

# Migrants in Neotropical bird communities: an assessment of the breeding currency hypothesis

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## Summary

1. Explanations for the integration of migratory and non-migratory (resident) birds in the Neotropics have been complicated by the paradox that arthropod abundances are low when bird abundances reach their annual peak. The breeding currency hypothesis offers an explanation for this paradox by postulating that resident birds are limited in the breeding season by the availability of large arthropods suitable for reproduction, whereas the carrying capacity of all birds in the non-breeding season is limited by the availability of arthropods suitable for self-maintenance of adults.
2. Field data from Jamaica supported this hypothesis. Among 19 sites, the ratio of migrant to resident bird abundance was correlated negatively with the ratio of large arthropod biomass in the breeding season to total arthropod biomass in the non-breeding season.
3. However, after controlling for effects of arthropod seasonality, migrant to resident bird abundance ratios were higher in human-disturbed than undisturbed sites.
4. Other factors may interact with the availability of food for nestlings to limit the populations of resident birds below carrying capacities set by non-breeding season arthropod abundance, thereby creating a set of resources available to non-breeding migrants.

*Key-words:* competition, consumer-resource model, food, insectivore, migration, seasonality.

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## Introduction

Neotropical–Nearctic migratory birds breed during the late spring and summer throughout much of North America, then migrate to Caribbean Islands, Central America, and South America during the autumn, where they spend up to 7 months before returning to the breeding grounds. The autumn arrival of migrants, many of which are insectivorous, dramatically increases the number of birds in tropical habitats (Keast & Morton 1980). A classic ecological question concerning the Neotropical–Nearctic migratory system has been: how do tropical communities support such an influx of consumers (Willis 1966; Ricklefs 1992; Greenberg

1995)? Searches for an answer to this question revealed a paradox: arthropod abundance often reaches its nadir during the winter dry season of the northern Neotropics, when migrants are found in high abundance (Janzen & Schoener 1968; Janzen 1973; Buskirk & Buskirk 1976; Emlen 1980; Hespeneheide 1980; Young 1994; Greenberg 1995). This resource paradox has led to a search for what limits bird abundances at various times of year in tropical ecosystems (Ricklefs 1992; Greenberg 1995; Martin 1996).

In this study, we first review briefly the breeding currency hypothesis proposed by Greenberg (1995) to explain the integration of migrants into tropical bird communities. Secondly, we assess two of its predictions using field data from Jamaica, West Indies. Thirdly, we discuss the potential for other factors to operate in concert with the breeding currency hypothesis to explain the integration of migrants into tropical bird communities.

As a potential explanation for the coexistence of migratory and non-migratory (hereafter, ‘resident’) birds in the Neotropics in the face of apparent resource shortages, Greenberg (1995) hypothesized that the productivity of breeding resident birds is a function of the

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abundance of large soft-bodied arthropods (i.e. 'breeding currency'), which are needed as food for growing nestlings (Greenberg 1981; Thiollay 1988). The carrying capacity of adult insectivorous birds, in contrast, may be a function of the total year-long biomass of all arthropods, many of which are too small to be used efficiently as breeding currency. The result, according to Greenberg's hypothesis, is that there are two carrying capacities for birds in the tropics: the first is lower and is set by the maximum availability of breeding currency; the second is higher and set by the minimum biomass of arthropods available to sustain adult birds. The difference between the two represents resources that resident birds cannot exploit and are therefore available to migratory winter visitors. Thus, by invoking the importance of quantitative as well as qualitative changes in food resources, the breeding currency hypothesis allows for higher carrying capacities of adult birds during periods of lower total arthropod abundance, thereby offering an explanation for the resource paradox.

