

# Effects of food availability on the distribution of migratory warblers among habitats in Jamaica

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## Summary

1. Theoretical arguments suggest that distributions of migratory birds in winter should match patterns of food availability, but in reality the match between migrants and their food may be imperfect because, for various reasons, birds may be unable to ‘track’ food resources. We tested the hypothesis that food availability influences the distribution of migratory canopy-foraging insectivorous warblers wintering in Jamaica.

2. Over a wide spatial scale (24 sites on the island), warbler abundance varied significantly among sites and habitats and was significantly dependent on measures of arthropod biomass. Alternative factors (vegetation characteristics, resident bird competitor abundance, predator abundance) were not correlated with warbler abundance.

3. Over a short temporal scale (about 2 weeks) at a single site, warbler abundance increased as predicted quantitatively after a natural, rapid increase in arthropod biomass.

4. Over a longer temporal scale (the duration of a winter), changes in density and persistence of individually marked American redstarts (*Setophaga ruticilla*, L.) on six sites corresponded with concurrent fluctuations in arthropod biomass.

5. These results document a strong association between arthropod biomass and warbler abundance in time and space, suggesting that warblers wintering in Jamaica distribute themselves in response to food resources.

6. We hypothesize that dominance hierarchies and variable movement strategies operate in concert with birds’ responses to food to influence the distribution of wintering warblers at different spatial scales. Whether food availability determines habitat quality remains to be investigated.

*Key-words:* American redstart, arthropod biomass, density, habitat use, insect abundance.

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## Introduction

Understanding the distribution and abundance of organisms – where they are found, how many individuals occur there, when, and why – is critical for the development of effective conservation plans and comprises the core of ecology as a science (Andrewartha 1961; Caughley & Sinclair 1994; Krebs 1994). The distribution of individuals among habitats is particularly important because conservation plans for animal species are usually realized through the management of their habitats (Morrison, Marcot & Mannan 1998).

Migratory birds move among habitats more than many other animals and are frequent subjects for distributional studies (Cody 1985; Bernstein, Krebs & Kacelnik 1991). Although most discussion of migratory bird habitat distributions has focused on breeding

populations, a simpler situation exists with birds outside the breeding season (i.e. the migration and winter periods), when they are free from confounding factors associated with reproduction (Hutto 1985a).

The influence of winter on a migrant’s fitness ultimately depends on its survival and preparation for an early spring departure for the breeding grounds to reproduce (Marra, Hobson & Holmes 1998). Winter survival and a successful spring departure, in turn, depend primarily on obtaining enough food for self-maintenance and fat storage (for spring migration), and avoiding predation (Price 1981; Moore & Yong 1991; Marra & Holberton 1998). Therefore, local distributions of migratory birds in winter should, in theory, match patterns of food availability (Fretwell 1972; Moreau 1972; Karr 1976; Hutto 1980, 1985a,b; Leisler 1990; Levey & Stiles 1992; Sherry & Holmes 1996). However, if food is not limiting or if migrants are unable to track differences in food availability among habitats, then their distributions may not correspond to food availability (Wiens 1976, 1977; Rotenberry & Wiens 1980;

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Recer *et al.* 1987, 1989). Alternatively, migrant distributions could be determined by predation risks (Rappole, Ramos & Winker 1989), habitat preferences from the breeding season (Morse 1971; Hutto 1980) or evolutionary responses to past ecological circumstances. In addition, migrant distributions may be further altered by intra-specific dominance hierarchies (Ornat & Greenberg 1990; Marra 2000) or the distribution of dominant resident species (Keast 1980; Greenberg 1986; Leisler 1992). The operation of one or more of such non-food factors could result in a poor match between the distribution of migratory birds in winter and the availability of their food resources.

Despite the potential role for winter studies to elucidate the ecological factors important in migratory bird distributions, much previous research has focused on documenting distributional patterns of migrants in winter (Karr 1976; Keast & Morton 1980; Lack 1986; Lynch 1989; Leisler 1990; Hagan & Johnston 1992; Wunderle & Waide 1993; Wallace *et al.* 1996), while investigation of the ecological mechanisms behind these patterns has received less attention (Petit *et al.* 1995; but see Hutto 1980 for Neotropics; Folse 1982 for Palaearctic migrants). The hypothesis that food influences the winter distribution of migrants is favoured by many avian ecologists (Leisler 1990; Hutto 1992; Wunderle & Waide 1993; Jones *et al.* 1996; Katti & Price 1996; Sherry & Holmes 1996), but few have quantified resources even at local scales (Hutto 1980; Folse 1982; Rabøl 1987; Greenberg, Caballero & Bichier 1993; Strong & Sherry 2000) and a comprehensive test is lacking (Petit *et al.* 1995).

Here, we evaluate the hypothesis that food availability influences the distribution of wintering migratory birds by testing three predictions: (1) variation in migrant abundance among sites is more dependent on food availability than on alternative factors; (2) migrant abundance responds predictably to a natural perturbation of food; and (3) overwinter changes in migrant abundance correspond with concurrent changes in food availability. First, if the winter distribution of migrants is influenced by food, then over a broad spatial scale, regressions of migrant abundance on food availability should be significantly stronger than on alternative factors, such as vegetation structural characteristics, competitor abundance or predation risk. Although indicative of an association between migrant abundance and food, such correlative results would not necessarily establish a causal link. If food availability explicitly influences migrant abundance in a habitat, then, secondly, a regression should permit one to predict the quantitative response of migrant abundance to a perturbation of food. However, even this kind of response could result primarily from the redistribution of wandering individuals or species capable of tracking ephemeral resources, it would not necessarily indicate that sedentary (territorial) migrants were also influenced by food availability. If food availability influences the distribution of territorial birds, which often comprise

the majority of individuals in some habitats (Rappole & Warner 1980; Holmes, Sherry & Reitsma 1989; Mabey & Morton 1992; Wunderle 1995), then, thirdly, overwinter changes in the density and site persistence of territorial species should correspond with concurrent changes in food availability.

We tested these three predictions for a guild of migrant warblers wintering in Jamaica, West Indies. We focused on canopy-foraging insectivorous warblers because they comprise a large proportion of all migrant land birds (up to 35% in some regions; Lack 1976) yet feed similarly, thereby lending generality to the study while permitting the quantification of an appropriately narrow resource (small canopy arthropods). Insectivorous, canopy-foraging migrant warblers (hereafter, 'warblers') in Jamaica consist of six species: The northern parula (*Parula americana*, L.), prairie warbler (*Dendroica discolor*, Vieillot) and American redstart (*Setophaga ruticilla*, L.) are widespread and common, the black-throated green warbler (*Dendroica virens*, Gmelin), yellow-throated warbler (*Dendroica dominica*, L.) and magnolia warbler (*Dendroica magnolia*, Wilson) are locally common in some habitats, but are not widespread (Lack 1976; Wunderle & Waide 1993; Johnson 1999).

## Materials and methods

### STUDY AREAS

We selected study sites to reflect the topographical and ecological diversity of Jamaica. Twenty-five sites differing in rainfall, elevation and degree of human disturbance were selected from six broad habitat types: wet limestone forest, dry limestone forest, coastal thorn scrub, mangrove forest, shade-coffee plantation and citrus orchard (Table 1; see Asprey & Robbins 1953, for detailed descriptions of the natural vegetation, and Johnson 1999, for detailed site descriptions).

