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COEXISTENCE OF RESIDENT AND MIGRATORY *CATHARUS* THRUSHES IN A MONTANE FOREST RESERVE OF THE NORTHERN NEOTROPICS: ON HABITAT USE AND MORPHOLOGY

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Resumen. – Coexistencia de zorzales (*Catharus*) residente y migratorio en un bosque de montaña al norte de la región Neotropical: sobre el uso de hábitat y morfología. – La interacción inter-específica en sitios de re-abastecimiento en la región Neotropical puede ser un factor que limita a las poblaciones de aves residentes y migratorias. Especies de aves congenéricas con características morfológicas similares podrían potencialmente competir por recursos limitados mientras coexisten, aunque la segregación ecológica puede reducir los efectos negativos de la competencia inter-específica. Aquí evaluamos la segregación ecológica entre el Zorzal de montaña (*Catharus frantzii*) y el Zorzal de Swainson (*C. ustulatus*) durante la primavera del 2002 y 2003 en una reserva de bosque montaña en los Altos de Chiapas. Para examinar la posible segregación de hábitat, comparamos las abundancias relativas de los zorzales de montaña y de Swainson a través de cinco tipos de hábitat de bosque. Además, comparamos sus características morfológicas para predecir la posición de forrajeo de cada especie en el sotobosque. Los zorzales de montaña y de Swainson coexisten en los mismos hábitat en la Reserva Huitepec durante el periodo migratorio hacia el norte del Zorzal de Swainson. Sin embargo, diferencias morfológicas implican que cada especie usa diferentes localidades de forrajeo dentro del sotobosque. No obstante esto, observaciones preliminares sugieren que los zorzales de montaña y de Swainson podrían requerir alimento de porciones del sotobosque en donde la otra especie parece estar mejor adaptada. Futuros estudios de la interacción entre zorzales de montaña y de Swainson pueden permitir un mejor entendimiento de las interacciones entre especies de aves residentes y migratorias en la región Neotropical.

Abstract. – Inter-specific interactions at stopover sites in the Neotropics may be an important factor limiting populations of both resident and migrant birds. Morphologically similar, con-generic bird species potentially compete for limited resources while coexisting, although ecological segregation can reduce negative effects of inter-specific competition. We evaluated ecological segregation between the resident Ruddy-capped Nightingale Thrush (*Catharus frantzii*) and the migratory Swainson's Thrush (*C. ustulatus*) during spring of 2002 and 2003 in a cloud mountain forest reserve in the Central Highlands of Chiapas. In order to examine possible habitat segregation we compared relative abundances of Ruddy-

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capped Nightingale and Swainson's thrushes across five forest habitat types. Furthermore, we compared morphological characters of these thrush species in an attempt to predict the foraging position of each species in the forest understory. The Ruddy-capped Nightingale and Swainson's thrushes coexist in the same habitats in the Huitepec Ecological Reserve during Swainson's Thrush's northward migration period. However, differences in morphology imply that each species may exploit different foraging locations within the forest understory. Despite this, preliminary observations suggest that Ruddy-capped Nightingale and Swainson's thrushes might require food from parts of the forest understory to which the other species seems better adapted. Further research on coexisting Ruddy-capped Nightingale and Swainson's thrushes could lead to a better understanding of interactions between resident and migrant bird species in the Neotropics. *Accepted 31 January 2006.*

Key words: *Catharus ustelatus, Catharus frantzii,* Resident-migrant coexistence, habitat-resource segregation, eco-morphology, and cloud montane thrushes.

INTRODUCTION

Morphologically similar, con-generic bird species occurring in the same area potentially compete for limited resources (e.g., Dilger 1956, Hamilton 1962, Raitt & Hardy 1970, Noon 1981, Grant & Grant 1982, Garcia 1983, Alatalo *et al.* 1987, Greenberg *et al.* 1993, Forstmeier *et al.* 2001). At the end of the Neotropical dry season, many types of potential food resources available to forest birds are at low levels (e.g., Wolda 1978, Rappole 1995). Yet this is a time when many resident species start breeding, possibly to time the rearing of young with the wet season increase in invertebrate abundance (Poulin *et al.* 1992, Stutchbury & Morton 2001). It is also at this time that Nearctic-Neotropical migrants require substantial amounts of energy while traveling through Middle America on their way to North American breeding grounds (Moore *et al.* 1995). Ecological theory proposes that the negative effects of inter-specific competition may be alleviated by the segregation of habitat or resource use (Schoener 1974, Greenberg 1995, Begon *et al.* 1996, Johnson *et al.* 2005). Thus, it is expected that morphologically similar, closely related species coexisting in the same area will differ in the use of one or more niche variables (MacArthur 1958, Schoener 1974, Carrete *et al.* 2005).