The breeding currency hypothesis makes two important assumptions concerning the arthropod community in tropical ecosystems. First, large and small arthropods must be taxonomically distinct (Greenberg 1995), for if they were not, birds harvesting small arthropods in winter could suppress the future growth of larger prey, i.e. breeding currency. Gradwohl & Greenberg (1982) found that most large insects were orthopterans and lepidopterans, while small arthropods were comprised largely of hard-bodied groups such as Formicidae, Coleoptera, etc. In turn, Poulin & Lefebvre (1996) found that these small hard-bodied taxa dominated the diets of migrant birds wintering in Panama, while residents ingested proportionally more large insects, especially orthopterans. The second assumption is that for unexploited resources to accumulate in the winter, the biomass of large arthropods must be more seasonal than that of small arthropods. It is not necessary that residents feed only on large prey all year, only that they rely on seasonal, large arthropods for breeding. Few data are available to examine this assumption, although the pattern has been observed in Panama (Smyth 1982). Additional data from more tropical locations are needed to fully assess the validity of these assumptions.

Other hypotheses exist for the integration of migrant and resident birds in the tropics (see Greenberg 1995 for review), some of which probably operate for particular migrant species. For example, hypotheses suggesting that migrants track irregular/ephemeral foods or habitats are probably appropriate for wandering frugivores (Willis 1966; Karr 1976; Alerstam & Enckell 1979; Leck 1987; Johnson & Sherry 2001). However, many wintering migrants remain locally resident, often territorial, and forage for small arthropods (Rappole 1995). Greenberg's hypothesis is the only one that adequately addresses the resource paradox for territorial migrant insectivores.

The principal prediction of the breeding currency hypothesis is 'that for a given region in the tropics, the ratio of standing crop of large arthropods during the

breeding season to total biomass of arthropods during the non-breeding season should be negatively correlated with the proportion of migrants in a particular community' (Greenberg 1995: 262). Unfortunately, the methods required to test this prediction are labour-intensive and the data must be collected in both breeding and non-breeding seasons in a large number of sites. Thus, despite its appeal and testability, 'the necessary data [have been] unavailable to test the major prediction of this hypothesis' (Greenberg 1995: 262).

Although data were lacking to test this prediction directly, Greenberg cited the high proportion of migrants in disturbed, ecologically 'non-buffered' habitats (e.g. edge, canopy or secondary forests, *sensu* Chesser & Levey 1998), as consistent with his hypothesis. Vegetation in disturbed tropical habitats is often comprised disproportionately of plants that are poorly defended chemically (Coley, Bryant & Chapin 1985), which results in high proportions of sucking herbivorous insects (e.g. Homoptera; Janzen 1973) and fewer chewing insects (e.g. Lepidoptera and Orthoptera; Schowalter 1994). Because Lepidoptera and Orthoptera comprise the majority of breeding currency in the tropics and Homoptera are typically small and soft-bodied, residents may avoid disturbed habitats because they contain few resources required for breeding.

This explanation for the often-cited observation that migrant to resident abundance ratios are high in disturbed areas (see papers in Keast & Morton 1980; Hagan & Johnston 1992) contrasts with that of an alternative hypothesis for the integration of migrants and tropical residents. Hutto (1980) suggested that in human-disturbed habitat, especially agricultural plantations, populations of resident birds may be kept low by the scarcity of safe nesting sites and high rates of nest predation. Residents tend to remain faithful to breeding sites year-round to ensure their repeated use, especially when nesting sites are limited (Alerstam & Enckell 1979; Greenberg & Gradwohl 1986; Switzer 1993; but see Levey & Stiles 1992). Therefore, according to Hutto's arguments disturbed habitats may remain chronically under-used during the non-breeding season, permitting migratory birds to exploit the resulting vacancies and surplus of winter food. Thus, Hutto's 'nest predation hypothesis' provides an explanation for spatial variation in migrant to resident ratios that does not rely on spatial and temporal variation in food availability. Hence, if the breeding currency hypothesis explains variation in migrant to resident ratios but the nest predation hypothesis does not, we make a second prediction. Once between-habitat differences in large and small arthropod biomass ratios are statistically controlled, migrant to resident ratios should be no higher in disturbed than undisturbed sites.

