Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird

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Identifying the factors that control population dynamics in migratory animals has been constrained by our inability to track individuals throughout the annual cycle. Using stable carbon isotopes, we show that the reproductive success of a long-distance migratory bird is influenced by the quality of habitat located thousands of kilometres away on tropical wintering grounds. For male American redstarts (*Setophaga ruticilla*), winter habitat quality influenced arrival date on the breeding grounds, which in turn affected key variables associated with reproduction, including the number of young fledged. Based on a winter-habitat model, females occupying high-quality winter habitat were predicted to produce more than two additional young and to fledge offspring up to a month earlier compared with females wintering in poor-quality habitat. Differences of this magnitude are highly important considering redstarts are single brooded, lay clutches of only three to five eggs and spend only two-and-a-half months on the breeding grounds. Results from this study indicate the importance of understanding how periods of the annual cycle interact for migratory animals. Continued loss of tropical wintering habitat could have negative effects on migratory populations in the following breeding season, minimizing density-dependent effects on the breeding grounds and leading to further population declines. If conservation efforts are to be successful, strategies must incorporate measures to protect all the habitats used during the entire annual cycle of migratory animals.

Keywords: migratory birds; carry-over effects; stable isotopes; population dynamics

1. INTRODUCTION

Understanding the factors that influence population dynamics in migratory animals requires knowledge of how events during one period of the annual cycle carry over to influence events in subsequent seasons (Sherry & Holmes 1996; Webster *et al.* 2002). Long-distance migratory birds typically spend six to seven months on the tropical wintering grounds, two to three months on the temperate breeding grounds and another two to three months in spring and autumn migration. In the last few decades, marked declines in the abundances of many long-distance migratory birds (Baillie & Peach 1992; Hagan & Johnston 1992) have led to increased attention concerning the major factors controlling population dynamics. In North America, migratory birds constitute more than 80% of avian breeding species in eastern forests and make up the most diverse terrestrial-vertebrate migration system in the world (Morton 1992; Rappole 1995).

Previous research suggests that migratory bird populations are limited by events related to reproductive success on the breeding grounds such as food abundance (Rodenhouse & Holmes 1992; Sillett *et al.* 2000), predation (Patton 1994; Donovan *et al.* 1997), brood parasitism (Hoover & Brittingham 1993; Robinson *et al.* 1995) and/or nest-site availability (Martin 1995). Other research has shown that birds may be limited primarily by habitat availability on the tropical wintering grounds (Marra *et al.* 1993; Stutchbury 1994), mediated through food abundance (Janzen 1980; Strong & Sherry 2000; Johnson & Sherry 2001) and/or global climate cycles (Baillie & Peach 1992; Sillett *et al.* 2000), or during the migration period (Moore *et al.* 1995). Within-season hypotheses, however, are probably overly simplistic if events throughout the annual cycle are inextricably linked. For example, the consequences of winter habitat occupancy could carry over to affect individual success on the breeding grounds (Marra *et al.* 1998; Gill *et al.* 2001). Assessing the relative importance of such carry-over effects will be a critical step towards understanding the population dynamics of migratory animals.

Using stable carbon isotopes, we tested whether habitat quality on tropical wintering grounds affected the reproductive success of American redstarts (*Setophaga ruticilla*) on the temperate breeding grounds. Redstarts are small (a body mass of *ca.* 8 g) neotropical–nearctic migratory passerines that winter in the Caribbean, Central America and northern South America and breed in deciduous and mixed forests throughout most of the USA and Canada (Sherry & Holmes 1997).

During the non-breeding season, redstarts occupying mesic habitats, such as coastal mangroves and lowland forests, are in better body condition, depart earlier on spring migration and have higher annual survival than individuals in arid scrub habitat (Marra 2000; Marra & Holmes 2001). High- and low-quality habitats yield distinct $\delta^{13}C$ values (Marra *et al.* 1998), which can be

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explained by differences in the photosynthetic pathways (C3 versus C4) and water-use efficiency (O'Leary 1981; Farquhar *et al.* 1989) of the dominant plant species in these habitats. Redstarts incorporate these $\delta^{13}C$ values into their tissues because they consume phytophagous insects from these habitats. Higher-quality winter habitats tend to be moister and result in depleted $\delta^{13}C$ values, whereas enriched $\delta^{13}C$ values indicate occupancy of drier low-quality habitat. Because the turnover rate of $\delta^{13}C$ in the red blood cells of birds is six to eight weeks (Hobson & Clark 1993), individuals arriving on the breeding grounds carry an isotopic fingerprint identifying the winter habitat in which they have spent the previous six to seven months.