### ARTHROPOD SAMPLING

Ornithologists have long recognized challenges in effectively quantifying food availability for forest insectivores (Cooper & Whitmore 1990; Wolda 1990). The principal problem is that due to birds' selection of prey and foraging microhabitats, the total abundance of arthropods in an environment does not necessarily correspond to the amount of food available for foraging predators (Hutto 1990). Our sampling design helped minimize effects of prey and microhabitat selection in three ways. First, a guild of six warbler species (see Introduction) was studied, whose combined foraging sites and diets more closely match the resources sampled by broad insect trapping techniques than for any one species alone. Secondly, 'branch clipping' (described below) was chosen because it samples microhabitats within canopy foliage most often used by feeding warblers (Johnson 2000a). Thirdly, parallel

**Table 1.** Study sites lettered alphabetically by sampling date (for Prediction 1), grouped by broad habitat types

Study site	Habitat type	Lat–Long.	Elevation range	Site
Description				
A Cope Mountain	Wet limestone forest	18°16'N 77°04'W	440–460 m	Tall, dense, old-aged wet forest fragment with several hurricane-formed gaps containing thick understories and vines
J Marshall's Pen	Wet limestone forest	18°3'N 77°32'W	600–620 m	Second growth moist forest fragment with continuing minor disturbance
N Windsor Cave	Wet limestone forest	18°21'N 77°30'W	230–240 m	Diverse, tall, dense, mesophyllc forest within large, relatively undisturbed forested landscape
W Ecclesdown	Wet limestone forest	18°05'N 78°54'W	210–320 m	Very wet forest at base of undisturbed forested mountain, limestone/shale soils
H Portland Ridge Upper	Dry limestone forest	17°44'N 78°09'W	100–120 m	Undisturbed arid forest in a valley where air was more moist, soils deeper, and trees taller than in surrounding areas
K Portland Ridge Lower	Dry limestone forest	17°44'N 78°09'W	80–100 m	Undisturbed arid forest, dense subcanopy with vines, canopy thin and lacking large trees
O Hellshire Hills	Dry limestone forest	17°51'N 78°12'W	10–20 m	Highly disturbed dry forest, dense thorny shrub layer, grasses in open areas
X Great Bluff	Dry limestone forest	17°52'N 77°45'W	10–30 m	Disturbed very arid forest, canopy sparse, cacti abundant, thorny understory
F Luana Point West	Thorn scrub	18°02'N 77°55'W	0–10 m	Heterogeneous grazed thorny thicket with some tall remnant trees
L Portland Cottage Inland	Thorn scrub	17°45'N 77°10'W	0–10 m	Homogenous grazed Mimosaceous dry savanna
M Portland Cottage Seaward	Thorn scrub	17°45'N 78°10'W	0–10 m	Heterogeneous woodland of dry thorn thicket, dry forest, and coastal woodland
R Luana Point East	Thorn scrub	18°02'N 77°54'W	0–10 m	Dense, thorny logwood thickets interspersed with grassy openings
P Negril	Mangrove	18°11'N 76°43'W	0–10 m	Tall, old/middle-aged diverse mangrove swamp
S Luana Point	Mangrove	18°02'N 77°54'W	0–10 m	Tall, mature black mangrove swamp in a landscape mosaic with thorn scrub
U Portland Cottage	Mangrove	17°45'N 78°10'W	0–10 m	Short dense mangrove scrub with shallow open pools
V Morant Point	Mangrove	18°04'N 78°57'W	0–10 m	Hurricane disturbed dense mangrove scrub thicket
B Kew Park Ortanique	Citrus	18°16'N 77°04'W	290–300 m	Small, little-managed orchard surrounded by pasture, occasional remnant tall wet forest trees
C Kew Park Orange	Citrus	18°16'N 77°04'W	300–310 m	Small little-managed orchard with small pockets of mesic trees and shrubs
E Trout Hall	Citrus	18°08'N 77°20'W	220–240 m	Large intensively managed relatively young orchard with many narrow wet ravines
T Comfort Hall	Citrus	18°10'N 77°34'W	200–210 m	Large, intensively managed orchard with small swampy hollows
D Kew Park	Shade-coffee	18°16'N 77°04'W	300–310 m	Very young small plantation surrounded by wet forest and pasture, diverse short planted shade trees among several tall remnant forest trees
G James Hill East	Shade-coffee	18°10'N 77°20'W	610–620 m	Moderately diverse area of plantation, tall, old shade trees of primarily two species, dense coffee understory with a small stream
I James Hill West	Shade-coffee	18°10'N 77°20'W	610–620 m	Relatively homogenous area of plantation, relatively open understory with abundant banana trees
Q Baronhall	Shade-coffee	18°13'N 77°22'W	550–560 m	Large, old, homogenous plantation shaded by <i>Inga vera</i> , wet forest, pasture, and pond near study area
Y Comforthall	Shade-coffee	18°15'N 77°34'W	680–700 m	Young homogenous plantation shaded by <i>Inga vera</i> , coffee trees pruned to form a short dense understory.

studies using emetics allowed the identification and analytical exclusion of prey that were not eaten by the study guild [Isoptera and all arthropods greater than 10 mm in length (except Lepidopteran larvae); Johnson 2000a; A. Medori & T. W. Sherry unpublished data].

To sample arthropods by branch clipping, a collapsible cloth bag was positioned in vegetation (up to 9 m with the aid of extension poles), placed quickly over the end of a branch, and the mouth of the bag was closed quickly and tightly around the branch with a drawstring. The branch was then clipped free with a telescoping tree pruner, and the bag and branch were lowered, and visually inspected for arthropods (Majer *et al.* 1990; Schowalter 1994; Johnson 2000a). All arthropods were immediately categorized by 1-mm size intervals and identified to order. Abundances per sample were converted to biomass using length-weight regressions generated from voucher specimens collected at the study sites (Johnson & Strong 2000). To standardize for variable amounts of clipped vegetation, each sample was expressed as total biomass of arthropods per 100 g of clipped vegetation (wet mass). The resulting branch clip arthropod biomass was normalized for analysis by log transformations. Details on the distribution of branch clip samples within study sites are explained for each prediction below.

Branch clipping tends to under sample keen sighted aerial insects such as Odonata and large Diptera (Johnson 2000a), which could result in underestimating food availability in habitats with proportionately high abundances of flies, such as those with standing water (e.g. mangroves). Therefore, a second complementary method, Malaise trapping, was used to improve aerial arthropod estimates. Standard Malaise traps (2 m high, pyramidal construction, Bioquip Corporation, Gardena, CA, USA) were operated for roughly 24 h (mean  $\pm$  1 SD operation length =  $23.7 \pm 1.9$  h). A pilot study indicated that Malaise traps hoisted into the canopy captured the same orders and ranked abundances as paired, simultaneously run traps placed on the ground (M. D. Johnson unpublished data). Therefore, ground traps were subsequently relied upon because they are far more convenient to operate. Trapped arthropods were sorted to the same taxa as the branch clip samples, dried to constant mass, weighed to the nearest 0.1 mg, and standardized to 24-h trap-periods. Malaise trap biomass was also normalized for analysis by log transformations.