Morphology can provide insight into the ecology of organisms (see Leisler & Winkler 1985, Miles *et al.* 1987, Landmann & Winding 1993, Ricklefs & Miles 1994). If it is accepted that current morphology reflects adaptations to abiotic and biotic interactions encountered by species during their life time (Ricklefs & Miles 1994, Martin 2001), then comparisons of some "ecologically important" morphological characters could be used to investigate potential ecological segregation among coexisting closely related species. Consequently, although morphology may not provide a complete picture of the niche width of individual species (Ricklefs & Miles 1994), within genus differences in morphology may indicate where one species is better adapted to forage compared to another species (Dilger 1956, James 1982, Leisler & Thaler 1982, Leisler & Winkler 1985, Martin 2001, Forstmeier *et al.* 2001).

The location of the Huitepec Ecological Reserve along a major migratory route provides an opportunity to study the ecology of a resident and a transient migrant thrush species in the understory of a northern Neotropical highland forest. The main objective of this study was to answer preliminary questions regarding habitat use and potential ecological segregation between the resident Ruddy-capped Nightingale Thrush (*Catharus frantzii*) and the migratory Swainson's Thrush

(*C. ustulatus*). Hamilton (1962) suggested that habitat segregation in closely related bird species can be observed at different spatial scales, including: segregation of different, but contiguous habitats and segregation of foraging positions in three-dimensional space within the same general habitat type (microhabitat segregation). We use this principle as a starting point in generating null-hypotheses about the distribution and morphology of each species. First, in order to investigate possible habitat segregation, capture frequencies of Ruddy-capped Nightingale and Swainson's thrushes caught during spring of 2002 and 2003 were used to compare relative abundance across five habitat types located within the Huitepec Ecological reserve. Secondly, morphological characters of Ruddy-capped Nightingale and Swainson's thrushes were also compared. Thereafter, once established, morphological differences were used to predict where in the forest understory each species is best adapted for foraging relative to the other species.

MATERIALS AND METHODS

Study site. The Huitepec Ecological Reserve is located 4.5 km northwest of San Cristobal de Las Casas in the highlands of Chiapas in southeastern Mexico (16°44'38"N, 92°40' 15"W). The reserve is situated on the northeastern slope of the inactive volcano Cerro Huitepec and covers 137 ha (flat area) of oak forest at altitudes between 2230 m and 2710 m. While the reserve consists of predominantly oak forest (*Quercus* spp.), the surrounding areas (where forested) are dominated by pine-oak forests, which are characteristic of the highlands of Mexico and Northern Central America. Despite this, the area immediately surrounding the protected reserve consists mainly of agricultural lands, cleared forest and human settlements, although, at higher elevations, the reserve is bordered by relatively undisturbed humid oak woodland. Due to its geographical location in the non-equatorial tropics, the study area is subject to a distinct wet period (May–October), when most of the mean annual 1300 mm of rain falls. However, higher regions of the reserve receive year round moisture through land level clouds, which in turn supports the remnant patch of cloud forest vegetation found at those altitudes.

Despite the homogeneity of the dominant oak forest, the reserve has been divided into five distinguishable, contiguous habitat types (or vegetation types). These habitat types reflect vegetation composition and structure, gradients in humidity and productivity as well as, to some extent, management history. The cloud mountain forest (CMF), at altitudes of 2400 m to 2700 m, is found at the highest regions of the reserve. The understory is continuous with shrubs, bushes and trees at different stages of development occupying a continuum from ground level to the canopy. The wet oak forest (WOF) found at 2450 m to 2620 m is structurally similar to the cloud mountain forest, although the understory is denser and trees support fewer epiphytes. In the western parts of the reserve, the wet forest ends abruptly, bordering open grass/scrub and agricultural areas. The riparian forest (RF) is found along two small streams that flow down the eastern slope of the mountain. This vegetation type has a cool, damp microclimate, which facilitates year-round lushness, making the area distinguishable from the surrounding drier forest: this is especially apparent during the dry season. Structurally, this habitat type is ravine like in parts, with steep wooded slopes on either side of the small streams. The vegetation along the streams consists largely of low bushes and small trees as well as dead trees that have fallen from the surrounding forest. The dry oak forest (DOF), at between 2200 m and 2350 m, has a relatively open understory and distinct strata consisting of the tree canopy and shrub layer characterize this vegetation type. The managed forest (MF), as the name suggests, is the habitat in the reserve most influenced by human actions in recent time. Wood, for among other things fuel, was harvested as recently as 1987, and tree structure and height reflect this. Trees in this forest are rarely higher than 19 m and exhibit "candelabra" growth patterns consistent with the management practice of pollarding (a method of cutting trees, such as oaks, above the levels reached by grazing animals). There is no real distinction between different strata, and the understory consists of trees at all stages of development.