2. MATERIAL AND METHODS

(a) *Field data*

We monitored arrival date and variables associated with the reproductive success of male and female American redstarts in 2001 and 2002 at the Queen's University Biological Station, Chaffey's Lock, Ontario, Canada (44°34′ N, 76°19′ W). To record the arrival dates of males and females we surveyed five forest plots (60 ha in total, 25 m × 25 m grids) daily (06.00–12.00 EST) from 1 May to 15 June. Males sing immediately upon arrival at the breeding grounds (Sherry & Holmes 1997). To record the arrival of females, we intensively monitored each male daily for 15–20 min. Decrease in song rate, switching song types from 'repeat mode' to 'serial mode' (MacNally & Lemon 1985), mate guarding, chip notes and frequent chases were reliable initial indicators that a female was present (Sherry & Holmes 1997). We confirmed the presence of a female through visual identification and then re-confirmed her presence 1–2 days following her initial sighting. On the rare ($n = 4$) occasions that the female was not present 1–2 days following her initial sighting, we re-visited the male the following day and confirmed that he was still unmated. When males lose females, they immediately revert back to a 'repeat mode' song type and increase their song rate dramatically.

All individuals were caught within 7 days of arrival (80% within 2–4 days) in mist nets using conspecific playback and a mounted redstart model. The number of days between arrival and capture were not correlated with $\delta^{13}C$ in either sex (males: $r^2 = 0.013$, $p = 0.266$, $n = 96$; females: $r^2 = 0.018$, $p = 0.466$, $n = 31$). Individuals were banded with a unique combination of two colour bands and a United States Fish and Wildlife Service aluminium band. Blood samples (10–50 μl) were taken from the brachial vein and placed on ice until they were centrifuged (within 4 h) for 8 min at 14 000 r.p.m. Red blood cells were immediately extracted with a Hamilton syringe and frozen (at −20 °C). Physical condition upon arrival was calculated as the linear residual of mass (in grams) over body size. Sexes were analysed separately (males: mass = 0.96 + 0.008 × body size; females: mass = 8.02 + 0.21 × body size). Principal-component (PC) scores were used as an index of body size (PC1 scores of tarsus–wing chord–bill depth; Marra & Holmes 2001). All three variables loaded positively on the PC1 axis with tarsus and wing chord having the largest effect. Body condition was not correlated with body size (males: $r^2 = 0.0008$, $p = 0.778$, $n = 100$; females: $r^2 = 0.004$, $p = 0.74$, $n = 29$). Nests were found, and monitored every 2–3 days. The first-egg date was defined as the date the first egg was laid in the first nest of the season. The number of young fledged was determined as the number of young present 1–2 days before fledging. To confirm a successful

fledging event, we recorded the presence of young 1–2 days after they left the nest.

(b) *Isotope analysis*

Isotope ratios (R) are expressed in δ units where $\delta = [(R_{sample}/R_{standard}) - 1] \times 1000$. $\delta^{13}C$ is reported as the ratio of $^{13}C/^{12}C$ relative to the Pee Dee belemnite standard. For analysis, blood samples were freeze-dried and powdered (Hobson *et al.* 1997). Samples were weighed in tin capsules, then combusted and oxidized in a NCS 2500 Elemental Analyser and introduced online into a Finnigan MAT 252 Mass Spectrometer. One in-house standard was run for every five unknowns. Samples were repeatable to within ±2 parts ml^{-1} ($n = 30$).

(c) *Path analysis*

We used path analysis to determine the relationship between $\delta^{13}C$ and reproductive success in American redstarts. Because there are several breeding events (e.g. arrival, mate searching, nest initiation) occurring between the time of habitat occupancy on the wintering grounds and ultimately fledging young at the end of the breeding season, a direct correlation between $\delta^{13}C$ and the number of young fledged was not anticipated. Instead, we were interested in how the variables potentially mediated this relationship. Path analysis allows for the calculation of not only direct effects (DEs) of one variable on another but also indirect effects (IEs) (Mitchell 1993). IEs are the product of all possible pathways from one variable to another. Each causal pathway is a DE and generates a path coefficient (standardized partial regression coefficients). Each indirect pathway is calculated from the product of the path coefficients in that path. The total effect (TE) is the sum of all IEs and DEs from one variable to another.

