ORIGINAL ARTICLE

Habitat choice shapes the spring stopover behaviour of a Nearctic-Neotropical migratory songbird

Nicholas J. Bayly[1] · Kenneth V. Rosenberg[2,3] · Camila Gómez[1,4] · Keith A. Hobson[5]

Abstract

The effect of habitat choice on fuelling behaviour and the organization of migration in birds has rarely been examined, despite the potential impact of widespread anthropogenic transformation of stopover regions. High energetic requirements in migrating birds mean that resource abundance, through its influence on fuel deposition rates (FDR), is expected to be the main determinant of stopover and migration strategy. We examined the spring stopover of Tennessee Warblers (*Oreothlypis peregrina*) in northern Colombia, evaluating how diet, FDR, stopover duration, departure mass and estimated flight range varied between two commonly used stopover habitats: shade coffee plantations and pre-montane forests. Diet included insects in both habitats, but fruit was only consumed in pre-montane forest, where FDR was highest (FDR forest = 2.4% LBM/day; coffee = 0.5% LBM/day). Three different estimates of stopover duration suggested longer stays in coffee but lengthier durations did not result in equivalent departure mass between habitats, such that estimated flight range was twice as long for birds departing forest (2000 km) relative to coffee (1088 km). We conclude that stopover performance differed between habitats, likely influencing the subsequent temporal and spatial organization of spring migration. On the basis of flight ranges, stopovers in shade coffee may also increase the risks of trans-Caribbean flights, suggesting a mechanism by which stopover habitat could directly influence survival. Given that fruit consumption in forest probably explains these differences, we recommend the identification of appropriate fruiting trees for Neotropical agroforestry systems that can tolerate a variety of conditions and increase the quality of these anthropogenic habitats for migratory and other frugivorous birds.

Keywords Agroforestry · Colombia · Diet · Fuel deposition rate · Flight range · Migration · Shade coffee · Stopover duration · Tennessee Warbler

Zusammenfassung

Habitatwahl beeinflusst die Frühjahrsrast eines nearktisch-neotropischen Zugvogels

Die Wahl des Habitats und ihr möglicher Einfluss auf das "Auftanken" und die gesamte Organisation des Zuges von Vögeln ist bislang noch kaum untersucht worden, trotz der potentiell großen Folgen der überall zu beobachtenden anthropogenen Veränderungen der Rasthabitate der Vögel. Die hohen Energieanforderungen ziehender Vögel bedeuten, dass das Vorhandensein ausreichend ergiebiger Nahrungsquellen wegen ihrer Auswirkungen auf die Energiespeicherung (fuel deposition rate – FDR) der wichtigste Einzelfaktor ist, der über das Einlegen von Zwischenstopps und die Zugstrategien generell entscheidet. Wir untersuchten die Frühjahrsrast des Brauenwaldsängers (*Oreothlypis peregrina*) in Nord-Kolumbien und versuchten einzuschätzen, inwieweit sich Nahrung, FDR, Dauer des Zwischenstopps, Körpermasse beim Abflug und Flugreichweiten von zwei üblicherweise genutzter Rasthabitate - schattige Kaffeeplantagen bzw. prämontane Wälder - unterschieden. Die Nahrung bestand in beiden Habitaten aus Insekten, wohingegen Früchte nur in den prämontanen Waldgebieten verzehrt wurden. Dort waren die FDR am höchsten (Wald: 2.4% LBM/Tag; Kaffeeplantage: 0.5% LBM/Tag). Drei unterschiedliche Methoden zur Einschätzung der Rastdauer zeigten allesamt eine längere Verweildauer in den Kaffeeplantagen, doch diese längeren Aufenthalte bedingten keine ähnlichen Abflugkörpermassen, woraus sich für Vögel der Wälder eine doppelt so weite, errechnete Flugdistanz ergab als für Vögel aus den Kaffeeplantagen (2000 km vs. 1088 km).

Communicated by C. G. Guglielmo.

Extended author information available on the last page of the article

🍀 Springer

Wir schließen daraus, dass sich das Rastvermögen der Vögel von Habitat zu Habitat unterscheidet und so wahrscheinlich die gesamte zeitliche und räumliche Organisation des Frühjahrszuges beeinflusst. Ausgehend von den Flugreichweiten erhöhen Zwischenstopps in den Kaffeeplantagen möglicherweise das Risiko des trans-karibischen Zugs und lassen einen Mechanismus vermuten, der über das Rasthabitat die Überlebenschancen der Zugvögel unmittelbar beeinflusst. Wenn tatsächlich in den Wäldern die Ernährung mit Früchten diese Unterschiede erklärt, empfehlen wir für die Landwirtschaft in den Neotropen herauszufinden, welche Früchte-tragenden Bäume ein möglichst weites Spektrum unterschiedlicher Bedingungen tolerieren und somit die Qualität anthropogener Habitate für Zugvögel und andere Früchtefresser erhöhen können.

Introduction

Migratory birds use a wide range of habitats during their annual cycle and it is now well recognized that not all habitats are of the same quality (e.g. Sherry and Holmes 1996; Faaborg et al. 2010; Bayly et al. 2016). Determining how habitat variability influences ecological processes throughout the annual cycle, especially where natural habitats have been transformed or lost, is fundamental if we are to protect high quality habitats and identify population-limiting processes (Holmes 2007). Indeed, variability in habitats occupied by migratory birds during the overwintering period not only affects overwinter survival (Johnson et al. 2006) but can also affect reproductive fitness through carry-over effects (Norris et al. 2004; Harrison et al. 2011).

For migratory birds, habitat quality may be decisive when meeting the energetic demands of long-distance migration (Newton 2006; Strandberg et al. 2010; Finch et al. 2014). Prior to crossing ecological barriers, for example, migratory birds deposit large energy stores at resource-abundant stopover sites (Bibby and Green 1981; Atkinson et al. 2007; Buler et al. 2007). Even small differences in habitat quality at such sites could influence the temporal (Gómez et al. 2017) and spatial organization of migration, and ultimately survival (Newton 2006; Sheehy et al. 2010, Duijns et al. 2017), but studies of how stopover behaviour varies among habitats are rare (Yong et al. 1998; Cohen et al. 2014; Liu and Swanson 2015).

For birds that migrate between North and South America, many of which are in steep decline (Sauer et al. 2014; Rosenberg et al. 2016), the northern coast of Colombia is an important stopover region during both autumn and spring migration (Bayly et al. 2012a, 2013, 2018; Gómez et al. 2015). Much of the natural habitat in northern Colombia has been transformed (Etter et al. 2006; IDEAM 2010) and pre-montane forests, which support high migrant diversity and abundance (Gómez et al. 2015), have been extensively replaced by coffee plantations. While shade coffee is recognized as an important habitat for overwintering migratory birds (e.g. Perfecto et al. 1996; Tejeda-Cruz and Sutherland 2004; Bakermans et al. 2012), representing a key component of conservation strategies for Nearctic-Neotropical migrant landbirds, its use during migration has rarely been assessed (Gómez et al. 2015). As a result, we do not know the implications of a stopover in shade coffee, although several indicators of habitat quality point to its inferior quality relative to native forest for some species (Bayly et al. 2016).