#### PREDICTION 1: REGRESSIONS OF WARBLER ABUNDANCE ON FOOD AND NON-FOOD VARIABLES

To test the prediction that warbler abundance was more strongly dependent on food availability than on alternative factors, data were collected in four representative sites in each of six broad habitat types (sites A–X; Table 1). During the middle to late winter months (January–March 1995–7), 10–20 study points were

established in each site depending on patch size (mean = 18.0), each separated by at least 100 m (75 m in the densest wet limestone forest sites) and 50 m from the nearest habitat edge. To estimate warbler abundance, a 10-min fixed radius (25 m) point count survey was conducted at each study point between 0530 and 1000 EST (Hutto, Pletschet & Hendricks 1986). To help detect vocally inconspicuous birds, taped songs and chip-notes (from Cornell Laboratory of Ornithology) of the three most common species in the study guild (prairie warbler, northern parula and American redstart) were played during the first 5 min of each point count (100 s of each species in a randomized order) from a portable cassette player fitted with a 7-watt speaker (SONY model SRS-A50) placed on the ground at each study point and directed vertically (Sliwa & Sherry 1992). A site-specific index of warbler abundance was calculated as the mean number of warblers (all six species combined) per count (within the 25-m radius) for use in regressions against independent variables hypothesized to influence warbler distribution (e.g. food, vegetation structure). For comparisons with other studies of the distribution of migrants among habitat types, differences in warbler abundance between and within the six broad habitat types used in this study were also examined (square-root transformed).

To estimate food availability in each study site, 16 branch clip samples and three Malaise traps were randomly distributed among the study points. If fewer than 16 study points were available at a site, additional points were randomly sampled until 16 were obtained. All arthropod sampling in each site was conducted within 6 days of the point count surveys. Arthropod data were analysed primarily as independent variables in regressions, but, like warbler abundance, differences in arthropod biomass between and within habitat types were also examined.

In addition to arthropod biomass, three other factors were quantified that could influence warbler abundance: vegetation structure, resident competitor bird abundance and predator abundance. Vegetation structure was quantified using foliage height profiles, which were measured using a plumb line and a vertically orientated camera with 15 etched grid points, as described by MacArthur & Horn (1969). In each site, profiles were measured at 30 points randomly distributed along five 30-m transects, which originated at randomly chosen study points. Foliage profile data for sites A–O were collected concurrently with the bird and arthropod data, data for sites P–X were collected 9–16 March 1998 and site V data were collected 8 June 1998. For each site, the mean number of leaves was calculated in each of the following height intervals: 0–1, 1–2, 2–3, 3–4, 4–6, 6–8, 8–10, 10–12, 12–15 and >15 m. The modal vegetation height and the number of height intervals with foliage were also determined, because these have correlated with migrant habitat use (Wunderle & Waide 1993). Because many of these 12 foliage distribution variables were intercorrelated, they were

**Table 2.** Resident bird guilds used to index competitor abundance

Non-ground-feeding insectivores/omnivores	Small insectivores	Small foliage-feeding insectivores
Jamaican tody <i>Todus todus</i> , L.	Jamaican tody	Jamaican tody
Jamaican elaenia <i>Myiopagis cotta</i> , Gosse	Jamaican elaenia	Jamaican elaenia
Jamaican peewee <i>Contopus pallidus</i> , Gosse	Jamaican peewee	Jamaican vireo
Sad flycatcher <i>Myiarchus barbirostris</i> , Swainson	Sad flycatcher	Blue Mountain vireo
Rufous-tailed flycatcher <i>Myiarchus validus</i> , Cabanis	Stolid flycatcher	Arrow-headed warbler
Stolid flycatcher <i>Myiarchus stolidus</i> , Gosse	Jamaican vireo	Yellow warbler
Jamaican becard <i>Pachyramphus niger</i> , Gmelin	Blue Mountain vireo	Bananaquit
Loggerhead kingbird <i>Tyrannus caudifasciatus</i> , d'Orbigny	Arrow-headed warbler	
Rufous-throated solitaire <i>Myadestes genibarbis</i> , Swainson	Yellow warbler	
White-eyed thrush <i>Turdus jamaicensis</i> , Gmelin	Bananaquit	
Jamaican vireo <i>Vireo modestus</i> , Sclater		
Blue mountain vireo <i>Vireo osburni</i> , Sclater		
Arrow-headed warbler <i>Dendroica phareta</i> , Gosse		
Yellow warbler (resident) <i>Dendroica petechia</i> , L.		
Bananaquit <i>Coereba flaveola</i> , L.		

collapsed for further analyses into three orthogonal foliage profile components with a principal components analysis (varimax rotation).

The mean number of resident competitors was categorized in three guilds, in increasing order of probable resource overlap with the warblers studied here (Table 2, based on Lack 1976): non-ground-foraging insectivores/omnivores, small insectivores and small foliage-feeding insectivores. The abundances of resident birds in these guilds were highly correlated with each other because they were nested subsets. Therefore, they were collapsed to a single resident competitor abundance component with a principal components analysis (varimax rotation).

The only consistent predators of adult canopy-foraging birds in Jamaica are two falcons (Lack 1976), the American kestrel (*Falco sparverius*) and merlin (*Falco columbarius*). Falcon abundance was indexed as the number of individuals detected in a site divided by the number of point counts.

To test the prediction that warbler abundance is more dependent on arthropod biomass than on alternative factors, a multiple regression was run using warbler abundance (dependent variable) against branch clip biomass and Malaise trap biomass (independent variables). Next, a stepwise multiple regression was run to determine what set of the following five alternative (non-food) independent variables could best predict warbler abundance: three foliage profile principal component scores, the resident bird competitor principal component score, and the predator abundance score. The relative strength of the two resulting regression models, one for food variables, one for non-food variables, was tested using a *z*-test of regression predictor sets (Tabachnick & Fidell 1996).

#### PREDICTION 2: PREDICTION OF SHORT-TERM WARBLER RESPONSE TO FOOD PERTURBATION

Within 2 weeks after the initial bird and food data were collected, a natural insect eruption occurred in one of

our thorn scrub sites (site R of the Prediction 1 test). This insect eruption was used as a 'natural experiment' to test the expectation that warbler abundance responds predictably to a natural perturbation of food availability.

After the eruption, warbler abundance was re-estimated with point counts, and arthropod biomass was simultaneously re-sampled with branch clips and Malaise traps as described above. Using the resampled arthropod biomass values, a 95% prediction interval was generated around the bird abundance value predicted by the multivariate regression of warbler abundance and arthropod biomass (from Prediction 1) to ascertain whether or not it included the re-estimated warbler abundance data point (Dillon & Goldstein 1984).

#### PREDICTION 3: NUMERICAL RESPONSES OF TERRITORIAL WARBLERS TO OVERWINTER FOOD FLUCTUATIONS

To measure numerical responses of warblers to overwinter changes in food availability, birds were colour-ringed and monitored in three habitats during the 1995–96 and 1996–97 winters. The labour-intensive methods used to capture, ring and monitor warblers dictated concentrating efforts for this test on just the American redstart, which is highly territorial in Jamaica and well enough studied for comparisons (Holmes *et al.* 1989; Marra, Sherry & Holmes 1993; Sherry & Holmes 1997; Marra & Holberton 1998). Five sites were monitored in the 1995–96 winter: two shade-coffee, two dry limestone and one citrus [sites I, Q, H, K, and B and C (combined), respectively]. Six sites were monitored in the 1996–97 winter: two shade-coffee, two dry limestone and two citrus [sites Y, Q, H, K, T, and B and C (combined), respectively]. Sites B and C, two small citrus sites on a single farm, were combined for Prediction 3 to generate adequate sample sizes for meaningful estimates of redstart density. Citrus, coffee and dry limestone forest habitats were chosen because they showed different seasonal patterns of arthropod

biomass. Each study site was gridded and flagged at 25-m intervals, and trails were cut along grid lines in dry limestone forest to facilitate moving quickly and quietly.