Unlike multiple regression, path analysis allows for the determination of causal relationships between an independent and a dependent variable as well as between multiple dependent (or independent) variables (Mitchell 1993). In this case, we considered $\delta^{13}C$ (measured upon an individual's arrival at the breeding grounds) as the independent variable and arrival date, first-egg date, fledging date and number of young fledged as the dependent variables. Path analysis is ideal for this investigation because the relationships between these variables flow in a time-series fashion, beginning with habitat occupancy the previous winter and ending with the number of young fledged at the end of the breeding season (see figure 1). We recognize that we may not have included all possible variables in the path models, and the depiction of the unmeasured variance is represented by latent variables ('*u*') included in the model.

The structures of the path models were designed based on previous knowledge of migratory-passerine ecology. For both the males and females, we predicted that individuals originating from higher-quality habitats would arrive earlier ($\delta^{13}C$ would positively influence arrival date). Individuals occupying high-quality winter habitat are in better body condition and depart earlier for spring migration (Marra 2000; Marra & Holmes 2001). Furthermore, individuals arriving early on the temperate breeding grounds have been shown to have more-negative $\delta^{13}C$ values, indicating occupancy of high-quality winter habitat (Marra *et al.* 1998). We also hypothesized that winter habitat quality could affect fledging date. Individuals originating from higher-quality winter habitat may also be in better condition throughout the breeding season, leading to improved parental care capabilities, fewer re-nesting events, faster nestling develop-
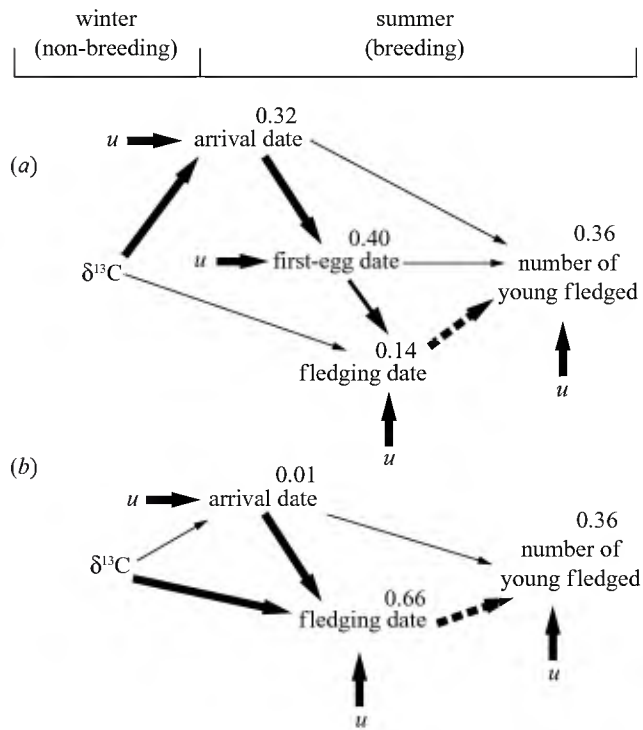
Figure 1. Path diagram of (*a*) adult male and (*b*) adult female American redstarts. $\delta^{13}C$ values represent the quality of habitat occupied by individuals the previous winter. Latent (unmeasured) variables are represented by '*u*'. The thicknesses of the arrows represent the magnitudes of the partial regression coefficients (βs) as well as significance. Thin arrows, $\beta < 0.10$, n.s.; middle-thickness arrows, $0.30 \leqslant \beta \leqslant 0.50$, $p < 0.05$; thick arrows, $0.50 < \beta \leqslant 0.70$, $p < 0.01$. Solid lines represent positive relationships and dashed lines indicate negative relationships. Values above dependent variables are r^2s, the proportions of the variance explained by the path model. For males, $n = 57$ (2001: $n = 31$; 2002: $n = 26$). For females, $n = 33$ (2001: $n = 15$; 2002: $n = 18$).

ment rates and earlier fledging dates (Hogstad 1993; Polomino *et al.* 1999). Because early-arriving males acquire females sooner than later-arriving males (Aebischer *et al.* 1996; Lampe & Espmark 2003), arrival date was predicted to have a positive influence on the first-egg date. We did not include a direct causal link between arrival date and number of young fledged based on results from a previous study on American redstarts (Lozano *et al.* 1996). First-egg date was predicted to have a negative influence on the number of young fledged (earlier first-egg dates result in higher numbers of young fledged) as earlier nests have larger clutches (Sherry & Holmes 1997; Nilsson 2000; this study). First-egg date was also predicted to correlate positively with fledging date because pairs with earlier nest-initiation dates should have more opportunities to re-nest after predation (Barba *et al.* 1995; this study).