Study species. The range of the Ruddy-capped Nightingale Thrush extends from central Mexico to Panama, where it is found at altitudes between 1500 m and 3500 m in humid pine, pine-oak and evergreen forests (Howell & Webb 1995, Clement *et al.* 2000). This species forages on invertebrates and berries at ground level and in dense understory (Clement *et al.* 2000), and breeds from February to August–September with an apparent peak in the study site in Chiapas during May–June (J. L. Rangel unpubl.). Swainson's Thrush breeds from the western United States, north to Alaska and across much of Canada and the northeastern regions of the U.S.A. The non-breeding period is spent from southern Mexico (although transient in the Huitepec Ecological Reserve) through much of Central America south to Brazil and northern Argentina (Clement *et al.* 2000). The habitat utilized during the non-breeding period consists of humid to semi-humid evergreen and semi-deciduous forest (Howell & Web 1995). However, during migration, a wider array of habitats is used, including parks, gardens and orchards (Clement *et al.* 2000). Behavioral studies in North America have revealed that Swainson's Thrush, while a predominant ground forager, is the most arboreal of the migratory *Catharus* thrushes (Dilger 1956, Holmes & Robinson 1988).

Field methods. We obtained relative abundance estimates and morphological measurements from mist-netting in conjunction with a long-term bird monitoring program conducted in the Huitepec Ecological Reserve. Birds reported here were caught during a 2-week period in late April and early May in 2002, and a 2-week period in April 2003. In each of the five sampled habitat types, ten standard-sized 12 m x 2.5 m mist-nets (12 in managed forest) were set up. We placed nets in groups of one, two or three along trails and purpose made mist-netting lanes; during sampling days, nets were opened just before local sunrise (between 06:15 and 06:30) and closed 5 h later, giving a sampling effort of 50 net-h per day and habitat. However, 60 net-h per day were conducted in the managed forest, as 12 nets were used in that habitat. During both 2002 and 2003 seasons, each of the five habitats were sampled on two consecutive days, equaling a total sampling effort of 100 net-h per habitat per season (120 net- h in managed forest). The capture procedure for each year was identical. However, the order in which habitats were sampled varied between years in order to minimize temporal bias in the long-term study capture-data.

We measured morphological characters according to Pyle (1997). Right tarsus, bill and keel were measured using dial calipers to the nearest 0.1 mm, and right unflattened wing length and tail length (length of the longest rectrix) were measured using a stopped wing ruler to the nearest 0.5 mm. Bill measurements, taken with dial calipers to the nearest 0.1 mm, consisted of exposed culmen, bill depth (at anterior end of nostrils) and bill width (at anterior end of nostrils). All birds were weighed to the nearest gram and banded.

