). However, if these conflicts are more equally weighted or the competitively superior species occurs at low densities, territories may be interspersed (Sherry 1979, Robinson and Terborgh 1995). Territories may also be overlapping if the costs and benefits of territory defense are more equally weighted (Cody 1974, Catchpole 1978, Sherry 1979, Garcia 1983, Leisler 1988, Robinson and Terborgh 1995).

Interspecific territorial defense has most commonly been studied during the breeding season (Tinbergen 1957, Brown 1964, Orians and Willson 1964, Brown and Gordon 1970, Cody 1974, Lyon et al. 1977, Sherry 1979, Robinson 1981, Garcia 1983), although some studies have occurred during the non-breeding season (Greenberg and Ortiz 1994, Greenberg et al. 1996, Dearborn 1998). Most studies in the non-breeding season have examined interspecific territoriality among resident species or among migrant species (but see Staicer 1992, Greenberg and Ortiz 1994). However, competition may be more intense between resident and migratory species because the potential for ecological divergence between residents and migrants can be limited by conflicting ecological pressures (see Chapter 1; Orians and Willson 1964).

Here, I examine the potential for interspecific territoriality between resident Adelaide's Warblers (Adelaide's; *Dendroica adelaidae*) and migrant American Redstarts

(Redstarts; *Setophaga ruticilla*), which both exhibit aggressive behavior against the other species (Chapter 6). I mapped territories of both species to determine if they overlapped. In addition, I also determined whether Adelaide's shifted their territories after Redstarts departed for their breeding grounds. Such shifts would strongly suggest that Redstarts restrict Adelaide's use of space. However, Redstarts typically depart near the onset of Adelaide's breeding season, which can induce changes in territorial behavior (Staicer 1991, Toms 2011). Therefore, I compared territory shifts in Adelaide's with and without Redstart neighbors, in order to control for any changes in Adelaide's territory use due to the onset of breeding.

Methods

This study was conducted in the upland forest of Guánica Dry Forest, a Commonwealth Forest and UNESCO International Biosphere Reserve located in southwest Puerto Rico (Figure 2). Upland forests in Guánica comprise a mixture of forest types: ridge-top scrub, deciduous, and semi-evergreen communities. Soil and litter depth, as well as moisture retained, increase along this gradient, with corresponding increases in average and maximum tree heights (Lugo et al. 1978). Ridge-top communities typically feature exposed limestone with shallow soils and little accumulation of organic material. The average canopy height ranges from 3–5 m, with scattered large trees of up to 7 m in height. Semi-evergreen communities feature relatively deep soils and relatively high accumulations of organic materials. The main canopy layer averages 5–8 m high, with scattered large emergent trees of 12–16 m in height. The deciduous communities are intermediate between these forest types, with gentle slopes, moderate soils and moderate accumulation of organic material. Canopy height averages 5–6 m in height, with scattered emergent trees of 8–10 m in height.

Three study sites were used, each centered on a trail. The La Joya site was a mixture of dry scrub, deciduous and semi-evergreen forest types. It was on the northern side of the forest, and was slightly wetter than the other two sites. The Fuerte site also included all three forest types, and was located closer to the coast. The Granados site was located along a long ridge dividing the coastal side of the forest from the northern valley, and comprised a mixture of dry scrub and deciduous forest, as well as a small area intermediate between deciduous and semi-evergreen forest. The study was conducted for three field seasons: January–May 2008, October 2008–June 2009, and February–June 2010. The La Joya and Fuerte sites were monitored for all field seasons, but the Granados site was monitored only during the second field season. Redstart territories had stabilized by the end of October. Redstart departure dates varied from late March to late April, depending on the study site and the year.

At each study site, I established a grid flagged at 15 m intervals, with narrow trails cut between grid points when needed. At all three sites, Adelaide’s and Redstarts were captured in mist-nets and given unique color-band combinations. Most netting was passive and occurred along the main trails. However, additional nets were also placed in the forest to target specific individuals. While target netting was usually passive, song playbacks were occasionally used at these nets in combination with decoys.

Territory mapping was conducted using focal-individual observations. An observer searched for individual color-banded birds at a site, then followed them for as long as possible while they moved through the site. Their position on the grid was recorded to the nearest meter each time they changed locations. Although most individuals were initially wary of observers, they typically became habituated to our presence within a few days, sometimes moving to within 1–2 m of us while foraging. Almost all observations were made after individuals were used to our presence. Individuals could often be followed as they moved through their territory, even when the observer was unable to obtain observations, which allowed us to quickly determine the rough locations of territory boundaries. Therefore, bias in detection of individuals within their territory is probably minimal. Some observations included several foraging movements by an individual at approximately the same location, which would artificially inflate the number of samples at that location. Therefore, all movements of less than 2 m were removed from the dataset before analysis. All other observations within a movement path were included, because obtaining a large number of locations would have been impossible if the individual needed to be relocated for each observation, and having a large sample size far outweighs any negative effect of autocorrelation among locations (Otis and White 1999, Fieberg 2007). Moreover, individuals are capable of flying across their entire territory within 20–30 sec (pers. obs.), suggesting that subsequent observations are autocorrelated by choice, rather than by necessity.

Most Adelaide's pairs monitored included at least one color-banded bird, but a few unbanded pairs were included when they could be easily distinguished from color-banded neighbors. In this study, Redstarts were comparatively uncommon, almost all female, and difficult to capture for color-banding. Therefore, several unbanded female Redstarts were included in this study. Locations from these individuals were included only if their identity could be determined by following them into an area known to be occupied only by a single Redstart, by establishing their location relative to other known Redstarts using counter-chips, or by finding them in an area used only by a single unbanded Redstart and one or more color-banded or after-second-year male Redstarts (I never observed more than one after-second-year male at a study site in a given year).

Home ranges were estimated using fixed-kernel density estimators that allowed the kernel bandwidth to vary along two independent axes (Duong 2007). Kernel bandwidth was optimized using a plug-in estimator that minimized the sum of the asymptotic mean squared errors (Duong 2007). Since Adelaide's remain pair-bonded year-round and both sexes defend their shared territory, home ranges were jointly estimated using observations from both members of a pair. Territory sizes were calculated using full (100%) utilization distributions (UDs) because territory boundaries appeared to be fairly sharp and extra-territorial movement was rare. Most UD's were calculated using at least 50 locations (68–75%; Figure 16). Territory sizes were compared among sites using Kruskal-Wallis rank sum tests, and between species using a two-sided Mann-Whitney test.

Overlap between Redstart and Adelaide's territories was estimated using a modification of the utilization distribution overlap index (UDOI). The UDOI provides an