Only individuals for whom we had complete reproductive data for the entire breeding season were included in the analysis. For example, if we sampled an individual for isotopes but failed to obtain data on some aspect of its nesting cycle, we did not include this individual in the analysis. Owing to a smaller sample of females (fewer females than males were captured because they were not as aggressive towards simulated intruders), we were constrained in the number of variables that could be used in the path analysis. Therefore, we removed the first-egg date from the

female model but kept the path relationships between the remaining variables the same as the male model. The model was then re-run, substituting the first-egg date for the arrival date. Variables were log transformed if they were non-normally distributed (Shapiro–Wilks test for normality). Data from 2 years (2001 and 2002) were pooled. To control for potential year effects, we performed the path analysis after variables were standardized by year (Lozano *et al.* 1996; Pacejka *et al.* 1998). Standardized variables met the assumption of normality. Yearling (first potential breeding season/second-year) males were not included in the path analysis. The few yearling males that paired ($n = 17$ over 2 years) exhibited significant differences in their reproduction (clutch size, first-egg date, number of young fledged) compared with adult (after second year) males, so we could not justify their inclusion in the model.

(i) *Winter habitat model*

We used the TE values from the path analysis to predict the reproductive consequences of occupying different-quality habitats on the wintering grounds. Unlike simple correlations (r), TE values for each sex summarize all indirect pathways from $\delta^{13}C$ to the number of young fledged. To produce the model, we first summarized the effect of $\delta^{13}C$ (measured upon arrival at the breeding grounds) on each reproductive variable using the TE values and standard deviations (s.d.) for each variable (Bart & Earnst 1999). For example, the effect of $\delta^{13}C$ on number of young fledged was expressed as: s.d.$(\delta^{13}C) =$ s.d.(young fledged) $\times$ TE. We then obtained actual $\delta^{13}C$ values from four different habitats on the wintering grounds. Differences in the $\delta^{13}C$ values from these habitats were then used to predict differences in reproductive variables by comparing individuals occupying different-quality winter habitats (figure 2).

3. RESULTS AND DISCUSSION

Adult males arrived before yearling males and females (adult male, mean arrival date: 14 May, s.e. $= 0.7$ days, $n = 72$; yearling male, mean arrival date: 24 May, s.e. $= 1.2$ days, $n = 29$; females, mean arrival date: 23 May, s.e. $= 1.1$ days, $n = 30$). Arrival date was correlated with winter habitat quality (positive relationship between arrival date and $\delta^{13}C$) for adult males in both years (2001: $r^2 = 0.38$, $p < 0.0001$, $n = 35$; 2002: $r^2 = 0.34$, $p = 0.0004$, $n = 32$), yearling males in 2002 (2001: $r^2 = 0.22$, $p = 0.53$, $n = 7$; 2002: $r^2 = 0.48$, $p = 0.0003$, $n = 22$) and females in 2001 (2001: $r^2 = 0.37$, $p = 0.027$, $n = 13$; 2002: $r^2 = 0.07$, $p = 0.29$, $n = 18$). We found no relationship between the physical condition of males or females upon arrival on the breeding grounds and $\delta^{13}C$ (males: 2001: $r^2 = 0.031$, $p = 0.268$, $n = 42$; 2002: $r^2 = 0.002$, $p = 0.749$, $n = 55$; females: 2001: $r^2 = 0.022$, $p = 0.649$, $n = 12$; 2002: $r^2 = 0.088$, $p = 0.266$, $n = 16$).