Stopover in forest or shade coffee could therefore influence subsequent migratory behaviour. In spring, birds departing from South America can either travel through Central America (e.g. Callo et al. 2013) or take a shorter and more direct route across the Caribbean Sea and Gulf of Mexico to northern Central America or directly to the USA (e.g. Gómez et al. 2017). The route birds adopt may depend on the availability and quality of habitats, where the energy stores for long over-water crossings are attained. If habitat quality influences migration behaviour in this way, we expect it to be mediated primarily through differences in fuel deposition rates (FDR), underpinned by variation in diet but also through variation in foraging rate and food availability (Bayly et al. 2016). Differences in FDR may in turn cause birds to adjust stopover duration (Alerstam 2011), altering the temporal organization of migration and potentially influencing arrival time at the breeding grounds, which can carry over to impact reproductive fitness (Harrison et al. 2011). Likewise, we expect that differences in FDR and stopover duration will lead to variation in departure mass and flight range, which can also affect the timing and speed of migration (Duijns et al. 2017; Gómez et al. 2017) and lead to reduced survival (Baker et al. 2004; Newton 2006).

In this paper, we assess how habitat use influences the spring stopover behaviour of Tennessee Warbler (*Oreothlypis peregrina*) in northern Colombia and by extrapolation their onward migration strategy. Previous work found differences in habitat quality between shade coffee and pre-montane forest for this abundant spring migrant in northern Colombia (Gómez et al. 2015; Bayly et al. 2016) and here we build on this finding by examining five metrics of stopover behaviour to determine how habitat choice influences (1) diet, (2) fuel deposition rate, (3) stopover duration, (4) departure mass and (5) potential flight range. By evaluating the consequences of variation in potential

flight ranges for onward migration, we demonstrate how the organization of spring migration in Tennessee Warblers may be mediated by habitat choice at a single stopover site.

Methods

Study site

This study took place in the Hacienda La Victoria (11°7′19.84″N, 74°5′34.14″W), a shade coffee farm in the Sierra Nevada de Santa Marta (SNSM), Colombia. Located on the north-eastern Caribbean coast, the SNSM supports a high diversity and abundance of Nearctic-Neotropical migrants during spring migration (Gómez et al. 2015). We worked in two dominant habitats at the study site: humid pre-montane tropical forest (≈ 300 ha) and shade coffee plantations (≈ 300 ha), both at an average elevation of 1200 m. Canopy cover in shade coffee varied between 30% and 60% and was dominated by the leguminous "guamo" tree (*Inga* sp.; 84% of trees), interspersed with *Albizia carbonaria* (1.6%) and *Trema micrantha* (7%). In pre-montane forest, canopy height varied from 10 m in young stands to 30 m in mature stands, with canopy cover greater than 75%.

Tennessee Warblers pass through this region in large numbers on spring migration and also overwinter at the study site (Bayly et al. 2016); the sampled population therefore included unknown proportions of "wintering" birds undergoing pre-migratory fuelling and passage birds on stopover. Of 746 birds captured in 2011 and 2012 just 14 (1.8%) were recaptured in subsequent years, suggesting that the number of overwintering individuals was low. During the study period both overwintering birds and those on stopover were fuelling for migration, we therefore do not attempt to distinguish between the two groups.

Data collection

To estimate fuel deposition rates, stopover durations, departure mass and flight ranges based on individual Tennessee Warbler captured on more than one occasion (Bayly et al. 2012a), we ran constant effort mist-netting stations in pre-montane forest and shade coffee (see below). We complemented captures with foraging observations to evaluate diet between habitats.

Captures We established four constant effort mist-netting stations during three consecutive spring migrations from 2011 to 2013. Stations were separated by at least 0.5 km horizontally (but ground distances were longer given the mountainous nature of the study site) and were divided equally between forest and shade coffee. Each station consisted of 6–9 mist-nets (12 or 18 m long, 32 mm and 36 mm mesh),

with mist-nets placed to maximize captures/recaptures. Specifically, we placed nets on ridges, where Tennessee Warblers regularly crossed between trees whose canopies were level with or below the ridge line, as well as distancing individual nets or groups of nets within a station (without overly extending net round length/duration) in an attempt to decrease the effect of net avoidance/learning on recapture rates. Stations were run between 12 March and 30 April, resulting in 4474 mist-net h in 2011, 4120 in 2012 and 2656 in 2013 (1 mist-net h = one 12 m net open for 1 h). Mist-nets were opened at dawn and operated for 5 h every day or every other day. Captured Tennessee Warblers (553, 163 and 291 individuals in 2011, 2012 and 2013, respectively) were fitted with a uniquely numbered Porzana-made metal ring (reporting address: http://www.aselva.co). For both new captures and recaptures, we recorded age and sex (Pyle 1997), fat score (visible fat deposits scored on a nine-point scale following Kaiser 1993), wing chord (± 1 mm) and body mass (± 0.1 g, using an electronic balance), prior to release.

Diet

To assess diet, we carried out focal observations on foraging birds located through random encounters while walking along tracks in each habitat (≈ 2 km/habitat). We recorded one sequence per individual taking note of the following: the number of attacks (directional pecking behaviours with bill) directed at two substrates, insects and fruit; habitat; and the duration of each sequence in seconds until a bird was lost from view (mean duration of 44 sequences = 48 s, range = 15–37 s).

To evaluate differences in diet between habitats, we first calculated the number of recorded attacks on each of two substrates in the two habitats. Using the percentage of attacks on each substrate from forest to generate expected values, we carried out a Chi-squared test to determine whether diet in shade coffee differed from that in forest.

Fuel deposition rate (FDR)

We examined differences in FDR between habitats by modelling change in body mass in 31 recaptured birds as a function of the number of days since first capture following Bayly et al. (2013). To account for differences in structural size, this method expresses mass changes as a percentage of each bird's estimated lean body mass (LBM). To estimate LBM, we took a subset of birds with fat score zero ($N = 14$) and regressed body mass against wing length, resulting in the following regression equation: $LBM = 2.763 + 0.0808 \times$ wing length ($r^2 = 0.155$, $P = 0.164$). Estimated LBM (7.85 g) for a bird of mean wing length (63 mm) is in good agreement with estimates from specimens after fat extraction: 7.94 ± 0.13 g (Connell et al. 1960).

Body mass changes were modelled in R using general linear models with normal errors (R Development Core Team 2017). Model selection was based on Akaike information criteria (AIC) and models with $\Delta i < 2$ were considered to be as plausible as the top model (Burnham and Anderson 2002), where Δi was the difference between each model and the model with the lowest AIC. Candidate models included the following variables: interval in days between captures (I); habitat (H)—two-level factor, forest and shade coffee; year (Y)—three-level factor (2011–2013); age (A)—two-level factor, immature (< 1 year old) and adult (> 1 year old); sex (S)—three-level factor (male, female, unknown); date at first capture (D)—day 1 = 1 March; starting body mass in grams (M); and the difference in hour of capture between captures (T). To determine whether FDR differed between habitats, we ran nine models designed to answer this question (Table 1).

Stopover duration

Three estimates of stopover duration were estimated via two methods.

(A) *Stopover after and total stopover* We estimated "stopover after" and "total stopover" through a mark-recapture analysis with data from 2011 (553 individuals, 19 recaptures), following the methods outlined in Schaub et al. (2001) and Efford (2005) in the program MARK (White and Burnham 1999). "Total stopover" estimates compare well with durations measured through the deployment of radio-transmitters on Grey-

cheeked Thrushes *Catharus minimus* at our study site, supporting the use of this method (Bayly et al. 2013; Gómez et al. 2017). Data from 2012 and 2013 were not analysed because of limited recaptures (≤ 6) and the concurrent lack of power for parameter estimation. For "total stopover" we used the following formula: 'total stopover' $= (-1/\ln \Phi) + (-1/\ln \gamma)$, where Φ is the parameter estimate for survival probability and γ the estimate for seniority probability. Given that certain stations were operated on alternate days, capture histories for each marked bird were created by pooling capture events across 2-day periods.