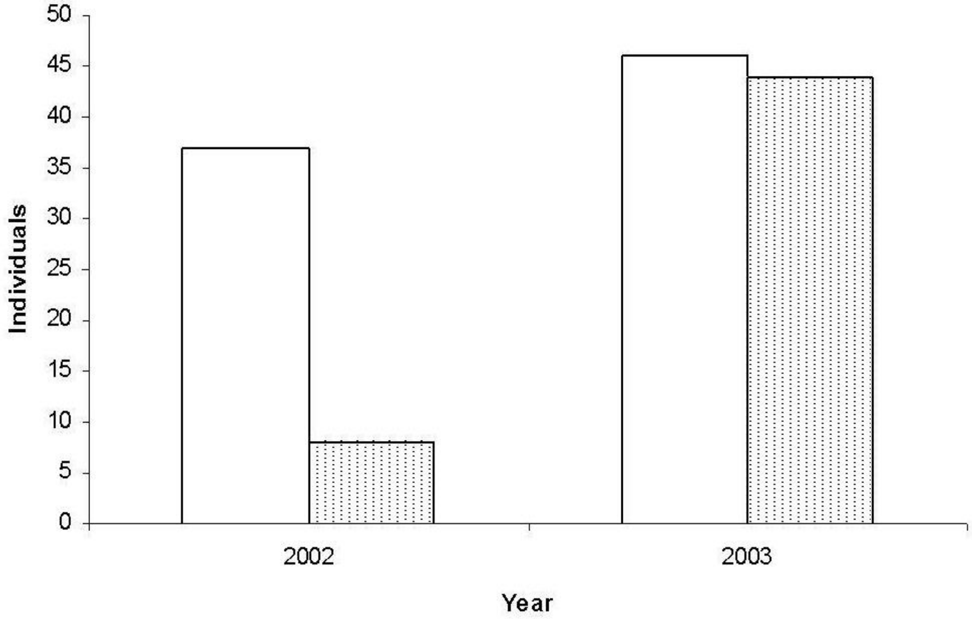

FIG. 1. Total number of Ruddy-capped Nightingale Thrushes (white bars) and Swainson's Thrushes (shaded bars) caught during mist-netting April–May 2002 and April 2003 in the Huitepec Ecological Reserve, Central Highlands of Chiapas, Mexico.

Data analysis

Distribution. Relative abundance was defined as individuals per 100 net-h, where net-h are calculated as 1 h of work for a standard-sized 2.5 m x 12.5 m mist net (Ralph *et al.* 1993). Relative abundance estimates from the managed forest were converted and rounded to nearest whole number in order to be comparable to the other habitat types. All individuals recaptured during the same sampling period were counted only once. Species associations to habitat types were tested using contingency analyses (likelihood ratio chi-square). However, due to low capture rates during the 2002 season, 20% of the expected frequencies were lower than 5, violating assumptions of chi-square tests (Quinn & Keough 2002, Sall *et al.* 2005). Therefore, species-habitat associations could not be statistically tested for distributional data obtained in 2002.

Morphology. Morphological data collected in 2003 for both species were used for this study. This was done partly because more morphological characters were measured during the 2003 season, and partly to reduce any bias caused by small differences in bander measuring techniques. After logarithm transformation of the selected variables, we used discriminant function analysis (DA) to test the hypotheses that morphological characters discriminate between Ruddy-capped Nightingale and Swainson's thrushes. Predictive models for the dependent, binary responses variables, defined as Ruddy-capped Nightingale Thrush and Swainson's Thrush, were developed to identify those morphological characters that best explain differences

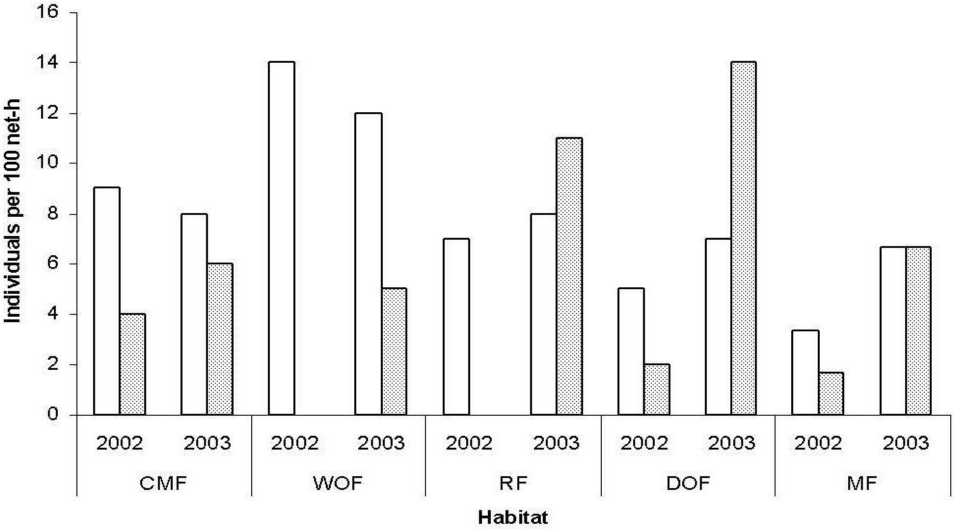

FIG. 2. Relative abundance of Ruddy-capped Nightingale Thrush (white bars) and Swainson's Thrush (shaded bars) in five different habitat types sampled during mist-netting April–May 2002 and April 2003 in the Huitepec Ecological Reserve, Central Highlands of Chiapas, Mexico. Habitats are: CMF = Cloud mountain forest, WOF = Wet oak forest, RF = Riparian forest, DOF = Dry oak forest, and MF = Managed forest.