For adult males, the path model provided a robust fit when compared with expected values (log-likelihood whole-model test: $\chi^2 = 2.1$, d.f. $= 4$, $p = 0.71$). As predicted, $\delta^{13}C$ influenced arrival date (more positive $\delta^{13}C$ values indicate poorer-quality winter habitats and later arrival dates) but had no DE on fledging date (figure 1*a*). In turn, arrival date affected the first-egg date, and the first-egg date influenced fledging date (figure 1*a*). Finally, fledging date negatively influenced number of young fledged (later fledging dates led to fewer young fledged).
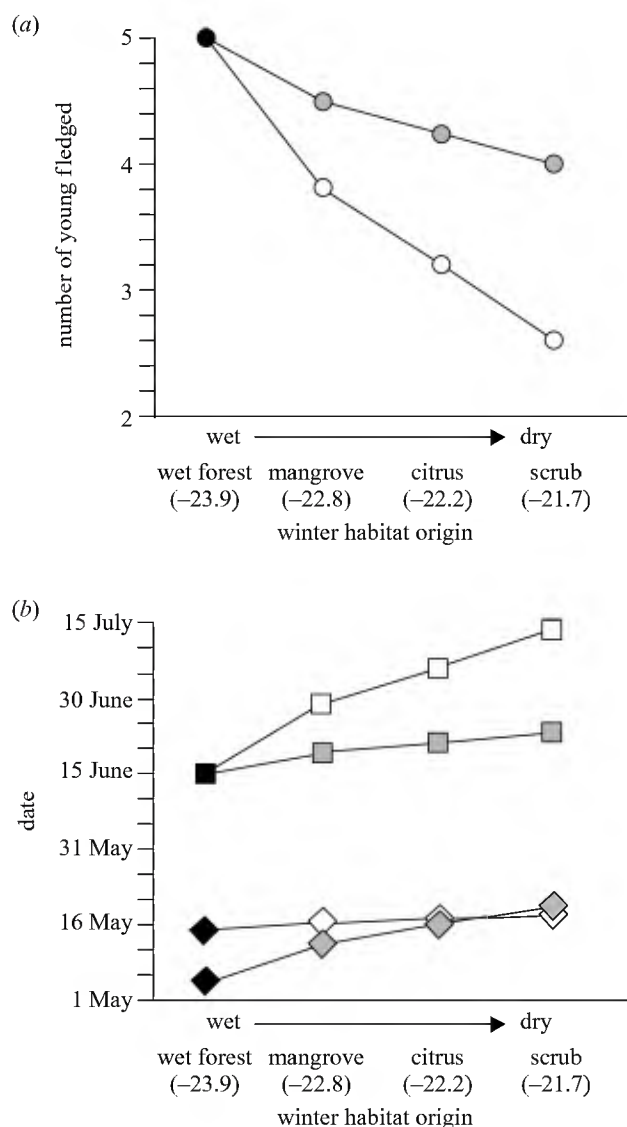
Figure 2. Predicted (*a*) number of young fledged (circles), (*b*) nest fledging date (squares) and arrival date (diamonds) for adult male (grey) and female (white) American redstarts as a function of hypothetical shifts in winter habitat occupancy. Ranges of $\delta^{13}C$ values (*x*-axis) from the four different winter habitats are based on samples taken from redstarts at three different locations on the wintering grounds (Jamaica, Honduras and Belize; Marra *et al.* 1998, P. P. Marra, unpublished data). Starting values on the left in black were chosen to represent individuals originating from the highest-quality winter habitat (number of young fledged, 5; fledging date, 15 June; male arrival date, 5 May; female arrival date, 15 May). Subsequent changes in the variables (*y*-axis) are based on the TEs of $\delta^{13}C$ on each variable calculated from the path analysis (figure 1), where path coefficients were converted to the units of each variable.

The female path model was also an excellent fit compared with predicted values ($\chi^2 = 0.09$, d.f. = 1, $p = 0.76$; figure 1*b*). In contrast to the situation in males, $\delta^{13}C$ did not influence arrival date, although arrival date directly affected fledging date. $\delta^{13}C$ positively influenced fledging date and, as in males, fledging date negatively affected the number of young fledged. This resulted in a large IE of $\delta^{13}C$ on the number of young fledged (-0.31; table 1). When the first-egg date was substituted for arrival date

(see § 2c), the results were almost identical: the main causal pathway remained from $\delta^{13}C$ to fledging date and from fledging date to number of young fledged ($\chi^2 = 0.37$, d.f. = 1, $p = 0.54$).