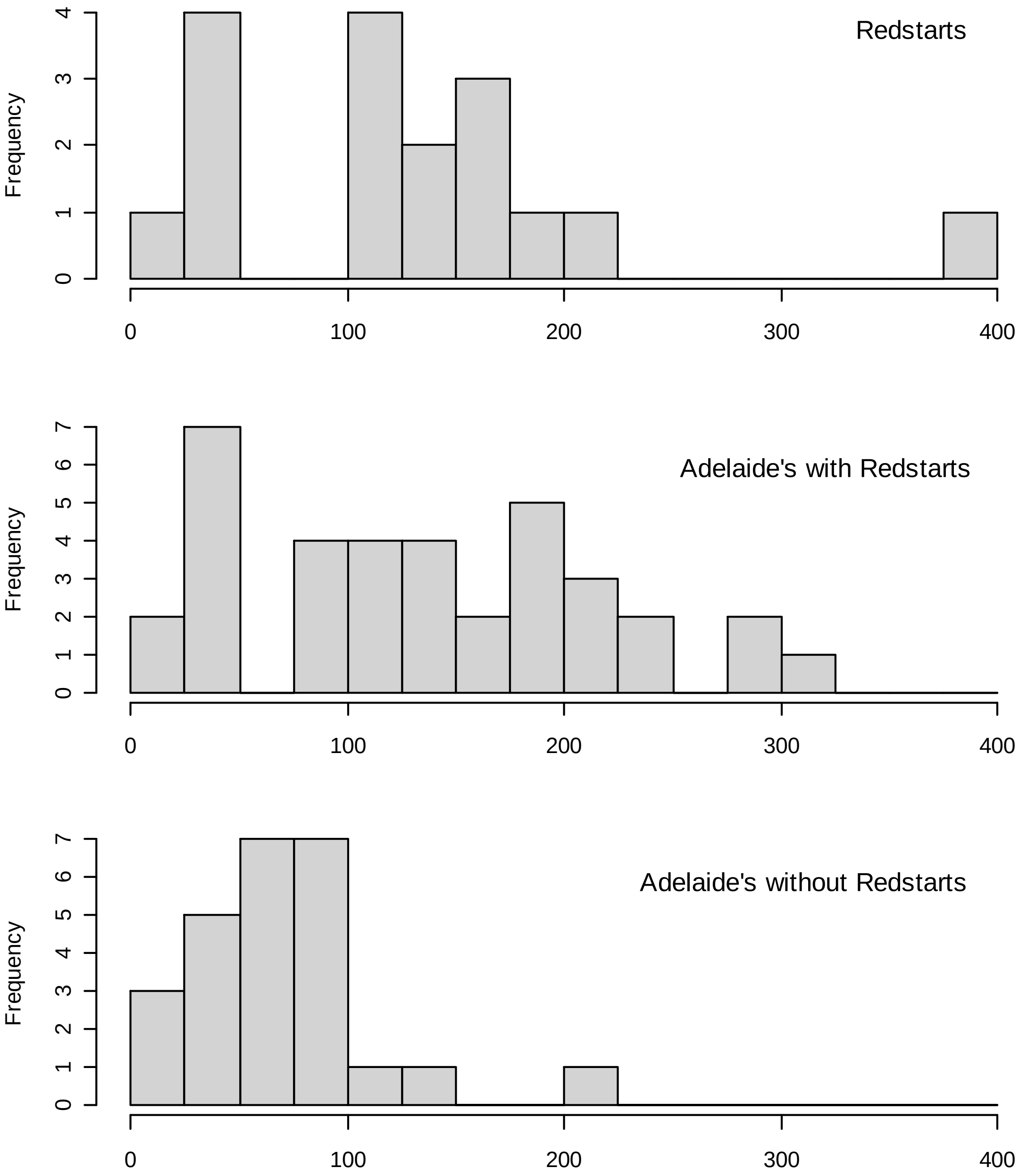

Figure 16. Distribution of sample sizes for the estimation of home ranges.

estimate of the degree to which two individuals use shared space (Fieberg and Kochanny 2005):

$$UDOI = A_{1,2} \sum_{i=1}^{n} \sum_{j=1}^{m} \widehat{UD}_1 \cdot \widehat{UD}_2 \cdot \Delta x \cdot \Delta y$$

where $A_{1,2}$ is the area of overlap between the two territories, Δx and Δy are the length and width of a grid cell, and the summations are made over all grid cells where the two UDs intersect. However, Redstart territories typically overlapped multiple Adelaide's territories, so pairwise comparisons of overlap were not a good measure of potential interspecific territoriality. Instead, a better estimate was a measure of the total overlap between one Redstart territory and multiple Adelaide's territories. Therefore, I modified the UDOI:

$$Total\, UDOI = A_{1,2:p} \sum_{i=1}^{n} \sum_{j=1}^{m} \widehat{UD}_1 \cdot \left[\sum_{k=2}^{p} \widehat{UD}_k \right] \cdot \Delta x \cdot \Delta y$$

where the second UD is replaced by the sum of $p-1$ UDs (here, Adelaide's territories), and $A_{1,2}$ is replaced by the total area of overlap.

This extension accounts for multiple overlapping UDs. However, an additional problem arises because Redstart non-breeding territories are held as individuals, while Adelaide's territories are typically held by pairs. Therefore, a given overlap with an Adelaide's territory has twice the impact that the same overlap would with a Redstart territory. One solution would be to estimate separate UDs for each member of the pair, and sum them using the formula above. However, it was more efficient to calculate a joint UD for the pair. Total UDOI can easily be modified to account for jointly estimated

UDs, simply by multiplying the joint UD by the number of individuals used to estimate that UD. In this study, the UD for each Adelaide’s pair was multiplied by two, because the likelihood of one individual of the pair using a particular point in space was twice that of a single individual. However, this modification could also be applied to any number of the UDs in the Total UDOI measure, with each UD potentially representing different numbers of individuals (e.g. if comparing overlap with a family group or flock).

The UDOI and Total UDOI do not have upper bounds, and can be difficult to interpret in isolation. Therefore, Total UDOI values were also calculated for Redstart-Redstart and Adelaide’s-Adelaide’s overlaps. If interspecific territoriality was about as strong as intraspecific territoriality, the Total UDOI values for interspecific overlaps will be similar to those for intraspecific overlaps. Conversely, if interspecific territoriality is weak or non-existent, the Total UDOI values for interspecific overlaps will be much greater than those for intraspecific overlaps. This hypothesis was tested using one-sided Mann-Whitney tests.

Differences in space use of individual Adelaide’s (or Adelaide’s pairs) when Redstarts were present and absent were quantified using Bhattacharyya’s affinity (BA; Bhattacharyya 1943, Fieberg and Kochanny 2005), which is a good measure of the similarity between utilization distributions (Fieberg and Kochanny 2005). BA ranges from zero (UDs have no similarity) to one (identical UDs). If Redstarts restrict Adelaide’s from using parts of their territory, Adelaide’s with Redstart neighbors would be expected to show greater territory shifts after Redstarts depart than would an Adelaide’s without Redstart neighbors, i.e. Adelaide’s with Redstart neighbors would have a smaller BA value. This hypothesis was tested using a one-sided Mann-Whitney test. Both overlap measures were calculated using full (100%) UDs. UDs were estimated using the package ks (Duong 2007) for R (ver. 2.9.1; R Development Core Team 2009), while both measures of home range overlap were calculated using functions I wrote in R.

Results

Both species had approximately the same mean territory size (Redstart mean 0.39 ha, SE 0.05; Adelaide's mean 0.42 ha, SE 0.07). Redstart territories did not differ in size between the La Joya and Fuerte sites ($\chi^2 = 0.205$, $p = 0.651$; the Granados site did not have any territorial Redstarts), but Adelaide's territories were significantly larger at the La Joya site (mean 0.48 ha; $\chi^2 = 8.244$, $p = 0.016$) than at the Fuerte (mean 0.40 ha) or Granados sites (mean 0.35 ha). Total UDOI was significantly greater for interspecific overlap than for overlap among Redstart ($W = 168$, $p \ll 0.001$; Table 5) and Adelaide's territories ($W = 732$, $p \ll 0.001$). Redstart territories had very little overlap, in part due to their low densities.

There was no difference in territory shifts of Adelaide's with and without Redstart neighbors ($W = 49$, $p = 0.145$). However, two Adelaide's without Redstart neighbors shifted their territories during this period, both in an area of the Granados site where one pair had disappeared. Average BA scores were moderate for both groups (Table 6).

Table 5. Mean and standard error of total UDOI values for three comparisons: overlap between Redstart and Adelaide's territories, overlap among Redstart territories, and overlap among Adelaide's territories.