between species. Candidate independent variables were selected for inclusion in the final model using stepwise selection procedure. Mahalonobis distances (minimum D^2) between group centroids were used for maximizing separation between species (McGarigal *et al.* 2000). Structure coefficients were obtained for determining correlations of variables with canonical discriminant functions (McGarigal *et al.* 2000, Gotelli and Ellison 2004). Positive parameter coefficients in the discriminant function indicated that an increase in the value of a variable increases the probability to identify the Ruddy-capped Nightingale Thrush. Conversely, a negative coefficient indicated that as variable values increase, the probability to identify Swainson's Thrush increases (Neter *et al.* 1996). DA allowed us to identify a linear composite of covariates, detect significant differences between group centroids and determine individual contribution of covariates to the overall discrimination function (McGarigal *et al.* 2000). All statistical differences were considered significant at $P < 0.05$. Statistical analyses were performed using JMP statistical software (Sall *et al.* 2005).

RESULTS

Results from mist-netting showed that the numbers of captured Swainson's Thrush varied substantially between 2002 and 2003, while Ruddy-capped Nightingale Thrush numbers differed to a lesser extent (Fig. 1). Due to low capture rates, it was not possible to conduct statistical tests for species associations to habitat types for the 2002 season (Fig. 2). However, during 2003, the frequencies of individuals represented by each species caught in all habitat types did not differ significantly from those expected by chance (G^2 =

TABLE 1. Weight (grams) and morphological measurements (mm) of Ruddy-capped Nightingale Thrush and Swainson's Thrush obtained during mist-netting in April 2003 in the Huitepec Ecological Reserve, Chiapas, Mexico. Measurements are given as means ± SE (30 < n < 45 for all morphological characters). * = Character selected by the canonical function analysis.

Characters	Ruddy-capped Nightingale Thrush	Swainson's Thrush
Weight	27.6 ± 0.28	27.8 ± 0.47
Wing *	86.5 ± 0.53	98.8 ± 0.40
Keel *	20.0 ± 0.18	22.8 ± 0.20
Tarsus *	35.1 ± 0.20	28.1 ± 0.13
Tail *	68.3 ± 0.69	67.6 ± 0.46
Culmen *	11.9 ± 0.10	11.0 ± 0.07
Bill depth	4.4 ± 0.04	4.4 ± 0.03
Bill width	5.3 ± 0.06	5.5 ± 0.06

6.25, df = 4, $P = 0.18$; Fig. 2). Thus, as similar numbers of both species were caught in all of the five habitat types, no positive association between species and habitat type could be determined.

The Ruddy-capped Nightingale Thrush significantly differs from the Swainson's Thrush in five of the eight morphological characters measured (Table 1). Discriminant function analysis revealed clear differences in these morphological characters between those two species (Wilk's λ, $\mu = 0.031$, $F_{5,91} = 579.99$, $P < 0.001$), and correctly classified 100 percent of the individuals of both species. Tarsus (r = 29.597), wing length (r = -26.701), tail (r = 6.681), and culmen (r = 2.826) were the characters most strongly correlated with the canonical discriminant function, producing the largest differences between species (Fig. 3).

DISCUSSION

Distribution. Capture frequencies from mist-netting during spring 2002 and 2003 confirmed that the breeding resident Ruddy-capped Nightingale Thrush and transient migrant Swainson's Thrush do coexist in the Huitepec Ecological Reserve during the latter's migration period. The 45 Ruddy-capped Nightingale Thrush and 43 Swainson's Thrush individuals captured during mist-netting in 2003 were distributed evenly across all sampled habitat types. Therefore, no evidence of habitat segregation between these two species could be established. Abundance data obtained in 2002 complicated conclusions regarding differences in habitat use, as a total of only eight Swainson's Thrush individuals were distributed among three habitat types. Even accounting for the fact that the riparian forest was sampled in early May 2002 (possibly after the migration period), numbers of captured Swainson's Thrush individuals were considerably lower during the 2002 season. Thus, results obtained from data collected in 2002 and 2003 indicate that the resident Ruddy-capped Nightingale Thrush does coexist with Swainson's Thrush in the same habitats in the Huitepec Ecological Reserve during Swainson's Thrush's northward migration period. However, the numbers of Swainson's Thrush individuals passing through the reserve may either fluctuate, vary spatially or differ temporally between years (e.g., absolute numbers of migrating individuals fluctuate, migration routes change or peak migration varies in relation to our netting period).