Each site was visited three times each winter: early (5 November–16 December 1995, 3 November–14 December 1996), middle (7 January–10 February 1996, 5 January–8 February 1997) and late winter (12 February–24 March 1996, 7 February–24 March 1997). Early and late winter dates were chosen to avoid periods when transient individuals pass through Jamaican habitats (Peter Marra and Robert Sutton personal communication). The order in which sites were visited between winter periods was the same in a given year, but changed between years, so that each site was visited at an interval of approximately 6 weeks (mean interval =  $45.5 \pm 2.5$  days SE).

During each visit, five to nine days were spent on a site to capture/ring (early and late winters only), census, and map movements of individual redstarts. Birds were captured in mist nets (6–12 m, four-tier, 30-mm mesh diagonal) using a combination of 'target netting' and 'blanket netting'. Target netting consisted of erecting a mist net near an unmarked bird, and luring the bird into the net with a combination of song and chip vocalization playbacks, a stuffed decoy and/or a temporarily held (<31 min) live decoy (Holmes *et al.* 1989). Blanket netting involved distributing 6–18 nets throughout a site, often within particular unmarked redstarts' territories. Each captured redstart was ringed with a unique combination of a numbered US Fish & Wildlife Service aluminium ring and two plastic coloured rings. In early winter, all territorial redstarts in each site were sought for capture, an average of 89% of those observed (range = 71–100%) were ringed.

The study plots were traversed repeatedly during each visit, and the locations and movements of all ringed and unmarked redstarts were recorded and tallied onto gridded maps (Holmes *et al.* 1989). All sightings of unidentifiable unmarked birds of the same age/sex class within 25 m of each other over a period of at least 2 days were considered sightings of a single individual for mapping purposes. Individual mapping was done to determine redstart density, and to assist in relocating birds rather than to establish strict territory boundaries or sizes. Therefore, minimal activity ranges were delineated by enclosing all observations of each individual onto summary maps generated after each site visit.

To examine numerical responses in warblers, two variables were quantified for each study site. 'Persistence' of redstarts in a site was calculated as the percentage of ringed birds that were detected in two consecutive winter periods (i.e. early middle and middle-late winter). 'Change in density' of redstarts was the factor by which density changed between consecutive winter periods (e.g. a factor of two indicated a doubling of density). Density was calculated as the number of ringed plus unmarked individual minimal activity ranges per hectare of gridded study plot. Individuals whose activity ranges fell on plot boundaries were considered within

the study site if greater than 50% of the estimated activity range fell within plot boundaries.

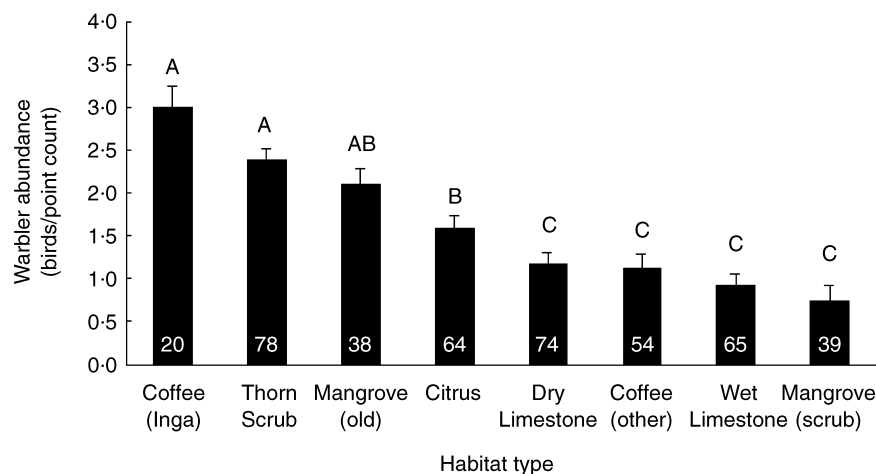
To quantify the temporal change in food availability on sites, branch clip samples were collected in each winter period from 20 points randomly distributed among 50-m grid intervals. Although branch clipping and Malaise trapping together probably better estimate the absolute availability of food across a diversity of sites, Malaise trap biomass contributed little in quantifying food availability in the habitats used in this test (citrus, coffee and dry limestone, see Results, Table 4). Thus, branch clipping alone was used for this test so that adequate within-season replication could be generated to calculate the relative change in arthropod biomass between site visits. Change in arthropod biomass, like change in redstart density, was calculated as the factor by which it changed between consecutive winter periods.

The prediction that overwinter changes in migrant abundance correspond to concurrent changes in food availability was tested by correlating the change in arthropod biomass between consecutive winter periods vs. (1) the persistence of ringed redstarts and (2) the change in density of all redstarts in a site between the same periods. Change in arthropod biomass was log transformed to linearize the predicted asymptotic relationship with redstart persistence. Over the course of the study, 22 data points for each correlation were generated: 10 points in 1995–96 (three visits to each site created two between-visit values per site  $\times$  five sites), and 12 points in 1996–97 (two values per site  $\times$  six sites). The changes in arthropod biomass and redstart density between periods, rather than the period-specific values themselves, were used to minimize the dependency of points in the correlations. However, each site contributed two data points to the correlations per winter (change from early to middle winter and from middle to late winter) and four sites were used in both winters. Therefore, Pearson's correlation coefficients and associated *P*-values are presented mainly for descriptive purposes, the correlations are evaluated graphically and in relation to the variance in redstart density (*sensu* Arcese *et al.* 1992). Analyses (for all predictions) were computed using SYSTAT 5.2.1 for the Macintosh (Wilkinson 1989).

## Results

### DIFFERENCES IN WARBLER ABUNDANCE AND ARTHROPOD BIOMASS BETWEEN HABITATS

Significant differences in warbler abundance among replicate sites within a broad habitat type were present only in mangrove forests and shade-coffee plantations, which were subsequently divided into finer habitat classifications for further analyses. Mangrove sites differed depending on age/stature (ANOVA:  $F_{3,73} = 12.51$ ,  $P < 0.001$ ): old growth black mangrove (*Avicennia germinans*) forests (sites P and S) contained more warblers than did short stature mangrove scrub sites (sites U and V). Coffee



**Fig. 1.** Abundance of warblers in eight habitat types in Jamaica (mean  $\pm$  1 SE). Habitats not sharing a letter have significantly different densities (on square-root transformed data; Tukey *post hoc* ANOVA tests,  $P < 0.05$ ). Samples sizes (shown at base of bars) are the number of point counts.