To evaluate the support for differences in duration between habitats, we created four models that included variation in Φ and recapture probability (p) with and without habitat but not with time because of the intensive data needs of time-dependent models (Efford 2005). We calculated c-hat ($\hat{c}$) to check model fit and all subsequent estimates were corrected for the resulting value ($\hat{c} = 1.03$). Model selection was based on ΔAICc values and Akaike weights.

(B) *Minimum stopover duration* To make use of recaptures from across all 3 years of the study ($N = 28$), we also calculated minimum stopover duration, as the number of days between the first and last capture of individual birds (Morris et al. 2006). Birds captured on the same day were excluded, as were birds captured between years, to minimize the influence of overwintering birds. To test for differences between habitats we carried out a T test, having first checked that the data met the assumptions of normality and equal variance.

Table 1 Model set to examine how habitat and other variables affect fuel deposition rates in Tennessee Warblers at a spring stopover site in northern Colombia. The model containing habitat (H) had the lowest AIC value and an Akaike weight (Wi) 62× greater than any other model. Parameter estimates and their 95% confidence intervals are given for the model containing habitat

Model (mass change =)	Parameters	AIC	ΔAIC	Wi
$I{:}H+T$	3	234.50	0.00	0.943
$I{:}D+T$	2	242.83	8.33	0.015
$I+T$	2	243.06	8.56	0.013
$I{:}M+T$	2	244.09	9.59	0.008
$I+I^2+T$	3	244.44	9.94	0.007
$I{:}A+T$	3	245.06	10.56	0.005
$I{:}Y+T$	4	245.59	11.09	0.004
$I+I^2+I^3+T$	4	246.37	11.87	0.002
$I{:}S+T$	4	246.67	12.17	0.002

| Factor	Coefficient	SE	95% CI
Hour difference	0.651	0.681	− 0.684 to 1.986
Forest	2.400	0.426	1.565 to 3.235
Coffee	0.446	0.387	− 0.313 to 1.205

I interval in days between captures; *H* habitat, 2-level factor; *T* time difference in hour of capture; *D* date, 1 = 1 March; *M* body mass at first capture; *A* age, 2-level factor; *S* sex, 3-level factor; *Y* year, 3-level factor

Maximum durations for each habitat (see calculation of flight ranges below) were based on the longest known durations in recaptured birds.

Departure mass and flight ranges

To estimate departure mass, we followed the methods described in Bayly et al. (2012a, 2013), entering stopover duration estimates into our models of body mass change for each habitat and adding the resulting estimate of mass change to 'starting body mass' (9.17 g). "Starting body mass" was taken as the mean mass of birds on first capture in shade coffee, given the limited evidence for fuelling in this habitat (see "Results"), such that body mass on first capture likely reflects body mass on arrival at the site. For each habitat we generated two estimates of departure mass: (1) entering the mean minimum stopover duration (MSD); (2) entering the longest known duration in a recaptured bird (see above). We did not use either "stopover after" or "total stopover", given uncertainty around estimated values (see "Results"), instead opting to estimate a range of departure masses bound by the mean and the maximum MSD. Studies on a range of species have found that "stopover after" and mean MSD typically provide similar values and that "total stopover" durations are around twice as long as "stopover after" durations (Morris et al. 2006; Bayly et al. 2012a). The mean MSD values found here follow this pattern, and maximum MSD were around twice as long as the mean MSD. Given the comparability of "total stopover" estimates and real durations in Grey-cheeked Thrush at our study site (see above), maximum MSDs in recaptured birds are treated here as a proxy for the average duration in the population.

Flight ranges were estimated in the program Flight 1.22 (Pennycuick 2008), entering a wingspan of 0.184 m (mean of seven live measurements taken at the study site), a wing area of 0.00668 m^2 (mean of five wings of live birds traced on graphical paper including the body area between the wing roots; see Flight 1.22 manual), a flight muscle fraction of 0.154 (mean of muscle fractions in Graber and Graber 1962) and a "Flight altitude" of 1300 m (the elevation of our study site). 'Fat fraction' was calculated following the 'Find fat fraction' guidelines provided in the Flight 1.22 manual, using a minimum mass (m_{min}) of 7.85 g, based on our LBM estimate. We estimated separate flight ranges for birds stopping over in forest and in shade coffee based on the range of departure mass described above, as well as an estimate for the highest departure masses recorded in forest (body masses > 13 g).
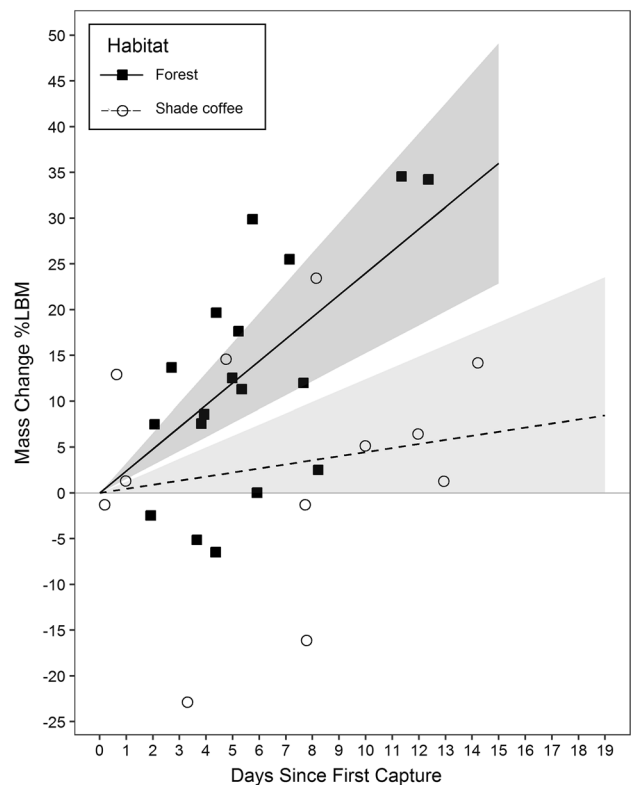
Fig. 1 Tennessee Warblers fuel faster in pre-montane forest than in shade coffee plantations at a spring stopover site in northern Colombia. Body mass change is expressed as a percentage of lean body mass (LBM) and plotted against the number of days since first capture (symbols). The predicted change in mass (lines) with 95% confidence intervals (grey shading) are shown separately for birds in shade coffee and birds in pre-montane forest based on the generalized linear model: mass change = days between captures × habitat + time difference in capture hour

Results

Diet

Diet was significantly different between habitats (Chi-square test, $X^2 = 65.4$, $P < 0.001$), with no observations of birds consuming fruit in shade coffee (based on 31 attacks by 9 birds), whereas fruit made up 67.8% of foraging attacks in forest (based on 223 attacks by 35 birds). Fruiting trees attracted flocks of Tennessee Warblers in forest and 94% of attacks on fruit involved birds piercing *Miconia* sp. fruits, a tree from the Melastomataceae family. Piercing, instead of swallowing whole, has been reported elsewhere (Stiles and Skutch 1989).