Ecomorphology. Overlap in habitat use suggests that ecological divergence in food choice and/or foraging positions within the same habitat (i.e., microhabitat segregation) may reduce resource overlap between Ruddy-capped Nightingale and Swainson's thrushes in the forests understory. However, data on the foraging behavior of these two species in the Huitepec Ecological Reserve during the migration period are not yet available. Therefore, ecomorphological theory (Leisler &

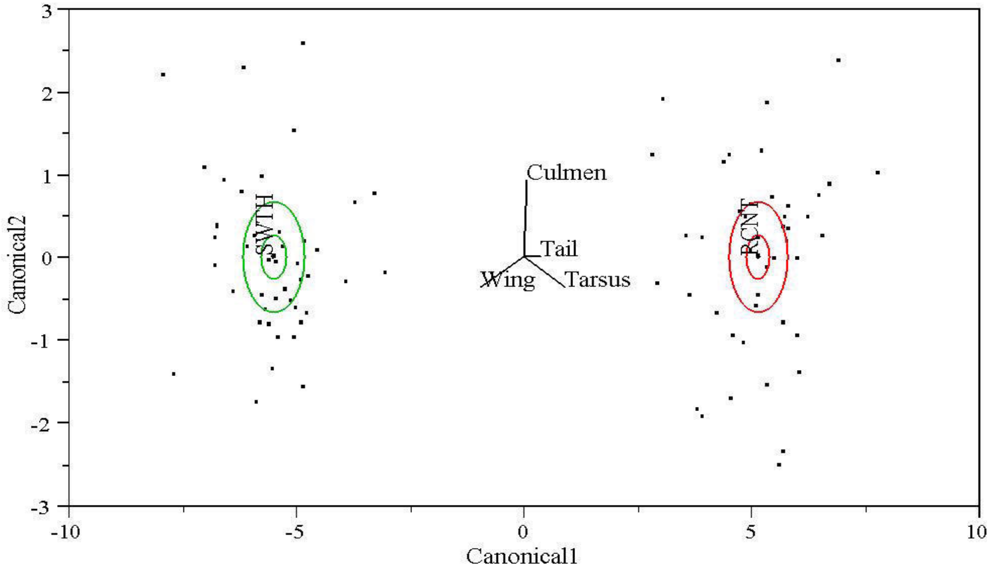

FIG. 3. Biplot with external circles including 50% of normal contours of canonical discriminant function analysis (DA) of standardized log of morphological characters for Ruddy-capped Nightingale Thrush (RCNT, right) and Swainson's Thrush (SWTH, left) caught during mist-netting in April 2003 in the Huitepec Ecological Reserve, Central Highlands of Chiapas, Mexico. Logarithm of selected characters (tarsus, wing length, tail, and culmen) revealed significant differences between species (Wilk's λ, $\mu = 0.031$, $F_{5,91} = 579.99$, $P < 0.001$). External circles included 50% of normal contours.

Winkler 1985, Wainwright & Reilly 1994) has been used to provide insight into the likely foraging positions occupied by Ruddy-capped Nightingale and Swainson's thrushes in the forest understory.

Members of the *Catharus* genus are generally described as terrestrial/ forest understory thrushes (Howell & Webb 1995, Clement *et al.* 2000). However, compared to other migrant *Catharus* species studied in temperate North America, Swainson's Thrush was observed to engage in arboreal foraging more frequently (Dilger 1956, Holmes & Robinson 1988). Dilger (1956) concluded that relatively longer hind limbs and a long slender bill were present in *Catharus* species more inclined to forage on the ground, while wing length and form were suggested to indicate levels of migratory behavior and/or arboreal feeding behavior (supported by Leisler & Winkler 1985).