**Table 3.** Biomass of arthropods in branch clip and malaise trap samples by habitat type

Habitat type	Branch clips			Malaise traps		
	Mean*	SE	n	Mean†	SE	n
Coffee ( <i>Inga</i> )	16.58 <sup>ab</sup>	3.26	16	7.64 <sup>abc</sup>	2.78	3
Thorn scrub	16.92 <sup>a</sup>	2.38	64	4.34 <sup>bc</sup>	0.77	12
Mangrove (old)	4.59 <sup>c</sup>	0.64	32	10.03 <sup>ab</sup>	2.97	6
Citrus	4.50 <sup>c</sup>	0.61	64	9.85 <sup>abc</sup>	1.45	12
Dry limestone	5.20 <sup>c</sup>	0.69	64	5.34 <sup>abc</sup>	1.14	12
Coffee (other)	11.16 <sup>bc</sup>	3.41	48	4.98 <sup>abc</sup>	1.07	9
Wet limestone	8.28 <sup>bc</sup>	1.06	64	2.61 <sup>c</sup>	0.32	12
Mangrove (scrub)	3.50 <sup>c</sup>	0.76	32	6.22 <sup>abc</sup>	2.17	12
	$F_{7,376} = 10.07\ddagger$ $P < 0.001$			$F_{7,64} = 4.36\ddagger$ $P < 0.001$		

\*Mg arthropods per 100 g clipped vegetation, habitats with different letters were significantly different ( $P < 0.05$ , Tukey *post hoc* tests).

†Mg arthropods per trap hour, habitats with different letters were significantly different ( $P < 0.05$ , Tukey *post hoc* tests).

‡Data were log-transformed for ANOVA.

sites varied according to shade-tree species ( $F_{3,70} = 9.77$ ,  $P < 0.001$ ): site Q, which was shaded primarily by *Inga vera*, contained more warblers than did sites D, G and I, which were shaded by other tree species. Among the resulting eight habitat types, the abundance of warblers varied significantly ( $F_{7,424} = 18.58$ ,  $P < 0.001$ , Fig. 1).

The biomass of branch clipped and Malaise trapped arthropods also varied significantly among habitats (Table 3). Mean branch clip and Malaise trap arthropod biomass were not correlated across sites or habitats (both  $r < 0.25$ ,  $P > 0.05$ ), and were therefore used as independent, complementary predictors of warbler abundance for testing Prediction 1.

#### TEST OF PREDICTION 1

The abundance of warblers increased significantly with arthropod biomass across the 24 sites (Table 4). Together,

branch clip and Malaise trap arthropod biomass accounted for 52% of the variation in warbler abundance. Warbler abundance was more strongly dependent on branch clip arthropod biomass ( $r = 0.58$ ) than on Malaise trap arthropod biomass ( $r = 0.30$ ), but the latter contributed significantly to the fit of the regression model once the effects of branch clip biomass were controlled ( $P < 0.05$ ). When analyses were restricted to coffee, citrus and dry limestone forest habitats (those used in the test of Prediction 3), only branch clip arthropod biomass contributed significantly to the model (Table 4).

Principal Components Analysis (PCA) reduced the number of foliage profile and resident bird competitor abundance variables to orthogonal components, which were then included with the other non-food factors in regressions with warbler abundance. PCA effectively reduced the 12 foliage profile variables to three components, which together explained 74.4% of the total foliage profile variance (Table 5). The first component was loaded with the tallest foliage profile intervals, the second with the mid-canopy 'scrubby' intervals and the third with the lowest intervals. Thus, the three components correspond to foliage canopy development, 'scrubbiness' and understorey development, respectively. The PCA of resident bird competitor abundance resulted in a single component explaining 91.8% of the total variance, which was most strongly loaded with the abundance of small insectivores (0.98), although it was also loaded with the abundances of other guilds (0.93–0.96).

Warbler abundance was not significantly correlated with any of the five non-food variables (Table 6). Stepwise multiple linear regression of warbler abundance against the non-food variables resulted in a model with one independent variable, which was also not statistically significant ( $P > 0.05$ ). The first foliage profile principal component, which corresponded roughly to canopy development, was weakly negatively associated with warbler abundance, accounting for 10% of its

**Table 4.** Regression coefficients of warbler abundance (dependent variable) on two sets of independent variables: (1) food (arthropod) availability and (2) non-food factors (vegetation structure, resident bird abundance, and predator abundance) across 24 sites. Food availability was indexed by the mean biomass of branch-clipped (mg arthropods/100 g vegetation) and Malaise-trapped arthropods (mg arthropods/trap/h). Non-food model was determined by a stepwise multiple regression of five variables (see Table 6). Regression model for food abundance in citrus, coffee, and dry limestone forest habitats only (the 12 sites used in Prediction 3) is also presented

Model	<i>n</i> (no. sites)	Variable	Coeff.	SE	<i>F</i>	d.f.	<i>P</i>	<i>r</i> <sup>2</sup>
All sites (food availability)	24	Constant	-0.67	0.50	11.17	2,21	<0.001	0.52
		Branch clip	1.61	0.38				
		Malaise trap	1.19	0.43				
All sites (non-food)	24	Constant	1.53	0.14	2.28	1,22	0.15	0.10
		Foliage profile component 1 score	-0.22	0.14				
Citrus, coffee, and dry limestone forest sites only (food)	12	Constant	0.45	0.46	5.55	1,10	0.04	0.36
		Branch clip	1.34	0.57				

**Table 5.** Significant loadings ( $P < 0.01$ ) of three principal components derived from 12 foliage profile variables from 24 sites in Jamaica

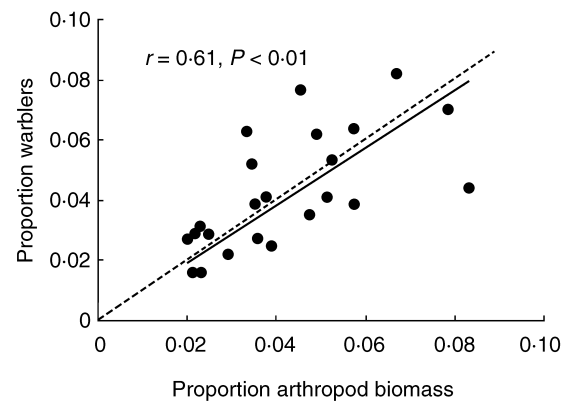
Foliage profile variable	Principal component		
	1	2	3
Amount of foliage: 0–1 m			0.516
1–2 m			0.703
2–3 m			0.572
3–4 m		-0.852	
4–6 m	0.624	-0.684	
6–8 m	0.861		
8–10 m	0.928		
10–12 m	0.847		
12–15 m	0.881		
>15 m	0.787		
Interval of maximum foliage	0.737		
No. intervals with foliage	0.737		
Cumulative percentage of total variance explained	46.4	62.0	74.4

**Table 6.** Correlations of non-food variables with warbler abundance across 24 sites in Prediction 1. See Table 5 and text for variable loadings of foliage profile and resident bird components, respectively. All  $P > 0.05$

Variable	Pearson's <i>r</i>
Foliage profile component 1	-0.31
Foliage profile component 2	-0.19
Foliage profile component 3	-0.04
Resident bird competitor	-0.21
Density component 1	
Predator abundance	0.14

variance (Table 4). Using a *z*-test of regression predictor sets (Tabachnick & Fidell 1996), total warbler abundance was significantly more dependent on arthropod biomass than on the best non-food model ( $z = 2.08$ ,  $P < 0.05$ , Table 4). Thus, the prediction that variation in migrant abundance among sites is more dependent on food availability than on alternative factors (Prediction 1) was supported.