Fuel deposition rate

Our model set provided strong support for a difference in fuel deposition rates between habitats (Table 1) based on

31 recaptures, and average FDR in Tennessee Warblers was predicted to be five times higher in forest than in shade coffee (Table 1; Fig. 1). Mean FDR was positive in both habitats and individual variation was especially high in shade coffee (mean FDR over 10 days: forest = 2.4% LBM, coffee = 0.45% LBM).

Stopover duration

We found limited support for a difference in "stopover after" (survival probability) between habitats in 2011 based on ∆AICs and Akaike weights, but stronger support for a difference in "total stopover" through the seniority probability (Table 2). In both cases the model explaining the most

Table 2 Models for estimating stopover duration that contained the variable habitat received the greatest support from ∆AICc values and Akaike weights (Wi), when entering capture-recapture data from Tennessee Warblers during the spring migration of 2011 in northern Colombia. In the case of the survival probability (Phi), models without habitat were also supported having a ∆AICc < 2

Model	Parameters	AICc	∆AICc	Wi
Survival probability				
Phi (habitat) p (.)	3	236.93	0	0.412
Phi (.) p (habitat)	3	238.12	1.19	0.227
Phi (.) p (.)	2	238.27	1.34	0.211
Phi (habitat) p (habitat)	4	238.94	2.01	0.151
Seniority probability				
Gamma (habitat) p (.)	3	238.68	0	0.552
Gamma (habitat) p (habitat)	4	240.71	2.03	0.200
Gamma (.) p (habitat)	3	241.04	2.36	0.170
Gamma (.) p (.)	2	242.61	3.93	0.077

variation in stopover duration included the variable habitat. Estimated mean "total stopover" duration was 12.2 days in forest and 32.6 days in shade coffee (Table 3); however, while mean durations differed markedly, 95% confidence intervals suggest considerable variation between individuals, with overlap between habitats, as well as a high degree of uncertainty. The lack of confidence in our estimates is likely due to the small number of recaptures (19) in the data set, resulting in unrealistically high maximum durations in coffee in particular (see 95% CI in Table 3).

Mean minimum stopover duration was longer in coffee (8.8 days, $N = 10$) compared to forest (6.6 days, $N = 18$) but this difference was not significant (T test, $t = 1.59$, $df = 26$, $P = 0.12$). Minimum stopover durations covered the greatest range in coffee (Fig. 2), with the longest known duration equating to 15 days in coffee and 13 days in forest (Table 3). Given the uncertainty around our estimates of "stopover after" and "total stopover", we used minimum stopover durations to estimate flight ranges (see "Methods").

Departure mass and flight range

Entering the longest known durations into our models for body mass change indicated that birds stopping over in forest could potentially increase their body mass by 31.2% LBM, while increases in shade coffee were predicted to be much lower (6.7% LBM). The resulting departure body mass (11.8 g) for forest is in good agreement with recorded masses in this habitat and gave rise to a potential flight range of 2000 km. In contrast, the span of flight ranges for birds in coffee was between 995 and 1088 km (Table 3; Fig. 3) and even when entering the "total stopover" estimate of 31 days, the estimate only increased to 1400 km. Birds at the upper

Table 3 For Tennessee Warbler stopping over in pre-montane forest in northern Colombia, mean stopover duration was shorter (based on three methods) relative to birds fuelling in shade coffee, while body mass gain, departure body mass and flight range were all higher

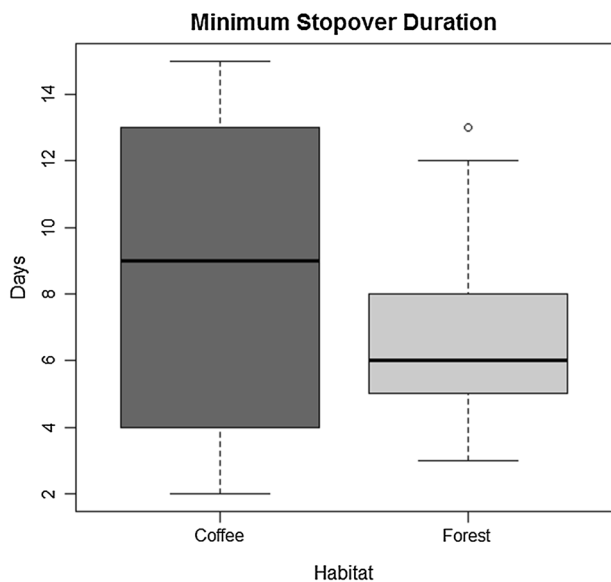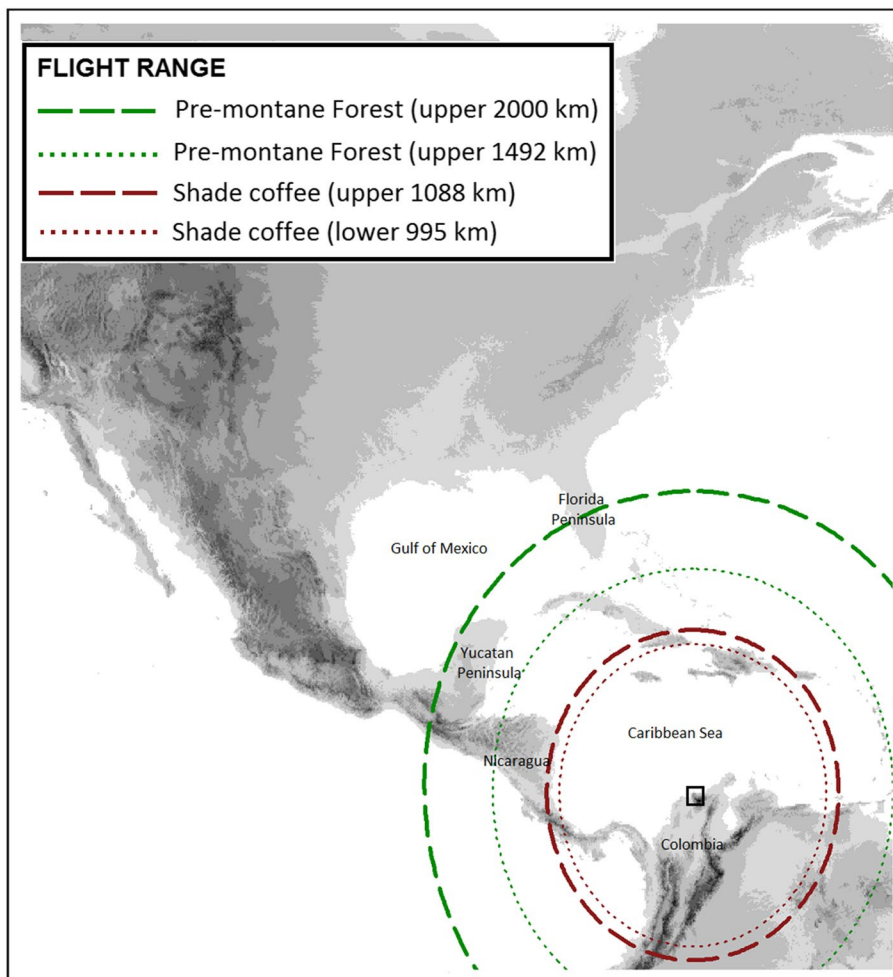|	Forest	Coffee
Stopover after duration (95% CI)	6.5 days (3.2–13.7)	9.4 days (4.1–22.4)
Total stopover duration (95% CI)	12.2 days (6.2–25.1)	32.6 days (8.0–172.1)
Minimum stopover duration (mean)	6.6 days	8.8 days
Longest known duration	13 days	15 days
Body mass gain	16.8–31.2% LBM	4.0–6.7% LBM
Departure mass	10.7–11.8 g	9.7–9.9 g
Potential flight range	1492–2000 km	995–1088 km
Max flight range from forest (departure mass > 13 g)	2500 km	N/A
Great circle distance from the Sierra Nevada de Santa Marta (SNSM)		
SNSM to Nicaragua or Cuba		1100 km
SNSM to Florida peninsula or Yucatan peninsula		1775 km
SNSM to Gulf Coast (Louisiana, Alabama, Florida panhandle)		2500 km