Comparison	**Median**	**Mean**	**SE**
Redstart-Adelaide's	0.512	0.874	0.191
Redstart-Redstart	0.060	0.057	0.015
Adelaide's-Adelaide's	0.087	0.219	0.044

Table 6. Mean and standard error of BA values for territory shifts in Adelaide's territories, for Adelaide's whose territory overlapped one or more Redstart territories and for those with no overlap.

Comparison	**Median**	**Mean**	**SE**
Did overlap Redstart territory	0.506	0.514	0.050
Did not overlap Redstart territory	0.637	0.577	0.070

Although some individuals had low sample sizes in one of these periods, which might have biased the UD (Figure 16), removing all comparisons involving a UD based on less than 50 observations did not change the conclusion of the hypothesis test.

Discussion

Even though Adelaide's and Redstarts are interspecifically aggressive (Chapter 6), this study shows that they are not interspecifically territorial. Instead, Redstart territories significantly overlap Adelaide's territories. During the breeding season, Redstarts interact with Least Flycatchers (*Empidonax minimus*) in a similar way: the two species are interspecifically aggressive but have overlapping territories (Sherry 1979, Sherry and Holmes 1988, Martin et al. 1996). However, in that system the dominant Least Flycatcher had much smaller territories than did Redstarts (Sherry 1979), while here Adelaide's and Redstarts had territories of similar size.

Adelaide's territories appeared to be saturated at all three study sites within Guánica, so the difference in average territory size among sites is most likely due to differences in habitat quality (Fretwell and Lucas 1969). Territory sizes were typically smallest in mesic habitats, with trees of moderate height and a well developed subcanopy and shrub layer, while the largest territories occurred in dry, scrubby habitats with exposed limestone (pers. obs.). Adelaide's typically forage in tree canopies, but I often observed Adelaide's foraging in the shrub and litter layers during the driest part of the winter. Although arthropod densities decline throughout the winter at Guánica (Chapter 3), arthropod densities may remain fairly constant at the forest floor (Poulin et al. 1992, Strong and Sherry 2000). Territories without substantial shrub and litter layers may need to be larger to compensate for the loss of this stable source of food.

Territory sizes of Adelaide's have not been reported in other studies, but estimated densities were 1.2 individuals per hectare in montane forest (Maricao; Cruz and

Delannoy 1984). In this study, densities on the three sites were approximately 6.2 individuals per hectare at La Joya, 8.5 individuals per hectare at Fuerte, and 10.0 individuals per hectare at Granados. Within Puerto Rico, Adelaide's are most abundant in dry coastal forest and scrub, and the montane forest site is probably marginal habitat (Toms 2010). A drier savannah-like habitat appeared to have larger territories, roughly 1.0 ha (based on territory maps; Staicer 1991). Population density may differ among habitat types, but no generalizations can be made with the limited data available.

Average Redstart territory sizes at Guánica (0.4 ha) suggest that the population density could be as high as 25 individuals per 10 ha, if Guánica was saturated with Redstart territories. However, none of the sites were saturated, so that the true density is no more than 10 individuals per 10 ha. This is among the lowest densities reported in other studies during the non-breeding season: 10.0–112.6 individuals per 10 ha in Jamaica (Holmes et al. 1979, Marra and Holmes 2001), 10 individuals per 10 ha in Mexico (Bennett 1980), 17.5 individuals per 10 ha in Puerto Rican mangroves (Bennett 1980), and 3.8–7.5 individuals per 10 ha on Grand Cayman (Bennett 1980). The comparatively low densities at Guánica may be due in part to habitat quality; in Jamaica, dry forests such as Guánica are of relatively low quality and support lower densities of Redstarts than higher quality habitats (Marra et al. 1993, Parrish and Sherry 1994, Marra 2000, Marra and Holmes 2001, Studds and Marra 2005). Moreover, the sex-ratio is highly female biased at Guánica, an indicator of low habitat quality in Jamaica (Marra et al. 1993, Parrish and Sherry 1994, Marra 2000, Marra and Holmes 2001, Studds and Marra 2005). At biogeographical scales, migrants are less common in Puerto Rico than in the other Greater Antillean islands, which would also lead to lower densities (Terborgh and Faaborg 1980, Wunderle and Waide 1993).

Adelaide's did not shift their territory in response to Redstart departure. Given the large degree of interspecific overlap among territories, the effect of Redstarts on Adelaide's seems to be relatively low in comparison to conspecific competitors. However, even though Adelaide's are dominant over Redstarts (Chapter 6), they do not exclude Redstarts from their territory. In part, this may result from the close spacing of Adelaide's territories: Redstarts may not be able to avoid Adelaide's completely in this habitat. However, behavioral differences between the species suggest another possible explanation. Redstarts are often silent while foraging (pers. obs.), but Adelaide's pairs vocalize frequently (Toms 2010). As a result, Redstarts may be able to keep track of the relative locations of Adelaide's and avoid direct confrontations, a strategy that would allow them to forage in Adelaide's territories by using temporary competition refuges.

Several observations suggest that some Redstarts are vagrants. At the La Joya site, most Redstarts appeared to be territorial, although some individuals appeared to roost off-site. The Fuerte site appeared to have a mixture of territorial and vagrant Redstarts: several individuals were followed as they transited the site, including one color-banded individual that was seen to move through the site several times. Moreover, an after-second-year male was followed through the site one morning. He vocalized frequently, and could not have been overlooked on other days. All Redstarts at the Granados site appeared to be vagrants. Netting at the Granados site in early February captured four Redstarts and 14 Adelaide's, including one Redstart captured twice.

However, although 13 of the 14 Adelaide's were resighted, not a single banded or unbanded Redstart was ever seen on the site after the netting session, even briefly. This strongly suggests that the Redstarts captured during the netting session were vagrants, as no shifts in Redstart territories were seen after late October. The ratio of territorial to vagrant Redstarts at a site could reflect differences in habitat quality. However, the size of Adelaide's territories at these sites suggests that this is not the case. Instead, Redstarts may not be able to hold territories in areas with high densities of Adelaide's.

In conclusion, even though aggressive behaviors implied that these species are competing (Chapter 6), such interspecific competition is not mediated by interspecific territoriality. Interspecific territories overlapped significantly more than intraspecific territories, and Adelaide's did not shift their territories in response to Redstart departure. Redstart densities at this site are relatively low, and some individuals appeared to be vagrant. Adelaide's territories appeared to be saturated at all study sites, and Adelaide's density was inversely correlated with the proportion of Redstarts that were territorial. This study suggests that Redstarts might be able to hold territories overlapping Adelaide's territories by using temporary competition refuges to avoid direct confrontations. However, this strategy may not be effective in areas with high Adelaide's densities, forcing some Redstarts to be non-territorial vagrants.

Chapter 6: An experimental test of interspecific aggression between American Redstarts (*Setophaga ruticilla*) and Adelaide's Warblers (*Dendroica adelaidae*) during the non-breeding season.

Abstract

Interspecific competition among migrant and resident species may be important in the dynamics of non-breeding bird communities, because migrants may not be able to ecologically diverge from resident species. Conditions in dry tropical and subtropical ecosystems appear to limit populations of avian insectivores, suggesting competition may be particularly important in structuring these communities. I used simulated territorial intrusions to determine whether resident Adelaide's Warblers (Adelaide's; *Dendroica adelaidae*) and migrant American Redstarts (Redstarts; *Setophaga ruticilla*) were aggressive towards the other species, a strong indicator that competition is occurring between these species. Decoys and vocalizations of these two species, along with a non-competitive control, were presented to individuals in a crossover experiment, and vocal and physical responses were observed. Both species had significant responses to decoys of conspecific and heterospecific competitors, while completely ignoring the heterospecific control. Repeatability of responses was extremely high in Adelaide's. Experimental results also matched behaviors observed outside of the experiment. This study provides strong evidence that Redstarts and Adelaide's compete for food during the non-breeding season.