The proportion of warblers in each site was correlated with the proportion of food in that site, the



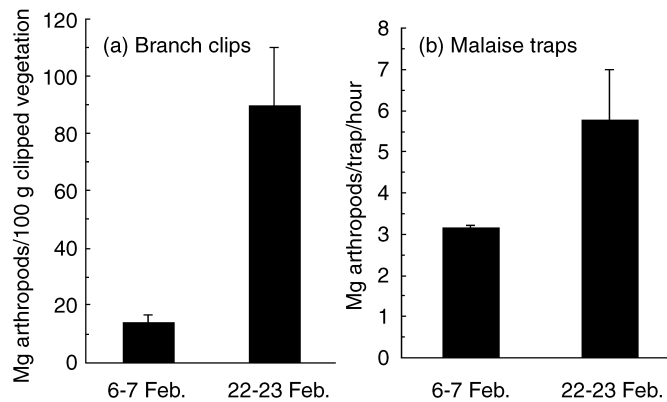
**Fig. 2.** Relationship between the proportion of warblers in each point count site (of total warblers detected among all sites;  $n = 24$  sites) and the proportion of arthropod biomass in that site (as mean of total branch clip and Malaise trap biomass proportions). Solid line indicates slope of the correlation (0.96) and dashed line indicated the expected slope of 1.0 if warblers exhibited exact 'habitat matching'.

so-called 'habitat matching' expectation of an ideal free distribution (Fretwell 1972; Fagen 1987; Ward, Austin & MacDonald 2000). Setting the intercept to zero, the proportion of warblers was significantly correlated with the proportion of arthropod biomass (as arithmetic mean of branch clip and Malaise trap biomass proportions), and the 95% confidence interval of the slope of this relationship (0.81–1.10) included 1.0, the value for exact habitat matching (Fig. 2).

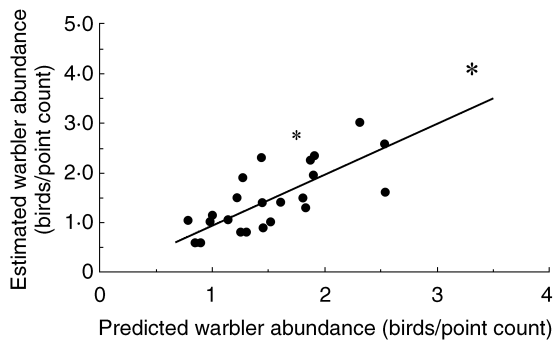
#### TEST OF PREDICTION 2

A localized insect eruption occurred between 7 and 22 February, 1996 at the Luana Point thorn scrub site (site R). Both branch-clip and Malaise trap arthropod biomass increased from sampling before (6–7 February) to after (22–23 February) the eruption, with branch clips showing a more than five-fold increase between the sampling dates ( $t = 3.65$ , 30 d.f.,  $P < 0.01$ , Fig. 3). The increase in arthropod biomass was primarily due to a sharp rise in the biomass of leaf hoppers (Homoptera: Cicadellidae), which are better sampled by branch clips than by Malaise traps. The biomass of Homoptera





**Fig. 3.** Arthropod biomass from (a) branch clips and (b) Malaise traps at the Luana Point West (site R) thorn scrub site before (6–7 February) and after (22–23 February) a natural insect eruption (mean  $\pm$  1 SE). Sample sizes were 16 branch clips and three Malaise traps per sampling date.



**Fig. 4.** Estimated and predicted warbler abundance based on measures of arthropod biomass among 24 sites across Jamaica (see Table 1 for site descriptions, Table 4 for regression statistics). The small and large asterisks represents data from the Luana Point (West) thorn scrub site before and after a natural insect eruption, respectively (see Fig. 3). The estimated abundance of warblers after the eruption fell within the 95% prediction interval (shown as bar) of the regression generated from pre-eruption data.

increased from 38.3% of the total branch clip biomass before the eruption to 74.5% afterwards.

Using post-eruption branch clip and Malaise trap biomass values in the regression equation generated in Prediction 1 (from Table 4), warbler abundance was predicted to be  $3.39 \pm 1.17$  warblers/point count after the eruption. The estimated abundance of warblers for the second sampling period, 4.10 warblers/point count, was within this prediction interval (Fig. 4). Thus, the prediction that migrant abundance responds as expected to a natural perturbation of food (Prediction 2) was also supported.

#### TEST OF PREDICTION 3

Due to the loss of individuals (emigration and/or mortality) and the arrival of new birds, the number of redstarts detected on our study sites changed between most winter periods (Table 7). In general, colour-ringed redstarts tended to disappear from sites more between the early and middle winter periods than between middle and late winter. For purposes of this study, we

were interested in how the fluctuations in arthropod biomass affected the total density and persistence of redstarts in a variety of sites; differences in patterns of persistence between ages, sexes and habitats are detailed elsewhere (Johnson 1999).

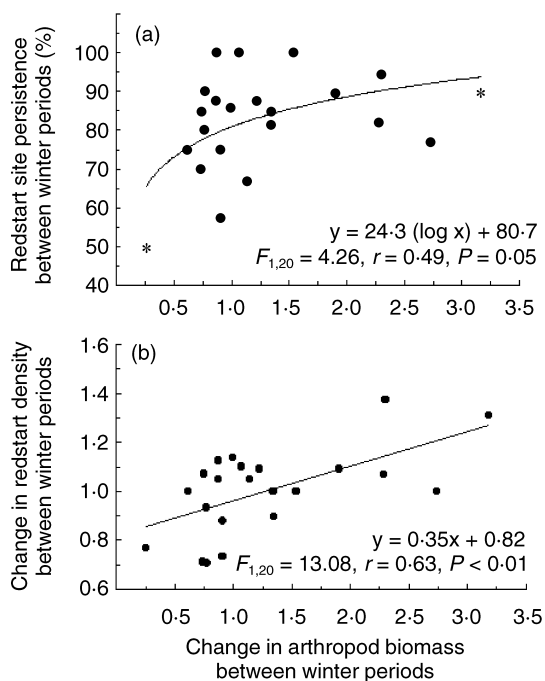
The site persistence of colour-ringed redstarts (percentage of birds remaining on a plot between winter periods) was correlated with concurrent log changes in arthropod biomass between visits (Fig. 5A). When arthropod biomass decreased between visits, redstarts tended to disappear from sites, but when food increased, redstarts tended to remain on sites, providing some support for the prediction that overwinter changes in migrant abundance correspond with concurrent changes in food availability (Prediction 3). However, the strength of this relationship was dependent on two influential sites (asterisks, Fig. 5A). The greatest decrease in arthropod biomass recorded in the study (a four-fold reduction) occurred on one of the dry limestone sites (site H) between the early and middle winter periods in 1995–96, when redstart persistence was also very low (50%). Coffee sites showed consistent large increases in insect abundance (mainly Homoptera: Psyllidae) between the middle and late winter periods, especially on *Inga vera* leaves (Johnson 2000b). The greatest of these blooms was a more than three-fold increase (site Q 1997), and occurred when redstart persistence on that site was high (90.5%). Both of these points had high statistical leverage (0.26 and 0.23, respectively), and when these points were removed from the analysis, the relationship between persistence and arthropod biomass lost statistical significance ( $F_{1,18} = 0.55$ ,  $P = 0.47$ ,  $r = 0.17$ ). Thus, the persistence of colour-ringed redstarts was most affected by large changes in arthropod biomass, but was less responsive to smaller food fluctuations.