The lower and upper limits for body mass gain, departure mass and flight range presented here are based on calculations using the mean and longest known minimum stopover duration. Maximum flight range reflects range for the heaviest birds captured during the study (mass > 13 g), all of which were captured in forest. Distances to potential stopover regions on leaving Colombia are also given

Minimum Stopover Duration

Fig. 2 The median value and the interquartile range for minimum stopover duration (days elapsed between first and last capture) in Tennessee Warbler varied between forest and shade coffee at a spring stopover site in northern Colombia

Fig. 3 Potential flight ranges of Tennessee Warblers fuelling in shade coffee and pre-montane forest at a spring stopover site in the Sierra Nevada de Santa Marta in northern Colombia, assuming that birds receive no wind assistance. Dashed lines bound the potential flight range of birds based on them fuelling for mean minimum stopover duration (lower) and the maximum known duration (upper). For birds fuelling in shade coffee, fuel stores are expected to be sufficient to reach the Caribbean coast of Central America but birds leaving with below average stores or meeting unfavourable weather conditions may run out of fuel over the sea

limit of estimated departure mass in forest could potentially fly directly to the Yucatan or Florida peninsulas (Table 3), while all birds leaving from coffee would require a stopover in Central America or on the Caribbean Islands in order to reach the Yucatan or North America (Fig. 3). Flight ranges for the heaviest known birds departing forest (2500 km) were sufficient to reach the US Gulf Coast, especially if birds have wind assistance. Birds leaving shade coffee were at greater risk of running out of fuel over the Caribbean, regardless of the route taken (Fig. 3).

Discussion

It is widely assumed that habitat quality, mediated through resource abundance, can affect the organization and success of migration in birds (Newton 2006; Moore and Buler 2011). In this study, we found that the stopover behaviour of Tennessee Warblers on spring migration in Colombia differed markedly between naturally occurring pre-montane forest and human-managed shade coffee plantations. Warblers increased their body mass (a surrogate for energy stores)

FLIGHT RANGE
- – – Pre-montane Forest (upper 2000 km)
- ⋯⋯ Pre-montane Forest (upper 1492 km)
- – – Shade coffee (upper 1088 km)
- ⋯⋯ Shade coffee (lower 995 km)

Florida Peninsula
Gulf of Mexico
Yucatan Peninsula
Nicaragua
Caribbean Sea
Colombia

at faster rates in forest, appeared to have shorter stopover durations and attained larger energy stores at departure than did birds stopping in shade coffee. These differences are expected to carry over to subsequent migratory phases, through earlier departure dates and a faster pace of migration requiring fewer stopovers for birds departing from forest (Fig. 4). To our knowledge, this is the first clear demonstration of how stopover habitat use may shape the stopover behaviour of a Nearctic-Neotropical migratory landbird.

Our results also provide evidence that tropical forest conversion could be negatively affecting the stopover ecology of these long-distance migrants, in addition to reducing available habitat for overwintering birds (Robbins et al. 1989). We hypothesise that forest loss at stopover sites has the potential to reduce survival rates during trans-Caribbean flights (Duijns et al. 2017), influence reproductive performance through carry-over effects (Fig. 4; Finch et al. 2014) and ultimately may contribute to the ongoing population declines in migratory landbirds (Rosenberg et al. 2016).

## Effect of habitat on stopover and the organization of migration

Migratory birds departing from the Sierra Nevada de Santa Marta during spring migration must undertake a long overwater flight across the Caribbean Sea (at least 1000 km) (Bayly et al. 2013) or make a major detour away from their optimal migration direction to follow the Central American mainland (Alerstam 2001). As in other situations where birds face an ecological barrier, the decisions made during stopover are expected to be adaptive, affecting both current stopover behaviour and onward migratory strategy (Delingat et al. 2007; Woodworth et al. 2015). Differences between the two habitats studied here resulted in marked variation in the primary metrics of stopover behaviour, further corroborating previously observed differences in several indicators of habitat quality (Bayly et al. 2016). Underlying these differences was a dissimilarity in the resource base, with the availability of small fruits in forest apparently driving faster fuel deposition rates—presumably aided by the higher lipid and

carbohydrate content of fruits versus insects (Bairlein 1998). A previous study also showed that Tennessee Warblers were more likely to form large flocks in forest (Bayly et al. 2016), presumably in response to clumped resources in the form of fruiting trees, and flocking may promote higher FDRs through a reduced need for vigilance (Fuller et al. 2013). Although small sample sizes for foraging observations in coffee may have precluded the observation of fruit consumption, shade coffee at our study site and in the wider SNSM region (Bayly, personal observation) was dominated by trees with large, hard-shelled fruits or non-fruiting species (see "Methods"), and we would not expect to observe fruit consumption in coffee even if sample size was increased.

As predicted by optimal migration theory (Alerstam 2011), variation in the rate of energy deposition by Tennessee Warblers at our study site led to an apparent divergence in stopover duration (Russell et al. 1994) and also in expected departure mass. Although differences were not statistically significant, all our estimates of stopover duration point to longer durations in shade coffee and further study would likely confirm this pattern. Despite longer durations, birds were predicted to depart with smaller energy stores and have shorter flight ranges from coffee, even when entering the "total stopover" estimate of 31 days. Habitat use therefore not only affected the timing of the current stopover but likely increased the overall duration of migration (Alerstam and Lindström 1990), with birds departing from shade coffee requiring more or longer stops in order to compensate for their reduced flight range (Fig. 4).