Introduction

Intraspecific and interspecific competition can be important in structuring non-breeding bird communities. American Redstarts (Redstarts; *Setophaga ruticilla*) show strong intraspecific interference competition in Jamaica, leading to habitat segregation by age and sex (Marra et al. 1993, Marra 2000, Marra and Holmes 2001, Studds and Marra 2005), and several other species of Neotropical migrant warblers show patterns of sexual habitat segregation that may result from intraspecific competition (Sherry and Holmes 1996, Wallace et al. 1996, Latta et al. 2003). Intraspecific competition can impact population dynamics and breeding success; Redstarts wintering in low-quality habitat have reduced reproductive success (Reudink et al. 2009) and are less competitive during the breeding season (Marra et al. 1998). Dugger et al. (2004) hypothesized that apparent-survival rates of winter residents might be related to interspecific competition with permanent residents, suggesting the effects of interspecific competition may also have important consequences for population dynamics of affected species. However, few studies have examined competition between migrant and resident species (but see Staicer 1992, Greenberg and Ortiz 1994).

The potential for winter-resident species to ecologically diverge from permanent-resident competitors using character displacement (Brown and Wilson 1956) may be limited, because they also face potentially conflicting ecological pressures from competitors during the breeding season. For example, Redstarts compete with different sets of flycatchers, warblers and other species on their breeding and wintering grounds (Kepler 1977, Bennett 1980, Martin et al. 1996), which may result in conflicting evolutionary pressures on their morphology (Wilson 1975, Bennett 1980, Moermond 1990). It is under just these sorts of conditions that interspecific competition is expected to occur most commonly (Orians and Willson 1964).

Dry tropical and subtropical forests are likely ecosystems where competition may occur among winter-resident and permanent-resident species. Seasonal rainfall patterns produce annual droughts during this overwintering period (in the Northern Hemisphere a pronounced dry season occurs from December through April; Ewel and Whitmore 1973, Murphy et al. 1995), reducing arthropod densities (Parrish and Sherry 1994, Strong and Sherry 2000, Van Bael et al. 2003, Jedlicka et al. 2006, Studds and Marra 2007). Arthropod densities are further depressed by avian insectivores (Borkhataria et al. 2006, Jedlicka et al. 2006, Kellermann et al. 2008), and limit the populations of some avian insectivores (Lovette and Holmes 1995, Wilson et al. 2011). Due to the seasonal climate, permanent-resident songbirds usually do not breed during the winter, minimizing the effects of competition for breeding-specific resources. In addition, risk of predation also appears to be comparatively low for adults, given high annual survival rates (Dugger et al. 2000, Sillett and Holmes 2002, Dugger et al. 2004). Thus, in this system there may be strong competition for food, without confounding from simultaneous competition for predator refuges or breeding-specific resources.

Simulated territorial intrusions (i.e. playback experiments) are commonly used to assess territorial aggression towards conspecifics or heterospecifics during the non-breeding season (Holmes et al. 1989, Mabey and Morton 1992, Marra et al. 1993, Stutchbury 1994, Marra 2000). The costs of territorial aggression can be substantial;

increased predation rates, energy expenditure, and loss of time for feeding, resting and preening (Orians and Willson 1964) could all affect individual fitness. Since natural selection should minimize misdirected or non-adaptive interspecific territorial aggression (Murray 1971), it is not surprising that several studies have shown that the results of playback experiments reflect underlying competition (Reed 1982, Marra et al. 1993, Durant 1998, Marra 2000, Martin and Martin 2001).

Here, I use playback experiments to determine whether migratory Redstarts and resident Adelaide's Warblers (Adelaide's; *Dendroica adelaidae*) use aggressive behaviors against the other species during the non-breeding season. Arthropods are a limiting resource in these forests during the winter dry season (Chapter 3). Redstarts and Adelaide's are of similar body mass (averaging 7.4 g and 7.1 g respectively; Arendt et al. 2004) and use similar foraging methods (Chapter 4). These forging niche overlaps possibly arise because seasonally-conflicting competitive pressures prevent Redstarts from ecologically diverging from Adelaide's (Wilson 1975, Bennett 1980). Dugger et al. (2004) suggested these species might be competing in the dry forests of Guánica, southwest Puerto Rico, but no studies have previously examined this hypothesis.

Methods

This experiment was conducted in March–April 2007, 2009 and 2010, in the Guánica Dry Forest (Guánica), a UNESCO Biosphere Reserve located in southwest Puerto Rico (Figure 2). Guánica is a seasonally dry forest that typically receives less than 20 cm of rain from December through March (M. Canals Mora, unpubl. data). The semi-deciduous vegetation is typically less than 5 m in height, with occasional larger emergent trees in favorable microsites (Ewel and Whitmore 1973, Lugo et al. 1978, Murphy and Lugo 1986b).

Adelaide's and Redstarts were captured in mist-nets, aged (as second-year or after-second-year) and sexed using plumage characteristics (Pyle 1997, Chapter 2), and given unique color-band combinations. Territories of most individuals were mapped using focal observations (Chapter 5). However, as Redstart densities were low, some unbanded individuals with unknown territory boundaries were included to increase the sample size. The experiment was conducted on 19 female and 23 male Adelaide's and 20 female and 9 male Redstarts.

The behavior experiment followed a cross-over design, where each individual was randomly assigned to a particular order (or sequence) of decoys (treatments). Each individual was presented with decoys of a Redstart, an Adelaide's, and a Black-whiskered Vireo (*Vireo altiloquus*; hereafter Vireo). Vireos were used as a non-competitive control because they are insectivorous and Redstarts and Adelaide's both interact with this species near the beginning and end of the winter, but they are unlikely to directly compete with it due to its much larger size (Puerto Rican individuals average 20.3 g; Arendt et al. 2004) and divergent foraging niche on other islands (Terborgh and Faaborg 1980). Female decoys were used because the sex-ratio of Redstarts is highly female-biased at Guánica (nearly 90% female; Dugger et al. 2004). After locating an individual, the first decoy was placed 5–10 m away and a speaker was attached to vegetation 25–50 cm away from the decoy. A three-minute recording of vocalizations for the decoy species, consisting of a mixture of songs and chips, was then played. Vocalizations were edited from recordings of Stokes (1997) and Oberle (2000), with additional Adelaide's chips I recorded at Guánica. Subsequent decoys were typically presented 0.5–2.0 min after completing the previous decoy, but occasionally individuals could not be easily re-sighted. In a few cases, experiments could not be completed until the following day.

Several components of aggressive behavior were quantified. The frequency of chips, songs (Adelaide's only, as only a single after-second-year male Redstart sang), chitbursts (Adelaide's only; Staicer 1991) and flyovers (flight passing above the decoy, within 3 m) were categorized as: 0 = none; 1 = occasional; 2 = frequent; and 3 = very many. Each species also uses stereotyped aggressive postures (Ficken 1962, Staicer 1991, Toms 2010), which were categorized as: 0 = no posturing; 1 = mild posturing; 2 = moderate posturing; and 3 = intense posturing. An overall score (1 to 4) was also quantified following Marra (2000), except that no physical contact with the decoy was required to attain the highest score (no decoy was ever physically hit). In all cases intermediate scores (on 0.5 point intervals) were also used. Two observers individually estimated scores for most individuals (a single observer was used for some individuals in 2007), with final composite scores determined by consensus.