Changes in the density of all mapped redstarts on sites between visits were correlated with concurrent changes in arthropod biomass (Fig. 5B). Like the relationship between redstart persistence and food, the relationship between redstart density and food also contained two influential points, the two largest Psyllid blooms in coffee sites (sites Q and Y 1997) had high

**Table 7.** Numbers of American redstarts, both ringed and unmarked, during each of three winter periods (early, middle, and late winter) on seven study sites in Jamaica during the 1995–96 and 1996–97 winters. See Table 1 for brief description of sites. Persistence of colour-ringed redstarts (percentage remaining on a given site between consecutive winter periods) is shown between winter period rows (percentages of numbers provided do not always yield integers because persistence was calculated from ringed birds only). Sites T and X were studied only in the 1996–97 winter, site G was studied only in the 1995–96 winter

		Study sites and habitat type						
		Dry limestone forest		Citrus orchard		Shade coffee plantation		
Winter period	Year	H (4.0 ha)*	K (6.0 ha)	B & C (8.25 ha)	T (7.0 ha)	Q (5.25 ha)	G (5.25 ha)	X (5.0 ha)
Early	1995	13	15	21		22	14	
Early mid		(50.0)	(57.1)	(66.7)		(89.5)	(84.6)	
Middle	1996	10	11	21		24	15	
Mid-late		(100.0)	(87.5)	(87.5)		(94.1)	(81.8)	
Late	1996	11	12	22		33	16	
Early	1996	8	15	31	18	33		17
Early mid		(100.0)	(80.0)	(70.0)	(81.3)	(75.0)		(76.9)
Middle	1997	8	14	27	19	27		17
Mid-late		(100.0)	(75.0)	(85.7)	(84.6)	(90.5)		(86.0)
Late	1997	9	14	25	17	38		15

\*This site was expanded from 3.0 to 4.0 ha in early winter 1996.



**Fig. 5.** Relationship of American redstart (a) persistence and (b) change in density to concurrent change in arthropod biomass in a total of 11 study sites over two winters. Changes were calculated as the factor by which values changed between consecutive winter periods (early, middle and late winter; approximately 6-week intervals). Change in arthropod biomass was log transformed to linearize (a) for regression analysis. Asterisks in (a) indicate points of high statistical leverage that resulted in a change in significance upon removal from the analysis.

statistical leverage. However, these points had relatively small residuals (and, hence, low Cook's distances). Therefore, when these high leverage points were removed from the analysis, the relationship between change in redstart density and arthropod biomass remained significant ( $F_{1,18} = 11.80$ ,  $P < 0.01$ ,  $r = 0.61$ ).

This result indicates that redstart density, unlike redstart persistence, responded similarly to both small and large changes in arthropod biomass, and provides additional support for Prediction 3.

## Discussion

### INFLUENCE OF FOOD ON WARBLER DISTRIBUTION

This study supports the hypothesis that food availability influences the distribution of migratory birds in winter by documenting associations between warbler abundance and food availability at three scales. First, over a wide spatial scale, warbler abundance varied significantly among sites and habitats (Fig. 1), and approximately half of this variation ( $r^2 = 0.52$ ) was accounted for by arthropod biomass (Table 4). Alternative factors (vegetation characteristics, resident bird competitor abundance and predator abundance) were not correlated with warbler abundance. Secondly, over a short temporal scale (about 2 weeks), warbler abundance responded to a natural increase in arthropod biomass as predicted in both direction and magnitude (Fig. 4). Thirdly, over a longer time scale (the duration of a winter), changes in the density and site persistence of American redstarts corresponded with fluctuations in arthropod biomass (Fig. 5), although persistence was responsive only to large changes in arthropod biomass. Taken together, these results suggest that the distribution of wintering warblers is influenced by food availability, resulting in a 'match' between the abundances of birds and their critical resources across habitats (Fig. 2; MacArthur & Levins 1964; MacArthur & Pianka 1966; Hutto 1985b).

Such 'habitat matching' could imply that wintering warblers track food and approximate an ideal free

distribution (Fretwell 1972; Fagen 1987), yet recent studies have documented the existence of behavioural sexual segregation (Ornat & Greenberg 1990; Wunderle 1995; Marra 2000), site tenacity (territoriality, Marra *et al.* 1993), and habitat differences in physiological condition (Marra & Holberton 1998) in wintering warblers, which could suggest a despotic distribution. Animal distributions may show features of both ideal free and despotic models (Parker & Sutherland 1986; Bernstein *et al.* 1991; Milinski & Parker 1991), and we do not view these extremes as mutually exclusive influences on warbler distributions in winter. Instead, as we detail below, we hypothesize that warblers respond to food resources and dominance hierarchies at different scales, and together these factors contribute to their overall distribution in winter (Morris 1987; Wiens 1989). In addition, we suggest that the match between distributions of warblers and their food in winter is enhanced by variation in movement strategies among individuals within species.

We hypothesize that wintering warblers concentrate initially in broad areas supporting abundant food resources, then, as behavioural hierarchies are established, they segregate such that dominant individuals concentrate into high quality sites at smaller spatial scales (*sensu* Whitham 1980). Two *post hoc* observations lend support for this hypothesis. First, covering approximately 24 ha, we found high abundances of warblers (including redstarts) and high arthropod biomass in both scrub forest and mangrove habitat at Luana Point in Jamaica (sites F, R, S). Working on 5-ha plots in the same area, Marra (2000) documented that behaviourally subordinate redstarts arriving in the autumn were gradually displaced from mangrove to scrub forest by dominant birds (mainly adult males) that concentrated into mangrove habitat, where a few insect types may be more abundant in late winter (Parrish & Sherry 1994). These findings suggest redstarts initially occupy Luana Point in response to high overall arthropod biomass and then behaviourally segregate between local sites based on more subtle seasonal changes in food availability. Secondly, we found that warblers similarly settled into food-rich shade coffee habitats at high abundance (see Fig. 1), where they may segregate between distinct canopy (shade tree) and understorey (coffee tree) layers. Although we have not quantified behavioural interactions between ages or sexes, adult male redstarts fed significantly higher than did females in Jamaican coffee plantations (M.D. Johnson unpublished data), and arthropods are five to seven times more abundant in the canopy than the understorey of shade coffee farms (Greenberg *et al.* 1997a; Johnson 2000b). An *a priori* prediction of our hypothesis, one that remains to be tested, is that birds occurring at low abundance in food-poor areas (such as in dry limestone forests) should similarly segregate among local sites differing in arthropod biomass.

Our observed match between the abundance of a guild of warblers and their food resources may have

been enhanced by variation in movement patterns among individuals within species. Multiple authors have suggested that movement patterns for migrants in winter lie along a continuum, the endpoints of which are characterized by birds belonging to two categories: those that hold persistent territories, and those that wander or 'float' over wider spatial scales (Rappole *et al.* 1989; Wunderle 1995; Johnson 1999). Cost-benefit analyses suggests that territoriality is most advantageous for the defence of predictable and moderately abundant resources (Brown 1969). Accordingly, strictly territorial warblers should not be responsive to small fluctuations in food; they should abandon a site only if conditions become very poor. Conversely, wandering warblers, by sampling many habitat patches, not only have less 'invested' in any one particular site than territorial individuals, but they could also be more aware of local changes in resource levels and thereby more responsive to small changes in food availability. With our capture methods, territorial redstarts were probably more likely to be colour-ringed than were wanderers (Conway, Powell & Nichols 1995). Therefore, the observation that the persistence of redstarts (which was calculated from ringed redstarts only) was less responsive to small changes in food than was the change in density (including both ringed and newly-arriving unmarked birds; compare Fig. 5a,b) is consistent with the hypothesis that wanderers are more capable of tracking small changes in food availability than are territorial individuals.