Results from the discriminant analysis reveal, in order of importance, that length of tarsus, wing, tail and culmen best separate individuals of both species. Consequently, our morphological comparisons (Table1) indicate that Ruddy-capped Nightingale Thrush with a mean tarsus length of 35.1 mm is better adapted to ground foraging than Swainson's Thrush (mean tarsus length = 28.1 mm). Wing length comparisons reflect migratory behavior with Swainson's Thrush having a mean wing length approximately 15% longer than Ruddy-capped Nightingale Thrush. In addition, shorter wing length may allow Ruddy-capped Nightingale Thrush to utilize more structurally complex layers of the forest understory (e.g., Forstmeier *et al.* 2001), leading to further microhabitat segregation. Bill measurements obtained in the field are particularly sensitive to small differences in measuring techniques and therefore should be viewed with caution. Ruddy-capped Nightingale Thrush and Swainson's Thrush bill dimensions were similar in size. However, despite overlap, mean exposed culmen and bill width measurements differed slightly but significantly. Ruddy-capped Nightingale Thrush's bill was on average longer and narrower than Swainson's Thrush's. This, according to Dilger (1956), would be consistent with Ruddy-capped Nightingale Thrush being the species better adapted to ground foraging. Thus, using morphological data and information available from literature to infer ecological relationships, it is predicted that Ruddy-capped Nightingale Thrush is the species more specialized for ground foraging and will spend a greater proportion of time foraging amongst leaf litter for ground living invertebrates and maneuvering in dense understory. In contrast, the morphology of Swainson's Thrush suggests that its arboreal abilities will allow it to utilize fruits and insects in understory trees more efficiently than Ruddy-capped Nightingale Thrush.

Research and conservation implications. Preliminary observations suggest that insects and fruits are an important part of Ruddy-capped Nightingale Thrush and Swainson's Thrush diet. C. Chavez-Zichinelli (unpubl.) found similar proportions of animal and vegetable matter in analyzed fecal samples of both species, indicating that they each utilize invertebrates and fruits while coexisting in the Huitepec Ecological Reserve. However, the specific types of invertebrates and fruits taken by each thrush species were not analyzed during that study. Thus, future research must include resource use analysis to answer whether Ruddy-capped Nightingale and Swainson's thrushes exploit the same food resources. If they do share resources when certain food types are possibly at low abundance in the Huitepec Ecological Reserve (e.g., Morón-Ríos and Huerta-Lwenga in revision), then competition could affect both the resident and migrant species. Stutchbury & Morton (2001) suggest that fruit may be utilized by non-migratory birds throughout the year in the tropics; even during the breeding season, and for migratory birds, low energy reserves during spring migration may have negative impacts for breeding performance (Martin 1987, Norris 2005).

Other issues that deserve immediate attention are the effects of forest loss/degradation on interactions between residents and migrants in highland ecosystems in the Neotropics (Mills 2006). Ruddy-capped Nightingale Thrush and Swainson's Thrush, may coexist non-interactively or migrant species may gain benefits and select habitats by heterospecific (or congeneric) attraction during migration as suggested by Thomson *et al.* (2003) for birds on breeding grounds. However, loss and modification of forested environments along migration routes in Middle America could alter factors affecting coexistence of those two species. For example, loss of suitable habitats to transient migrants could lead to crowding in remaining areas (Moore *et al.* 1995), leading to increase resource depletion and even interference with resident species. Furthermore, human modification of forested environments can lead also to changes in food abundance (Burke & Nol 1998, Zanette *et al.* 2000), soil invertebrate abundance and plant phenology (Saunders *et al.* 1991), and forest structure and vegetation (Young & Mitchell 1994). Thus, interactions between Ruddy-capped Nightingale Thrush and Swainson's Thrush could change as forest habitats are reduced and modified.

CONCLUSIONS

Overlap in distribution across distinguishable vegetation types in the Huitepec Ecological Reserve in the highlands of Chiapas indicate that the resident Ruddy-capped Nightingale Thrush and the transient migrant Swainson's Thrush utilize the same habitats at this locality. Comparisons of morphological characters and considerations from literature suggest that each species is better adapted to forage in different positions within the forest understory. Longer tarsi, shorter wings and slightly longer culmen indicate that Ruddy-capped Nightingale Thrush is better adapted for foraging at ground level and maneuvering through dense understory. In contrast, the shorter tarsi and longer wings of Swainson's Thrush suggest morphological adaptations more suited to arboreal foraging in relatively open understory. Additional detailed studies on the behavior and ecology of these two coexisting *Catharus* thrushes could provide information on resident-migrant interactions from a Neotropical conservation perspective in tropical montane forest ecosystems.

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