Data were analyzed using linear mixed-effects models, which included fixed effects for treatment and sex, and a random effect of individual nested within sequence. In addition, models included fixed effects for time period (first, second or third decoy presented), sequence, carryover effects and a time period by treatment interaction term, to account for potential effects of the experimental design. Linear mixed models are preferred above ANOVA analyses when the number of individuals is not equal among sequences (Díaz-Uriarte 2001). Models were fit with restricted maximum likelihood using Proc Mixed in SAS 9.2.

In 2007, a Vireo decoy was not used. Analyses excluding 2007 data showed that no carryover or time period effects were present for any of the response variables (unpubl. data). Moreover, no individual of either species showed any aggressive behaviors towards the Vireo decoy (i.e. all behaviors were scored as no response for all individuals tested). Therefore, Vireo responses were imputed for 2007 data (using mean scores), after randomly assigning them to decoy presentation orders (maintaining the order of the Adelaide's and Redstart decoy presentation).

Eight Adelaide's were tested in both 2009 and 2010 (three after-second-year females and five after-second-year males). Only 2009 data for these individuals were included in the main analyses to avoid pseudoreplication. However, both years of data were used to conduct a test of repeatability, the proportion of among- plus within-individual variance attributable to among-individual variation (Lessels and Boag 1987, Dewitt et al. 1999). For this analysis, an additional term was included in the linear mixed-effect model, a random effect of year nested within individual. This provided an estimate of within-individual variation.

I also observed occasional interactions between Redstarts and Adelaide's during field studies of territorial and foraging behaviors. A summary of these ad-hoc observations is included to support the generality of the experimental results.

Results

Experimental responses

Both species showed significant overall responses to decoys of conspecific and heterospecific competitors (p « 0.001 for Adelaide’s, p = 0.002 for Redstarts), while exhibiting no response to the decoy of a non-competing heterospecific. Adelaide’s responded significantly more aggressively to conspecific competitors than to heterospecific competitors, while Redstarts responded only slightly more aggressively to conspecifics than to heterospecific competitors (Figure 17). Male Redstarts were more aggressive than females (p = 0.026), but there were no differences in aggression between the sexes in Adelaide’s (p = 0.993).

Both species used chips in similar ways against conspecifics and heterospecifics, with a slightly higher rate of use against conspecific decoys, and a significantly higher rate of use than against Vireos (p « 0.001 for Adelaide’s, p = 0.021 for Redstarts; Figure 18). Adelaide’s also used chitbursts and songs against both conspecifics and heterospecifics (p = 0.042 for chitbursts, p « 0.001 for songs), although the confidence bounds for their use against Redstarts were not significantly different to their use against Vireos. Differences in use of vocalizations were seen between sexes in both species. Male Redstarts were more likely to chip than females (p = 0.021). In contrast, female Adelaide’s were more likely to chip (p « 0.001) or chitburst (p = 0.004) than males. Only male Adelaide’s sang in response to playbacks (leading to a highly significant difference, p « 0.001).

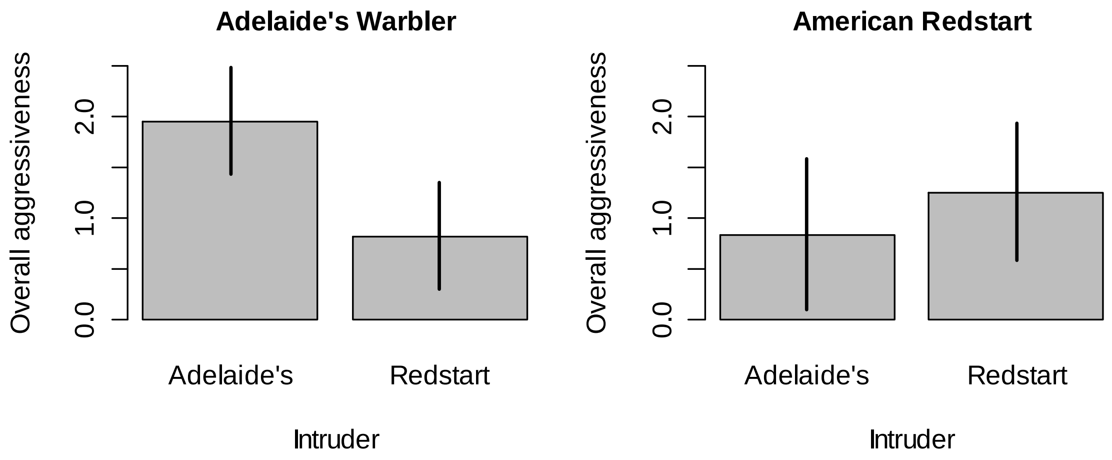

Figure 17. Estimated effect sizes and 95% confidence intervals for the overall response of Adelaide's Warblers and American Redstarts to decoys of each species, relative to the response to Black-whiskered Vireo decoy.

Adelaide's also used aggressive postures and flyovers against both species ($p \ll 0.001$ for both responses; Figure 19), although only the responses to conspecific decoys were significantly different from those to Vireos. There was also a trend for Redstarts to use aggressive postures and flyovers against conspecifics, but this was not significant ($p = 0.173$ for aggressive postures and $p = 0.093$ for flyovers; Figure 19). Aggressive postures and flyovers were occasionally used against heterospecific decoys, but were relatively uncommon. Males and females of both species were equally likely to use aggressive postures ($p = 0.660$ for Adelaide's and $p = 0.266$ for Redstarts). Adelaide's of both sexes also used flyovers ($p = 0.266$), but male Redstarts were more likely to flyover than females ($p = 0.021$).