We collected no data on variation in site tenacity among individuals within species other than redstarts, but previous studies have found other migrant species to be flexible in their winter movement patterns (Lack 1986). Individual northern parulas have ranged from strictly territorial to wandering to occasionally participating in mixed flocks (Eaton 1953; Post 1978; Ewert & Askins 1991; Staicer 1992). Prairie warblers have also been variously described as wandering widely (Staicer 1992) to occasionally territorial (Steve Latta, personal communication). Although not canopy foragers, wood thrushes (*Hylocichla mustelina*, Gmelin), black-throated blue warblers (*Dendroica caerulescens*, Gmelin) and ovenbirds (*Seiurus aurocapillus*, L.) have also varied from being territorial to wandering on their wintering grounds (Rappole *et al.* 1989; Wunderle 1995; Strong 1999). Indeed, most studies capable of detecting intra-specific variation in movement strategies in wintering migrant songbirds have found them, and we suspect that species less well-studied exhibit similar variation. By locating and exploiting local abundances of food, wandering warblers could exploit ephemeral or unpredictable resources under-used by territorial birds, and their presence within populations could contribute to an overall match between the distributions of wintering warblers and their arthropod prey.

Variation in habitat use and movement patterns within species could facilitate a match between resource availability and warbler distribution as we have described,

but our results could have arisen by an alternative pathway. If we assume that food availability affects the quality of a habitat (i.e. warbler survival), then by distributing themselves randomly, but remaining faithful between winters to areas where they were successful (i.e. those with abundant resources), birds would, over time, become concentrated in areas with abundant food. This alternative is unlikely to be solely responsible for our results, however, because warbler density both decreased and increased in our sites as arthropod biomass changed (Fig. 5b), even over a period of only 2 weeks (Fig. 4). This finding suggests that birds both emigrated from and immigrated into sites in response to changing food availability. If warbler distributions matched food resources only by an indirect pathway, such responses would not be expected.

#### HABITAT SELECTION IMPLICATIONS

Although this study suggests that food availability influences the distribution of wintering warblers, it does not indicate that warblers select among available habitats based on the availability of food. Habitat selection differs from habitat distribution in two ways. First, the distribution of birds among habitats (also called habitat use) must be evaluated within the context of habitat availability to examine selection (Manly, McDonald & Thomas 1993). Secondly, habitat selection refers to the decision-making processes (behavioural and evolutionary) by which organisms come to occupy some habitats and not others (Cody 1985). We know of no study, including this one, that has rigorously quantified the use and availability of habitats for wintering migrants, thus, migrant winter habitat selection remains unresolved.

However, numerous studies, including this one, have quantified various habitat characteristics that could serve as proximate or ultimate factors of a habitat's quality and be employed by migrants as cues in selecting among habitats (Hildén 1965). Various authors have found high migrant abundance to be positively associated with annual rainfall (or habitat moisture), foliage heights and/or canopy cover (Askins, Ewert & Norton 1992; Baillie & Peach 1992; Wunderle & Waide 1993; Jones *et al.* 1996; Marra & Holberton 1998; Sillett, Holmes & Sherry 2000). Conversely, other workers have found migrant abundances to be high in dry and/or disturbed habitats characterized by low canopy covers and heights (Lack 1986; Blake & Loiselle 1992; Hutto 1992; Wallace *et al.* 1996; Greenberg, Bichier & Sterling 1997b). Despite such differences, most authors have suggested that food resources influence migrant distributions, arguing either that insects and fruit are more abundant in second growth than in mature tropical forests (Janzen 1973; Levey 1988; Loiselle & Blake 1991) or that insects remain most plentiful throughout the winter in sheltered, mesic, mature habitats (Parrish & Sherry 1994; Marra *et al.* 1998). Clearly, 'direct sampling of insect populations [is] necessary to determine

some of the causes for habitat differences in wintering migrant abundance' (Wunderle & Waide 1993).

This study is one of the first to sample arthropods in relation to wintering migrants on a large scale (see also Strong & Sherry 2000), and it provides some of the first quantitative comparisons of the effects of food availability vs. non-food factors on migrant distributions. Here, we found that warbler abundance was significantly more dependent on arthropod biomass than on non-food factors (Table 4). This suggests that wintering warblers select habitats by assessing food availability directly, in which case previously described associations of warblers with particular habitat characteristics may have arisen because those characteristics were themselves correlated with food availability, as some authors have suspected (Lack 1986; Wunderle & Waide 1993; Jones *et al.* 1996). However, Folse (1982) documented clear bird-vegetation associations in the Serengeti plains and did not detect significant relationships with arthropod biomass, although his arthropod sampling may have been inadequate to quantify food availability meaningfully, and he did not distinguish migrants from residents in his analyses. Results confirming or refuting food as the ultimate factor influencing habitat selection in wintering migrants await controlled experimentation.

#### CONSERVATION IMPLICATIONS

Our findings have three conservation implications. First, understanding that food influences winter distributions of warblers is important because it indicates that migrants can be indirectly affected by habitat disturbance through the alteration of food resources. With this knowledge, examination of avian foraging behaviour and patterns of food availability can help elucidate why some species are more vulnerable to certain types of habitat disturbance than others. For example, the fragmentation of moist forests can lead to drying and decreased leaf litter- and foliage-arthropod abundance (Strickland 1947; Janzen & Schoener 1968), but to increased abundance of small fruits (Blake & Hoppes 1986; Levey 1988; Petit *et al.* 1995). Consequently, alteration of tropical forested landscapes through logging may be especially harmful to forest insectivore populations (Thiollay 1992), while densities of frugivores may increase in response to higher food availability (Johns 1989; Petit *et al.* 1995).

Secondly, understanding mechanistic pathways provides insight into the ecology of overwintering migrants that could permit the extension of conservation efforts beyond simple habitat-based plans to pro-active management techniques (Petit *et al.* 1995). In agricultural habitats for example, the adoption of farm management practices that enhance populations of economically benign insects can lead to higher bird abundances (Greenberg *et al.* 1997a; Johnson 2000b). Similarly, the success of tropical reserves intended to protect habitat for migrants will depend on their ability to support abundant food resources, especially in late-winter.

Lastly, the spatial distribution of preserved areas will likely affect their capacity to support viable wintering migrant populations. Our results suggest that at least some individuals of even 'territorial' insectivorous species track food resources in space, and numerous studies suggest the same for frugivores (Leck 1972; Lack 1986; Martin & Karr 1986; Rappole *et al.* 1989; Loiselle & Blake 1991). Therefore, successful landscape-level conservation efforts must consider all sites that may be used at various periods of the winter, as well as their proximity to one another (Bernstein *et al.* 1991). For example, access to habitats that provide abundant food late in the dry season, such as mangroves (Parrish & Sherry 1994; Marra & Holberton 1998), mesic forests (Wunderle & Waide 1993), and coffee plantations shaded by *Inga* sp. (Johnson 2000b) may be necessary for migrants to prepare for a timely spring migration back to their breeding grounds (Marra & Holberton 1998), which in turn may influence breeding productivity (Marra *et al.* 1998). Thus, the proximity of these food-rich areas to less optimal habitats that support high densities of migrants earlier in the winter (such as drier disturbed sites) may determine the capacity of the latter to support viable wintering migrant populations.

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