These findings suggest that differences in the quality of habitats that birds encounter or select can have a dramatic impact on the timing and organization of the migratory journey. Nonetheless, a number of cautionary points should be raised here. While rates of mass change were, on average, five times faster in forest, three individuals gained mass in coffee at similar rates to birds in forest (Fig. 1). It could be argued that birds in coffee with negative or very slow rates were first recaptured prior to the initiation of premigratory fuelling (Neto et al. 2008). Indeed, the low percentage (1.8%) of between-year recaptures suggests that a

Fig. 4 Habitat choice at a stopover site in northern Colombia affects fuel deposition rates and stopover durations, leading to shorter stopover durations and higher departure mass in birds fuelling in pre-montane forest relative to shade coffee. These differences may have carry-over effects on stopover site use, route selection and arrival date at breeding grounds
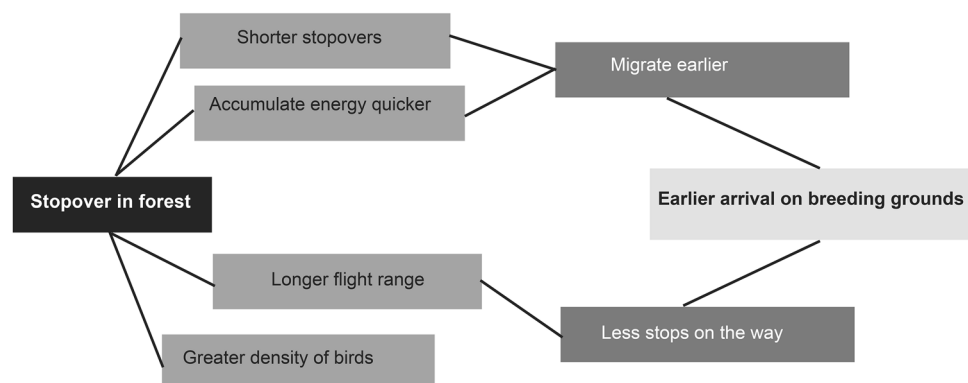
small proportion of birds at the study site were overwinter residents. Coffee may therefore provide sufficient fuelling conditions for some birds. That said, densities of Tennessee Warbler during spring migration were found to be six times higher in forest compared to coffee in the SNSM (Bayly et al. 2016), implying that per unit area, coffee plantations support far fewer birds at the population level when compared to forest during migration.

Given the large confidence intervals around our stopover duration estimates (Table 3), we are cautious in interpreting this result, despite the biologically important differences across all our stopover estimates (2–20 days). Durations may also have been overestimated in shade coffee as a result of the extended presence of non-fuelling birds. However, over-wintering and non-fuelling birds were as or more likely to be present in forest, given that 70% of birds recaptured between years, which likely overwintered at the study site, were captured in forest. Finally, even if stopover durations were the same between habitats, estimated departure fuel loads in coffee would be lower still, with the same implications for onward flight range and subsequent stopover use.

Migration strategy of Tennessee Warblers

Tennessee Warblers at our study site increased their energy stores by 4–31% depending on the habitat they occupied, giving rise to potential flight ranges between 995 and 2000 km. These estimated flight ranges imply that most individuals were not capable of direct flights to North America, in contrast to Grey-cheeked Thrushes departing from the SNSM (Bayly et al. 2013; Gómez et al. 2017). Rather, most Tennessee Warblers likely require a stopover to refuel or top up stores in northern Central America or Cuba. This necessity for additional stopovers could in turn determine departure dates (Fig. 5), which in Tennessee Warbler are up to a month earlier than species making direct flights to North America (e.g. Heckscher et al. 2011; DeLuca et al. 2015; Gómez et al. 2017).

According to our flight range estimates, the heaviest individuals (> 13 g) recorded in forest could safely reach North America without stopping to refuel (Table 3), suggesting that a direct flight to the Gulf coast or the Florida peninsula is possible. Further, our flight ranges did not account for wind assistance, yet we know that trans-Caribbean spring migration routes take advantage of favourable trade winds (La Sorte et al. 2014). If we assume that birds received wind assistance equivalent to 10 km/h, Tennessee Warblers stopping over in forest for 13 days or more could have flown direct to either Florida or the Gulf coast east of Louisiana. An examination of the relative timing of migration through northern Colombia and the US Gulf coast provides some support for such direct flights, given the minimal time lag
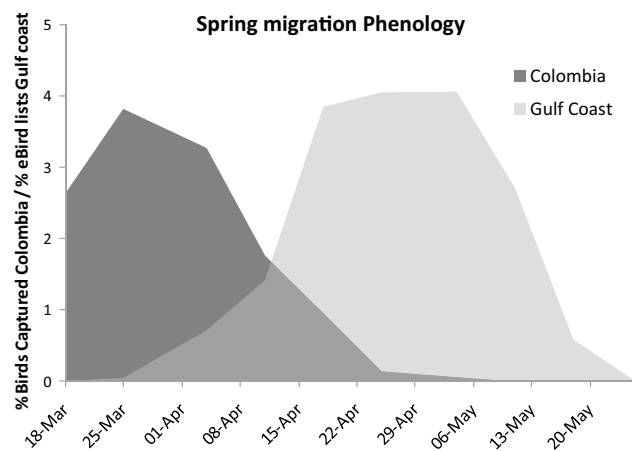
Fig. 5 Comparison of spring migration phenology between the Sierra Nevada de Santa Marta, Colombia and the Gulf Coast Prairie Bird Conservation Region in North America (coastal Mississippi, Alabama, Florida panhandle). The phenology in Colombia was based on daily mist-net captures, which were first transformed into a percentage of total seasonal captures for 2011, 2012 and 2013 before being converted into weekly means. For the Gulf Coast, we used the weekly average for the percentage of eBird lists in the Gulf Coast Prairie Conservation region containing Tennessee Warbler as of 2017

between numbers decreasing in Colombia and increasing on the Gulf Coast (Fig. 5).

While estimated flight ranges of most birds from premontane forest were likely sufficient for flights to southern Florida or the Yucatan peninsula, the same is not true for birds fuelling in shade coffee (Fig. 3). Our estimated departure loads and flight ranges from shade coffee suggest that birds with smaller fuel stores or encountering unfavourable weather conditions could run out of fuel just before reaching Central America and possibly perish in the sea. Whether this occurs depends on the spread of migration directions taken by birds departing Colombia and whether birds with smaller energy stores take a more westerly bearing in order to increase the chance of making landfall in Panama and Costa Rica, or even make landscape-scale movements within Colombia in search of more favourable fuelling conditions (Mills et al. 2011; Taylor et al. 2011). However, if we do assume that such a danger zone exists for birds migrating over the Caribbean Sea, then stopover-habitat choice at our study site in northern Colombia could influence survival rates on spring migration (Duijns et al. 2017).

Many of the conclusions drawn above depend on the relative accuracy of flight ranges calculated using Flight 1.22. While no direct validation of the predictions of Flight 1.22 exists for free-living birds undertaking migratory flights, there is support from Grey-cheeked Thrushes tracked from northern Colombia through the Motus automated telemetry array (Gómez et al. 2017). Potential flight ranges calculated using Flight 1.22 (Bayly et al. 2013) agreed closely with

documented non-stop flights of birds fitted with radio-transmitters, suggesting that accurate flight range estimates are attainable for birds departing northern Colombia. Nonetheless, while we have confidence that relative differences in flight range for Tennessee Warblers in this study are reliable, we must be cautious when interpreting the actual distances and we recommend that our predictions are tested through the application of radio-transmitters or similar tracking technologies.

Implications for full life cycle conservation

Tennessee Warblers on spring migration in northern Colombia made long stopovers, gaining sufficient energy to cover a significant proportion of their total migratory journey. This result supports the emerging recognition of northern Colombia as a major stopover region for Nearctic-Neotropical migratory birds (Bayly et al. 2013; Gómez et al. 2015, 2017), as well as confirming that Neotropical forests provide critical stopover habitat (Welton et al. 2012; Bayly et al. 2012a; Gómez et al. 2015). Given that in the wider SNSM region less than 50% of the original pre-montane forest cover remains (146 of 348 km^2; Bayly et al. 2012b), protection of remaining forests is a conservation priority for both Nearctic-Neotropical migratory birds and for 21 bird species endemic to the SNSM (Botero-Delgadillo et al. 2015). Identifying similarly important stopover sites and habitats elsewhere in northern South and Central America remains a top research priority (Faaborg et al. 2010; Bayly et al. 2018).