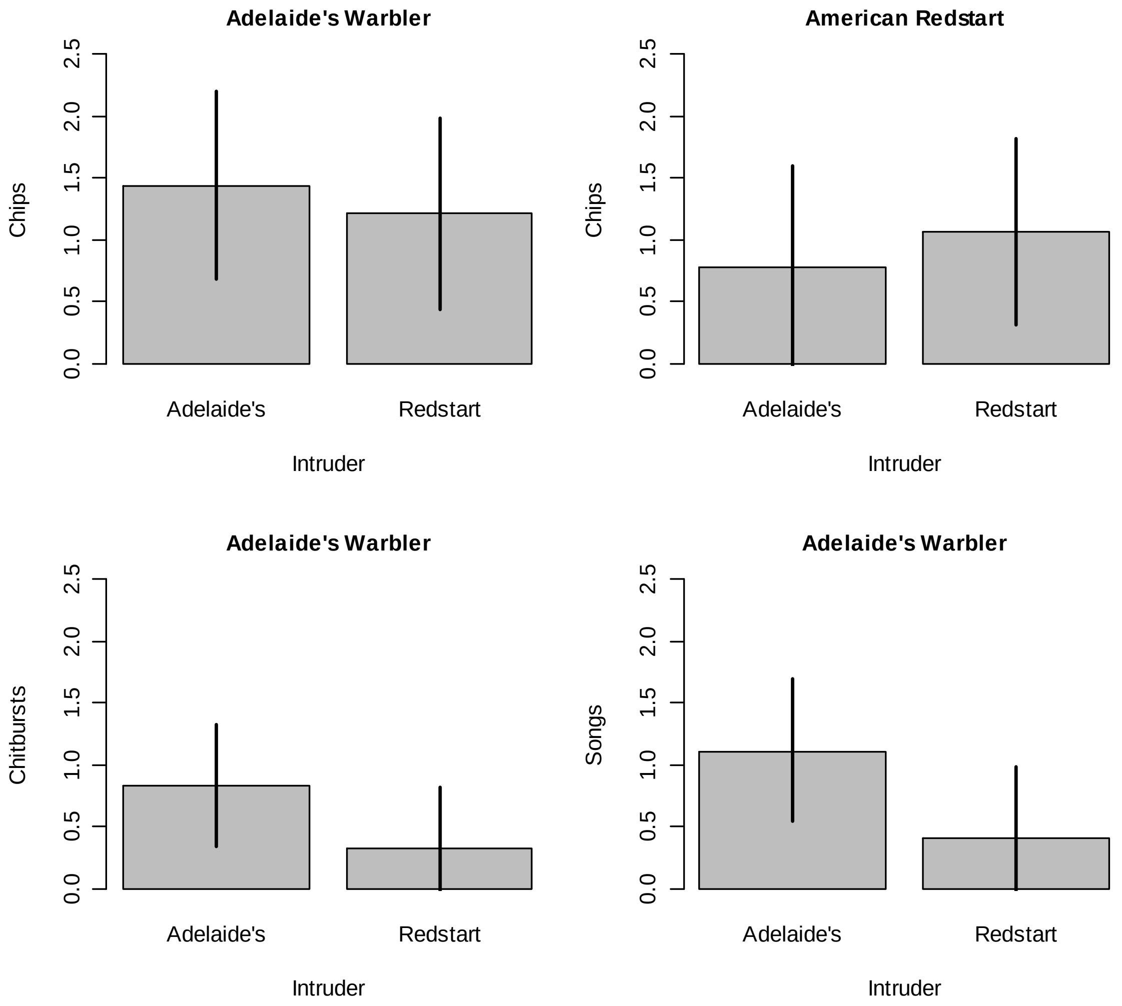

Figure 18. Estimated effect sizes and 95% confidence intervals for the vocal responses of Adelaide’s Warblers and American Redstarts to decoys of each species, relative to the response to Black-whiskered Vireo decoy. American Redstarts do not chitburst, and male song was noted only in a single individual, so these responses were modeled only for Adelaide’s Warblers.

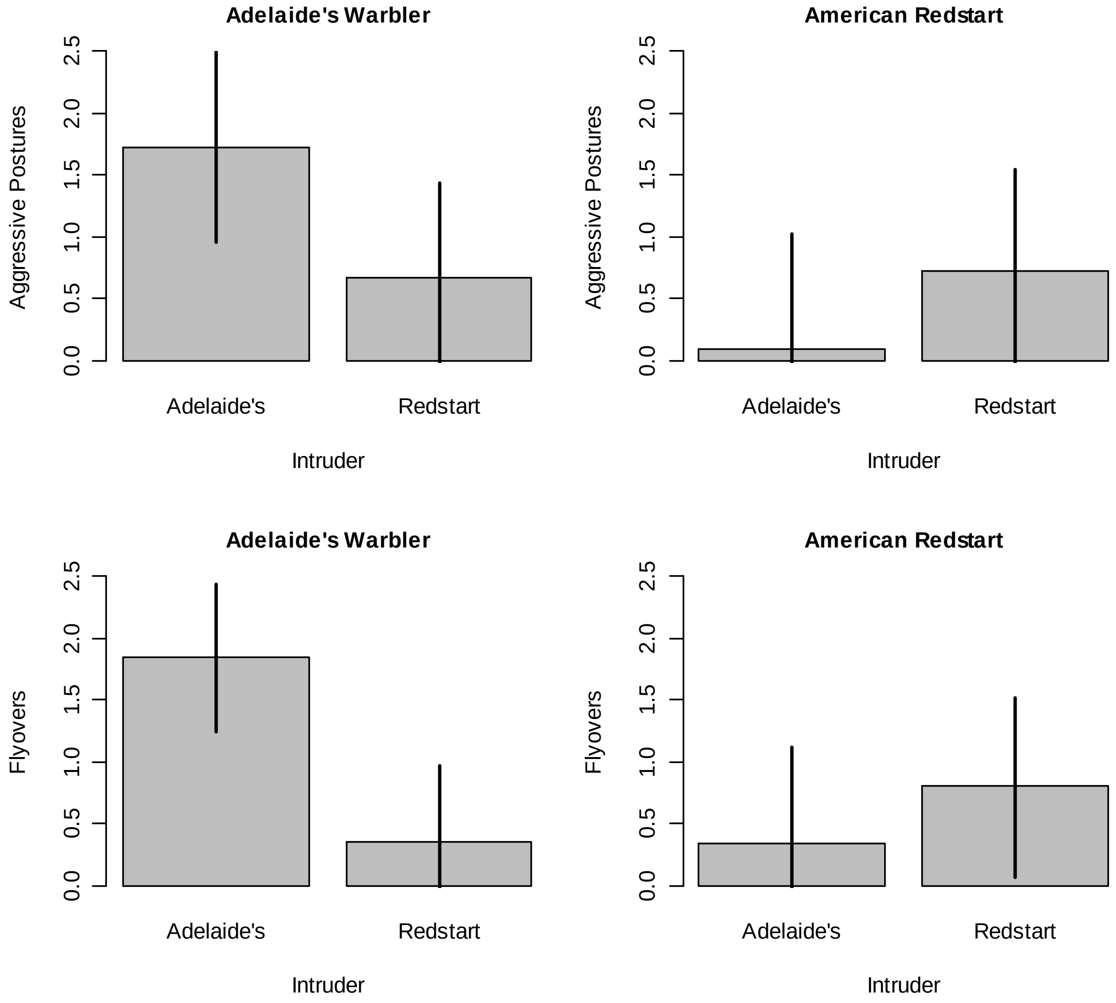

Figure 19. Estimated effect sizes and 95% confidence intervals for the postural responses of Adelaide's Warblers and American Redstarts to decoys of each species, relative to the response to Black-whiskered Vireo decoy.

Table 7. Estimated repeatability of responses for eight Adelaide's Warblers sampled during both 2009 and 2010.

Response	**Among-individual Variation**	**Within-individual Variation**	**Estimated Repeatability**
Overall Response	0	0	N/A
Chips	0.1577	0	1
Chitbursts	0.1085	0	1
Songs	0.1049	0	1
Posturing	0.0883	$1.91\ e^{-4}$	0.998
Flyovers	0	0	N/A

Repeatability was extremely high for all responses in Adelaide's, except for the overall response and flyovers, where it could not be estimated because variance estimates were zero (Table 7).

Carryover effects were not significant (p » 0.10 in all cases, except p = 0.10 for a negative carryover of Adelaide's on the overall response of Redstarts and p = 0.07 for a positive carryover of Redstarts on the songs of Adelaide's). In these two instances where carryover effects were nearly significant, conspecific carryover effects were negligible. Similarly, other design effects (sequence, period and period*treatment effects) were almost always not significant (p » 0.10 in all cases, except p = 0.035 for order of decoy presentation on posture of Adelaide's). In this case, the effect of order seemed to be inconsistent, with no patterns suggesting why order might be important. Given the inconsistency of the carryover and design effects, these effects were likely spurious effects resulting from the large number of hypothesis tests conducted, and were ignored in the hypothesis tests of interest (the effect of playback type on the response variables).

Ad-hoc behavioral observations

Outside of the experiment, Redstarts and Adelaide's were most commonly observed interacting vocally. Redstarts used *metallic chip* or *tsip* calls in response to Adelaide's calls and songs (see Sherry and Holmes 1997 for a description of these vocalizations). Similarly, Adelaide's responded to Redstart calls with chips and songs, and occasionally even chitbursts. Vocal interactions were observed to occur throughout the over-wintering period.