For adult males, the winter-habitat model predicted a maximum change of one offspring (figure 2*a*) and a shift in fledging date of approximately one week (figure 2*b*). Depending on the winter habitat type occupied, arrival date shifted by a maximum of two weeks, a large difference given that more than 80% of males arrive within a three-week window during the month of May. Importantly, the model also predicted that males originating from the poorest-quality winter habitat would arrive several days later than females. As is the case with most species of migratory birds, the advantage of early arrival in males is high (Lozano *et al.* 1996; Hasselquist 1998). Early-arriving males pair earlier (2001: $r^2 = 0.128$, $p = 0.045$, $n = 32$; 2002: $r^2 = 0.09$, $p = 0.107$, $n = 29$) and mate with females that have depleted $\delta^{13}C$ values (2001/2002 combined: $r^2 = 0.20$, $p = 0.037$, $n = 22$) suggesting that males may enhance their own reproductive success by pairing with females from high-quality winter habitat.

Based on the winter-habitat model, females originating from high-quality habitat were predicted to produce two additional offspring (figure 2*a*) and have a fledging date of almost one month earlier (figure 2*b*) compared with females from low-quality habitat. Such changes are highly important considering that redstarts raise single broods, lay clutches of only three to five eggs per season (Sherry & Holmes 1997) and have a nesting season of only about two-and-a-half months in duration. A change in fledging date by a month would probably have major consequences for the ability of parents to feed fledglings prior to departure on autumn migration.

Unlike the case for males, winter habitat quality for females did not influence arrival date on the breeding grounds (figures 1*b* and 2*b*). The trade-off between early arrival and survival is likely to be different between the sexes. Whereas reproductive success in males appears to be tightly linked to arrival date, all females are likely to obtain mates and breed (Marra & Holmes 1997), regardless of their arrival date on the breeding grounds. In years where temperatures are low during early spring migration, females may delay departure from the wintering grounds and/or extend the migration period. Along the migration route in the eastern USA (Maryland), average temperatures between 15 April and 15 May were 2 °C colder in 2002 than in 2001 (Smithsonian Environmental Research Center, unpublished data). Correspondingly, for females, there was a significant relationship between arrival date and $\delta^{13}C$ in 2001 but not in 2002.

The findings reported here have important consequences for understanding the dynamics of migratory animal populations. First, our study provides direct evidence that the quality of tropical wintering habitat influences reproductive success thousands of kilometres away on the temperate breeding grounds and emphasizes the importance of conserving habitat throughout the annual cycle of migratory animals. Second, events in one season are thought to act as a regulatory mechanism (via density dependence) against negative effects in the previous season (Fretwell 1972; Sutherland 1996). For example, the

Table 1. DEs, IEs and TEs (calculated from standardized partial regression coefficients) of male and female $\delta^{13}C$ on reproductive variables.
(TE, TE of $\delta^{13}C$ on each reproductive variable (see figure 1). Years are combined.)

reproductive variable	males			females		
	DE	IE	TE	DE	IE	TE
arrival date	0.57	—	0.57	0.10	—	0.10
first-egg date	—	0.36	0.36	0.01	—	0.01
fledging date	0.09	0.12	0.21	0.44	0.06	0.51
number of young fledged	—	−0.11	−0.11	—	−0.31	−0.31

loss of tropical habitat may increase the *per capita* winter mortality but could also result in an increase in *per capita* reproduction in the following breeding season (Cox 1985). By contrast, our results suggest that a loss of high-quality winter habitat may have a negative carry-over effect on individuals during the following season. The magnitude of this effect on female redstarts is equal to or greater than density-dependent effects on reproduction found for neotropical migratory passerines (Sillett & Holmes 2003). Negative breeding-ground effects from loss of high-quality winter habitat, therefore, may outweigh the benefits gained from increases in density-dependent fecundity, leading to a further decrease in population abundance.

Negative carry-over effects such as those reported here might be especially pertinent to species that prefer to over-winter in mesic habitats, such as coastal mangroves and tropical lowland forests. These habitats are among the most threatened ecosystems in the world (Ellison & Farnsworth 1996; Whitmore 1997). In the tropics, the late-winter dry season can result in a reduction in insect biomass (Janzen 1980), a key food resource for most over-wintering migrants. Mesic habitats provide enriched food resources for insectivorous birds, particularly at the end of the dry season, resulting in individuals that are in better body condition and have higher survival. Based on our results, the continued destruction of these habitats would have serious negative effects on the population dynamics of temperate–tropical migratory birds.

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