Despite the clear value of pre-montane forest, some Tennessee Warblers were able to accumulate moderate energy stores in shade coffee plantations. Given that large tracts of pre-montane forests have been converted to coffee production throughout the Neotropics (Etter et al. 2006), appropriate management of coffee and other agroforestry systems may increase their value as stopover habitats. For example, the inclusion of shade trees with fruits consumed by migratory birds could improve habitat quality for a range of frugivorous migratory and resident species (Smith et al. 2007); especially as the predominant shade trees in Neotropical coffee farms are leguminous trees with large, shelled fruits, inappropriate for consumption by most migratory birds (Komar 2006). Tennessee Warblers were largely observed consuming fruits of the tree *Miconia* sp. (Melastomataceae) in this study, and unpublished observations include large flocks feeding on fruits in *Ficus* sp. in the same region. The inclusion of these and other suitable trees within agroforestry systems may partly offset past and ongoing forest loss at Neotropical stopover sites (Wassenaar et al. 2007).

References

Alerstam T (2001) Detours in bird migration. J Theor Biol 209:319–331. https://doi.org/10.1016/S0169-5347(01)02258-3
Alerstam T (2011) Optimal bird migration revisited. J Ornithol 152:5–23
Alerstam T, Lindström A (1990) Optimal bird migration: the relative importance of time, energy and safety. In: Gwinner E (ed) Bird migration: the physiology and ecophysiology. Springer, Berlin, pp 331–351
Atkinson PW, Baker AJ, Bennett KA et al (2007) Rates of mass gain and energy deposition in red knot on their final spring staging site is both time- and condition-dependent. J Appl Ecol 44:885–895. https://doi.org/10.1111/j.1365-2664.2007.01308.x
Bairlein F (1998) The effect of diet composition on migratory fuelling in garden warblers *Sylvia borin*. J Avian Biol 29:546–551
Baker AJ, González PM, Piersma T et al (2004) Rapid population decline in red knots: fitness consequences of decreased refuelling rates and late arrival in Delaware Bay. Proc R Soc Lond B 271:875–882. https://doi.org/10.1098/rspb.2003.2663
Bakermans M, Rodewald AD, Vitz AC, Rengifo CG (2012) Migratory bird use of shade coffee: the role of structural and floristic features. Agrofor Syst 85:85–94
Bayly NJ, Gómez C, Hobson KA et al (2012a) Fall migration of the Veery (*Catharus fuscescens*) in northern Colombia: determining the energetic importance of a stopover site. Auk 129:449–459. https://doi.org/10.1525/auk.2012.11.188
Bayly NJ, Paez A, Gómez C, Mora C (2012b) Conservation hotspots for migratory landbirds in the Sierra Nevada de Santa Marta. Colombia, Bogotá
Bayly NJ, Gómez C, Hobson KA (2013) Energy reserves stored by migrating Gray-cheeked Thrushes *Catharus minimus* at a spring stopover site in northern Colombia are sufficient for a long-distance flight to North America. Ibis 155:271–283. https://doi.org/10.1111/ibi.12029
Bayly NJ, Gomez C, Hobson KA, Rosenberg KV (2016) Prioritizing tropical habitats for long-distance migratory songbirds—an assessment of habitat quality at a stopover site in Colombia. Avian Conserv Ecol 11:5
Bayly NJ, Rosenberg KV, Easton WE et al (2018) Major stopover regions and migratory bottlenecks for Nearctic-Neotropical landbirds within the Neotropics: a review. Bird Conserv Int 28:1–26
Bibby CJ, Green RE (1981) Autumn migration strategies of reed and sedge warblers. Ornis Scand 12:1–12
Botero-Delgadillo E, Bayly NJ, Gómez C et al (2015) An assessment of the distribution, population size and conservation status of the Santa Marta Foliage-gleaner *Automolus rufipectus*: a Sierra Nevada de Santa Marta endemic. Bird Conserv Int 25:451–465
Buler JJ, Moore FR, Woltmann S (2007) A multi-scale examination of stopover habitat use by birds. Ecology 88:1789–1802. https://doi.org/10.1890/06-1871.1
Burnham KP, Anderson DR (2002) Model selection and multinomial inference: a practical information-theoretic approach. Springer, New York

Callo PA, Morton ES, Stutchbury BJM (2013) Prolonged spring migration in the Red-Eyed Vireo (*Vireo olivaceus*). Auk 130:240–246. https://doi.org/10.1525/auk.2013.12213

Cohen EB, Pearson SM, Moore FR (2014) Effects of landscape composition and configuration on migrating songbirds: inference from an individual-based model. Ecol Appl 24:169–180. https://doi.org/10.1890/12-1867.1

Connell CE, Odum EP, Kale H (1960) Fat-free weights of birds. Auk 77:1–9

Delingat J, Bairlein F, Hedenström A (2007) Obligatory barrier crossing and adaptive fuel management in migratory birds: the case of the Atlantic crossing in Northern Wheatears (*Oenanthe oenanthe*). Behav Ecol Sociobiol 62:1069–1078. https://doi.org/10.1007/s00265-007-0534-8

DeLuca WV, Woodworth BK, Rimmer CC et al (2015) Transoceanic migration by a 12 g songbird. Biol Lett 11:20141045

Duijns S, Niles LJ, Dey A, Aubry Y, Friis C, Koch S, Anderson AM, Smith PA (2017) Body condition explains migratory performance of a long-distance migrant. Proc R Soc B 284:20171374. https://doi.org/10.1098/rspb.2017.1374

Efford MG (2005) Migrating birds stop over longer than usually thought: comment. Ecology 86:3415–3418

Etter A, McAlpine C, Wilson K et al (2006) Regional patterns of agricultural land use and deforestation in Colombia. Agric Ecosyst Environ 114:369–386. https://doi.org/10.1016/j.agee.2005.11.013

Faaborg J, Holmes RT, Anders AD et al (2010) Conserving migratory land birds in the New World: do we know enough? Ecol Appl 20:398–418

Finch T, Pearce-Higgins J, Leech DI, Evans K (2014) Carry-over effects from passage regions are more important than breeding climate in determining the breeding phenology and performance of three avian migrants of conservation concern. Biodivers Conserv 23:2427–2444. https://doi.org/10.1007/s10531-014-0731-5

Fuller RA, Bearhop S, Metcalfe NB, Piersma T (2013) The effect of group size on vigilance in Ruddy Turnstones *Arenaria interpres* varies with foraging habitat. Ibis 155:246–257. https://doi.org/10.1111/ibi.12020

Gómez C, Gómez-Bahamón V, Cárdenas-Ortiz L, Bayly N (2015) Distribution of Nearctic-Neotropical migratory birds along a South American elevation gradient during spring migration. Wilson J Ornithol 127:72–86

Gómez C, Bayly NJ, Norris DR et al (2017) Fuel loads acquired at a stopover site influence the pace of intercontinental migration in a boreal songbird. Sci Rep 7:3405

Graber RR, Graber JW (1962) Weight characteristics of birds killed in nocturnal migration. Wilson Bull 74:74–88

Harrison XA, Blount JD, Inger R et al (2011) Carry-over effects as drivers of fitness differences in animals. J Anim Ecol 80:4–18. https://doi.org/10.1111/j.1365-2656.2010.01740.x