In addition, physical interactions between these species were seen, particularly early in the over-wintering period when Redstarts were establishing territories (October and early November). Redstarts were sometimes observed to use aggressive posturing during these encounters, but no Adelaide's were observed using stereotyped aggressive displays. Physical attacks typically did not include vocalizations, but a few Redstarts were observed chipping between attacks. Physical attacks were sometimes repeated, with the level of aggression typically increasing each time. Both Redstarts and Adelaide's were observed to initiate aggressive interactions, typically by flying directly at the heterospecific. Initiation of attacks was balanced between species early in the over-wintering period, but Adelaide's usually initiated attacks later in the season. Redstarts and Adelaide's were occasionally seen foraging in close proximity without interacting, particularly later in the winter, although one of the individuals typically moved away after a short time (most often the Redstart).

Discussion

This study strongly supports the hypothesis of interspecific aggression between resident Adelaide's Warblers and migratory American Redstarts in this ecosystem. For both species, responses to the presentation of conspecific decoys were stronger than responses to heterospecific decoys, while no individual responded to the control decoy. In addition, responses of Adelaide's were consistent across years, and the results matched observational data.

Although both species exhibited aggressive responses to decoys of heterospecific competitors, Adelaide's responses were more aggressive when compared on an absolute scale. Field observations of aggressive interactions generally concur with the experimental results, and suggest that Adelaide's are dominant over Redstarts. Previous studies have found the dominant species to be more aggressive when responding to playbacks (Prescott 1987, Robinson and Terborgh 1995, Martin and Martin 2001). Nevertheless, relative to a conspecific competitor, Redstarts responded more strongly to an Adelaide's decoy than Adelaide's responded to a Redstart decoy. Adelaide's maintain pair-bonds and territories year-round (Staicer 1996b), while Redstarts have to establish individual winter territories each year (Holmes et al. 1989). Prior occupancy of territories has been shown to provide an advantage in competitive contests among conspecifics (Tellería and Pérez-Tris 2004), and may provide a similar advantage in heterospecific contests. Thus, Adelaide's may pose a greater relative threat to Redstarts than Redstarts do to Adelaide's. Similar patterns of response are seen in Great Tits (*Parus major*) which respond more strongly to dominant Chaffinches (*Fringilla coelebs*) than Chaffinches do to Great Tits (Reed 1982), and in Reed Warblers (*Acrocephalus scirpaceus*) which respond more strongly to the larger and dominant Great Reed Warbler (*A. arundinaceus*) than Great Reed Warblers do to Reed Warblers (Leisler 1988).

Adelaide's used the same set of aggressive behaviors with conspecific and heterospecific decoys. However, although Redstarts chipped almost as aggressively towards heterospecific decoys as to conspecific decoys, they showed reduced levels of aggressive posturing and flyovers. On the breeding grounds, Redstarts avoid flying in response to playbacks of Least Flycatchers (*Empidonax minimus*) because Least Flycatchers physically attack Redstarts only after visual recognition (Martin et al. 1996). It is likely that Redstarts use a similar avoidance behavior when facing a dominant competitor on the wintering grounds. Avoidance of the dominant species by the subordinate is known from other species (Martin and Martin 2001) and is thought to be an important part of niche partitioning (Morse 1970, 1971, 1974). Male Redstarts were significantly more aggressive overall than females at Guánica, chipping and flying over decoys more frequently. Although male and female Redstarts were equally aggressive to conspecific playbacks in mangrove sites in Jamaica (Holmes et al. 1989), males are substantially more aggressive than females in dry Jamaican scrub (Marra 2000). Male Redstarts are dominant over female Redstarts in the non-breeding season (Marra et al. 1993, Marra 2000), and may be more aggressive to other species as well.

As in previous studies, responses to conspecific competitors were stronger than to heterospecific competitors (Reed 1982, Prescott 1987, Martin and Martin 2001). When combined with the uniform lack of response to a non-competitive decoy, this suggests that Adelaide's and Redstarts both have nuanced responses to intruders, whereby they assess and respond to a potential threat appropriately. Even a short period between decoy presentations was sufficient for individuals of both species to return to a normal state, suggesting that this evaluation occurs rapidly. Individuals of many species learn to identify and respond selectively to competitors (Catchpole 1978, Catchpole and Leisler 1986, Prescott 1987, Jankowski et al. 2010).

Observations of species interactions were consistent with the experimental results. Aggressive interactions were more common in the fall, as seen in other studies (Chipley 1976, Holmes et al. 1989). The experiment was conducted in the late winter, when ad-hoc observations of aggressive interactions were less common. This suggests that experimental results might actually have underestimated the potential strength of responses to heterospecifics. However, Adelaide's seem to respond in the same manner over both the short- (Staicer 1991) and long-term (this study), so it is also possible that responses to "strangers" do not change over the winter.

Based on a previous conspecific playback experiment, Staicer (1991) hypothesized that male Adelaide's use song for longer-range disputes with known neighbors, and use calls, flyovers and posturing for close-range disputes with neighbors or with strangers. The songs used in this experiment were from "strangers", and therefore might have been expected to elicit few songs in response. However, male and female Adelaide's typically used a variety of vocally and physically aggressive behaviors in response to conspecific decoys. It is possible that males are more likely to sing when a decoy is visible; Staicer (1991) did not use decoys in her playback experiments. Female and male Adelaide's were equally aggressive. Female Adelaide's are strongly territorial, except when nesting (Staicer 1991, Toms 2011).

Adelaide's are known to be aggressive to other warblers, attacking Northern Parulas (*Parula americana*) and Prairie Warblers (*D. discolor*) in savannah-like habitat (Staicer 1992). They also respond aggressively to playbacks of their close congeners, Olive-capped (*D. pityophila*), Grace's (*D. graciae*) and Yellow-throated Warblers (*D. dominica*; Staicer 1991). However, this is the first study to show that Adelaide's sometimes use the stereotyped chitburst display against heterospecifics. Redstarts might invoke a stronger response than the species tested by Staicer (1991), which were uncommon or absent from her study site. Alternatively, even though a decoy is not necessary to elicit chitburst displays (Staicer 1991), decoys may induce Adelaide's to use aggressive postures at a lower threshold of aggression.

The aggressive response of Redstarts and Adelaide's towards each other, but not to other heterospecifics, would not be adaptive unless they competed for food or other resources (Orians and Willson 1964, Murray 1971). The limited availability of arthropods in Guánica during dry years (Chapter 3) and the similarity in their foraging techniques (Chapter 4) suggests that they are indeed competing for food. The resident Adelaide's appear to be behaviorally dominant over migrant Redstarts. Residents were also found to be dominant over migrants in previous studies (Leisler 1992, Staicer 1992).

However, Adelaide’s do not exclude Redstarts from their territories (Chapter 5). Instead, Redstarts seem to avoid Adelaide’s while foraging. Indeed, the relationship between Redstarts and Adelaide’s during the non-breeding season is highly reminiscent of that between Redstarts and Least Flycatchers during the breeding season, where interspecific competition has been shown (Sherry 1979, Sherry and Holmes 1988, Martin et al. 1996). This experiment provides strong evidence that Adelaide’s do compete with Redstarts.

Chapter 7: Do Adelaide's Warblers and American Redstarts compete for food in the non-breeding season?

Competition will not occur among species unless they share the same resources, and those resources are limiting. In the non-breeding bird community of the Guánica Dry Forest, southwest Puerto Rico, food is the only resource that is likely to be limiting because predation on adults is low. This study tested the hypothesis that Adelaide's Warblers (Adelaide's; *Dendroica adelaidae*) and American Redstarts (Redstarts; *Setophaga ruticilla*) compete for food during the non-breeding season when both are sympatric in Guánica. These species may be the most ecologically similar pair of resident and migratory passerines in the West Indies, with similar foraging techniques and body sizes (Oberle 2000).