Heckscher CM, Taylor SM, Fox JW, Afanasyev V (2011) Veery (*Catharus fuscescens*) wintering locations, migratory connectivity, and a revision of its winter range using Geolocator technology. Auk 128:531–542

Holmes RT (2007) Understanding population change in migratory songbirds: long-term and experimental studies of Neotropical migrants in breeding and wintering areas. Ibis 149:2–13. https://doi.org/10.1111/j.1474-919x.2007.00685.x

IDEAM (2010) Leyenda Nacional de Coberturas de la Tierra. Metodología CORINE Land Cover adaptada para Colombia Escala 1:100.000. Bogotá, Colombia

Johnson MD, Sherry TW, Holmes RT, Marra PP (2006) Assessing habitat quality for a migratory songbird wintering in natural and agricultural habitats. Conserv Biol 20:1433–1444. https://doi.org/10.1111/j.1523-1739.2006.00490.x

Kaiser A (1993) A new multi-category classification of subcutaneous fat deposits of songbirds. J Field Ornithol 64:246–255

Komar O (2006) Ecology and conservation of birds in coffee plantations: a critical review. Bird Conserv Int 16:1–23. https://doi.org/10.1017/S0959270906000074

La Sorte FA, Fink D, Hochachka WM et al (2014) The role of atmospheric conditions in the seasonal dynamics of North American migration flyways. J Biogeogr 41:1685–1696

Liu M, Swanson DL (2015) Stopover duration, movement patterns and temporary home ranges of fall migrant yellow-rumped Warblers *Setophaga coronata* in native and anthropogenic woodlands of the Northern Prairie region, USA. J Avian Biol. https://doi.org/10.1111/jav.00672

Mills AM, Thurber BG, Mackenzie SA, Taylor PD (2011) Passerines use nocturnal flights for landscape-scale movements during migration stopover. Condor 113:597–607

Moore FR, Buler JJ (2011) Migrant–habitat relationships during stopover along an ecological barrier: extrinsic constraints and conservation implications. J Ornithol 152:101–112

Morris SR, Larracuente AM, Covino KM, Mustillo MS, Mattern KE, Liebner DA, Sheets D (2006) Utility of open population models: limitations posed by parameter estimability in the study of migratory stopover. Wilson J Ornithol 118:513–526

Neto JM, Encarnação V, Fearon P, Gosler AG (2008) Autumn migration of Savi's Warblers *Locustella luscinioides* in Portugal: differences in timing, fuel deposition rate and non-stop flight range between the age classes. Bird Study 55:78–85. https://doi.org/10.1080/00063650809461507

Newton I (2006) Can conditions experienced during migration limit the population levels of birds? J Ornithol 147:146–166. https://doi.org/10.1007/s10336-006-0058-4

Norris DR, Marra PP, Kyser TK et al (2004) Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. Proc R Soc Lond B 271:59–64. https://doi.org/10.1098/rspb.2003.2569

Pennycuick CJ (2008) Modelling the flying bird. Elsevier, London

Perfecto I, Rice RA, Greenberg R, van der Voort M (1996) Shade coffee: a disappearing refuge for biodiversity. Bioscience 46:598–608

Pyle P (1997) Identification guide to North American birds, Part II: Columbidae to Ploceidae. Slate Creek Press, Bolinas

R Development Core Team (2017) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Robbins CS, Sauer JR, Greenberg RS, Droege S (1989) Population declines in North American birds that migrate to the neotropics. Proc Natl Acad Sci USA 86:7658–7662

Rosenberg KV, Kennedy JA, Dettmers R et al (2016) Partners in flight landbird conservation plan: 2016 revision for Canada and continental United States. Cornell Lab of Ornithology, Ithaca

Russell RW, Carpenter FL, Hixon MA, Paton DC (1994) The impact of variation in stopover habitat quality on migrant Rufous Hummingbirds. Conserv Biol 8:483–490. https://doi.org/10.1046/j.1523-1739.1994.08020483.x

Sauer JR, Hines JE, Pardieck KL et al (2014) The North American breeding bird survey, results and analysis 1966—2013. In: Version 01.30.2015. http://www.mbr-pwrc.usgs.gov. Accessed 20 Aug 2015

Schaub M, Pradel R, Jenni L, Lebreton JD (2001) Migrating birds stop over longer than usually thought: an improved capture-recapture analysis. Ecology 82:852–859

Sheehy J, Taylor CM, McCann KS, Norris DR (2010) Optimal conservation planning for migratory animals: integrating demographic information across seasons. Conserv Lett 3:192–202. https://doi.org/10.1111/j.1755-263X.2010.00100.x

Sherry TW, Holmes RT (1996) Winter habitat quality, population limitation and conservation of Neotropical–Nearctic migrant birds. Ecology 77:36–48

Smith SB, McPherson KH, Backer JM et al (2007) Fruit quality and consumption by songbirds during autumn migration. Wilson J Ornithol 119:419–428

Stiles FG, Skutch AF (1989) A guide to the birds of Costa Rica. Cornell University Press, Ithaca

Strandberg R, Klaassen RHG, Hake M, Alerstam T (2010) How hazardous is the Sahara Desert crossing for migratory birds? Indications from satellite tracking of raptors. Biol Lett 6:297–300. https://doi.org/10.1098/rsbl.2009.0785

Taylor PD, Mackenzie SA, Thurber BG, Calvert AM, Mills AM, McGuire LP, Guglielmo CG (2011) Landscape movements of migratory birds and bats reveal an expanded scale of stopover. PLoS One 6(11):e27054. https://doi.org/10.1371/journal.pone.0027054

Tejeda-Cruz C, Sutherland WJ (2004) Bird responses to shade coffee production. Anim Conserv 7:169–179. https://doi.org/10.1017/S1367943004001258

Wassenaar T, Gerber P, Verbury P et al (2007) Projecting land use changes in the Neotropics: the geography of pasture expansion into forest. Glob Environ Chang 17:86–104

Welton MJ, Anderson DL, Colorado GJ et al (2012) Spring migration stopover by Cerulean Warblers in northen Middle America. Ornitol Neotrop 23:289–305

White GC, Burnham KP (1999) Program MARK: survival estimation from populations of marked animals. Bird Study 46:120–139

Woodworth BK, Mitchell GW, Norris DR et al (2015) Patterns and correlates of songbird movements at an ecological barrier during autumn migration assessed using landscape- and regional-scale automated radiotelemetry. Ibis 157:326–339. https://doi.org/10.1111/ibi.12228

Yong W, Finch DM, Moore FR, Kelly JF (1998) Stopover ecology and habitat use of migratory Wilson's Warblers. Auk 115:829–842. https://doi.org/10.2307/4089502

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Affiliations

Nicholas J. Bayly[1] · **Kenneth V. Rosenberg[2,3]** · **Camila Gómez[1,4]** · **Keith A. Hobson[5]**

✉ Nicholas J. Bayly
nick.bayly@selva.org.co

1 Asociación SELVA: Investigación para la Conservación en el Neotropico, Diagonal 42A No 20-37, Bogotá, DC, Colombia

2 Cornell Lab of Ornithology, 159 Sapsucker Wood Road, Ithaca, NY 14850, USA

3 American Bird Conservancy, The Plains, VA 20198, USA

4 Laboratorio de Biología Evolutiva de Vertebrados, Universidad de Los Andes, Bogotá, D.C, Colombia

5 Environment Canada, 11 Innovation Blvd, Saskatoon, SK S7N 3H5, Canada