Adelaide's and Redstarts are both generalist insectivores, consuming a wide range of arthropod taxa (Wetmore 1916, Lefebvre et al. 1992, Sherry and Holmes 1997, Toms 2010). Differences in prey species taken by insectivores are typically due to differences in foraging locations or methods, rather than to different preferences for particular taxa (MacArthur 1958, Robinson and Holmes 1982, Radford and Du Plessis 2003). I have shown that these species have a very high degree in overlap of both foraging location (vegetation type, relative location within tree canopies and height from ground) and attack type (foraging method and substrate attacked), both when assessed at the level of the population and at the level of individuals (Chapter 4). In addition, both species have flycatcher-like bill morphology (Chapter 4). This suggests that they are consuming the same arthropods, a conclusion which is supported by dietary studies (Wetmore 1916, Lefebvre et al. 1992, Sherry and Holmes 1997, Toms 2010).

Moreover, arthropods do seem to be limiting in this system in some years (Chapter 3). I monitored arthropod densities through two non-breeding seasons. In the drier of the two years, leaf fall was pronounced in all vegetative layers and total arthropod density declined. In contrast, during the wetter year, leaf fall was largely limited to the shrub layer and total arthropod density remained fairly constant (Chapter 3). No mortality was observed in either bird species throughout the non-breeding season. However, the body condition of both species declined during the drier year, even though they appeared to forage for a higher proportion of the day, while they were able to maintain body condition in the wetter year (Chapter 3). Decreased body condition may delay the departure of migratory Redstarts (Studds and Marra 2005, 2007, 2011), which is correlated with increased mortality during migration and reduced reproductive success (Marra et al. 1998, Bearhop et al. 2004, Smith and Moore 2005, Reudink et al. 2009). Similarly, decreased body condition in the resident Adelaide’s may delay their response to conditions favorable for breeding, thereby limiting their reproductive success (Staicer 1991, Toms 2010). Thus, food is limiting these species not through direct mortality, but through indirect sub-lethal carryover effects.

My behavioral experiment supports my contention that these species compete (Chapter 6). Aggressive behaviors have high costs, and should be used only if the benefits of aggression outweigh these costs (Orians and Willson 1964, Murray 1971). I simulated territorial intrusions to determine whether each species was aggressive towards the other species. Both species were significantly more aggressive to decoys of the other species than they were to a decoy of a non-competitive control (Chapter 6). In addition, responses to conspecifics were somewhat stronger than responses to heterospecifics, confirming that the aggressive behaviors are used in a manner consistent with an adaptive response. Field observations supported the experimental results, and showed that Adelaide's were the dominant species (Chapter 6).

These results indicate that Redstarts and Adelaide's are competing for food, but do not reveal the form that this competition takes. The high degree of similarity in foraging niches when both species are present (Chapter 4) shows that they do not partition food resources directly. However, Redstarts might still be preventing Adelaide's from using preferred resources (Alatalo et al. 1985). Therefore, I determined whether Adelaide's shifted their foraging niches when Redstarts left, using Adelaide's without Redstart neighbors as a control for any changes related to the onset of the breeding season. Adelaide's did not differentially shift either their foraging location or attack type after Redstarts left (Chapter 4), indicating that depletion competition does not occur.

Alternatively, each species could defend territories against the other species, as well as against conspecifics. However, detailed territory mapping showed that interspecific overlap of territories was significantly greater than the intraspecific territory overlap of both species (Chapter 5). In addition, Adelaide's did not shift territories when Redstarts left, demonstrating that Redstarts were not restricting the space use of Adelaide's (Chapter 5). Thus, interference competition is not occurring.

By process of elimination, my results suggest that the subordinate Redstarts integrate into this community by using a vagrant fugitive strategy (Figure 1). Other observations support this hypothesis. Redstarts are often silent while foraging (pers. obs.), while Adelaide's vocalize frequently (Toms 2010). As a result, Redstarts may be able to keep track of the relative locations of individual Adelaide's and avoid direct confrontations. This would allow them to forage in Adelaide's territories by using temporary competition refuges. Similar avoidance of the dominant species by the subordinate is known from other species (Martin and Martin 2001) and is thought to be an important part of niche partitioning (Morse 1970, 1971, 1974). However, this strategy may not be effective in areas with high Adelaide's densities, forcing some Redstarts to be non-territorial vagrants (Chapter 5).

Adelaide's are constrained by strong intraspecific competition to defend their territory year-round. Adelaide's are dominant over Redstarts, which are comparatively uncommon at this site, so intraspecific competition is a stronger source of evolutionary pressure for Adelaide's than is competition with Redstarts. In turn, Redstarts may not have evolved to minimize competition with Adelaide's because they face conflicting selective pressures from competitors on their breeding grounds and from migration itself. Instead, the behavioral flexibility of Redstarts seems to allow them to coexist with a dominant competitor.

Such competition between migrants and residents may be unusual within the West Indies. On the other Greater Antillean islands, migratory warblers are present at much higher densities and resident warblers tend to occur only in a restricted set of habitats or areas (Terborgh and Faaborg 1980, Wunderle and Waide 1993, Raffaele et al. 2003). In contrast, in the Lesser Antillean islands, migratory warblers are uncommon to rare and resident warblers use most habitats available. Thus, Puerto Rico may be the only island where migrants and residents are both present in moderate numbers.

Nevertheless, this study may be applicable to other regions. I have argued that competition may be more intense between migrants and residents than it is among residents or among migrants because ecological character displacement is restricted in migrants (Chapter 1). Moreover, it may be more intense or frequent during the non-breeding season when survival is the only strong selective force. Since direct mortality is uncommon in adult songbirds (Dugger et al. 2000, Sillett and Holmes 2002, Dugger et al. 2004), the pressure to ecologically diverge from competitors in the non-breeding season may well be reduced compared to that of competitors during the breeding season, where limiting resources directly impact population growth rates through reduced reproductive success.

In conclusion, Adelaide's and Redstarts do seem to be competing for food, but not through niche partitioning or interspecific territoriality. Instead, the evidence suggests that Redstarts listen to the frequent vocalizations of Adelaide's, and forage in areas of their territory that minimizes the risks of confrontation at any given time: they use temporary competition refuges. Redstarts are not territorial where Adelaide's densities are high, suggesting that Redstarts may be vagrant in these areas, or avoid them entirely. Competition does occur between these species, and appears to be mediated through aggressive confrontations and the behavioral flexibility of Redstarts.

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VITA

Judith Toms was born in Port Alberni, British Columbia, Canada. She lived in Vancouver and Nanaimo before moving to Victoria for her undergraduate studies. She received an Honors degree in Biology, with a minor in Statistics, from the University of Victoria in 1997. As an undergraduate, she obtained work experience in many areas of biology, including cancer research, fisheries, avian ecology and forest ecology.

After her undergraduate degree, Judith spent several years travelling and working as a statistician and ecologist. In 2001 she returned to academia, working with Susan Hannon at the University of Alberta. She completed her M.Sc. in Ecology in December 2003, and immediately started a M.Math. degree at the University of Waterloo. In 2005 she moved to the University of Missouri to work with John Faaborg. Her dissertation research combined her interests in competition, the effects of migration on species' life histories and animal behavior, and lead her to conduct research in many aspects of ecology that she did not expect.

Judith's interests are focused on community ecology, particularly interactions among species. However, her research also touches on many other aspects of ecology, and her interest extends to taxa other than birds. Her work often involves novel statistical approaches to data analysis, and she has a strong interest in improving the statistical education of biologists. She has been a lecturer for an introductory statistics course for biologists at the University of Waterloo, worked as a lab instructor for several biology courses at the Universities of Alberta, Missouri and Nebraska, and worked as a statistics tutor at the Universities of Waterloo and Auckland. She intends to continue in academia.