## Materials and methods

Nineteen sites differing in rainfall, elevation and degree of human disturbance were selected from six broad

habitat types in Jamaica, West Indies: wet limestone forest, dry limestone forest, thorn scrub, mangrove forest, shade-coffee plantation and citrus orchard (Appendix S1 in Supplementary material); (see Asprey & Robbins 1953 for detailed descriptions of natural vegetation). Accessibility constraints precluded selecting sites randomly, so sites were selected to reflect the topographical and ecological diversity of Jamaica without a priori knowledge of migrant to resident ratios. The sites spanned the entire east–west axis of the island, most of the north–south axis (> 75%), ranged from 0 to 620 m in elevation, had approximate rainfall rates of < 130 to > 500 cm year<sup>-1</sup> (Lack 1976), and ranged from intact native plant communities to heavily disturbed agricultural plantations.

To quantify the relative abundances of migrant and resident birds in each study site, we surveyed bird abundance at 10–20 study points (mean 18.0) depending on patch size, each separated by at least 100 m (75 m in the densest wet limestone forest sites), and 50 m from the nearest habitat edge. All counts were conducted during the non-breeding season, January–March 1995–97. Over a period of 2–3 mornings per site, we conducted a 10-minute fixed-radius point count (Hutto, Pletschet & Hendricks 1986) at each study point, recording all birds seen or heard within a 25-m radius. All counts were conducted between 0530 and 1000 EST. Accessibility again constrained the timing of our visits, but we spread visits over sites via a rotation among habitats so that there were no significant differences in mean sampling date among habitats. There was also no significant correlation between sampling date and the ratio of migrant to resident bird abundance nor the ratio of breeding currency to total arthropod biomass (both  $r < 0.17$ ), the principal variables for assessing the breeding currency hypothesis (details on these variables below). Therefore, we attributed differences in bird and arthropod ratios among the sites and habitats to ecological variation and not to sampling date.

Sliwa & Sherry (1992) demonstrated that the detectability of vocally inconspicuous species, such as wintering migrants, is increased by the use of broadcast vocalizations during point counts. Although using playbacks of all relevant species is impossible within a reasonable point count duration, multiple species are attracted to migrant songs and chip-notes (Sliwa & Sherry 1992). Therefore, we played the songs and chips of three of the most common migrants in Jamaica [American Redstart, Northern Parula and Prairie Warbler (see Appendix S2 for scientific names of bird species used in analyses) 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, placed on the ground at each study point with the speaker facing upward. We quantified the relative abundance of migrants and residents in a site as the mean number of migrant and resident individuals detected per point count, and calculated the ratio of migrant to resident abundance for analyses. Although several of the species used in

analyses are partially frugivorous or nectarivorous (Lack 1976), evidence suggests that even these species rely on arthropods for food for nestlings (Lack 1976; Greenberg 1995). Residents that do not typically bring insects to nestlings (e.g. pigeons and hummingbirds) were excluded from the analysis. All migrants that are at least partially insectivorous in the winter were included.

The detectability of birds may at times differ among sites due to varying densities of vegetation (Hutto *et al.* 1986), but all that is necessary for our relative comparisons is that detectability of residents and migrants varies in parallel. Residents probably have higher absolute detectability than migrants (only the former sing appreciably in the tropics), and this difference could be magnified in dense habitats that visually obscure quiet migrants. However, playbacks can help equalize detectability of wintering migrants across varying densities of vegetation by drawing into view birds otherwise overlooked (Sliwa & Sherry 1992; Turcotte & Desrochers 2002). Our relatively small radius (e.g. 25 m) also helped minimize detectability differences across vegetation types (*sensu* Hutto *et al.* 1986). Thus, our point counts yielded satisfactory indices of relative migrant and resident bird abundance across sites.

The breeding currency hypothesis offers an explanation for the integration of all species of migratory and non-migratory insectivorous birds in a given tropical region. Because each bird species is characterized by unique patterns of prey selection and foraging microhabitat use, no single sampling technique could accurately measure the availability of food for all bird insectivores in all habitats (Cooper & Whitmore 1990). Therefore, we did not attempt to quantify absolute prey availability for all species. Instead, we used a general arthropod sampling technique, ‘branch clipping’ (described below), and made the assumption that calculated values were correlated with actual arthropod prey availability (*sensu* Hutto 1985).

To sample arthropods by branch clipping, we positioned a collapsible cloth bag around the end of a branch in the understorey or canopy (up to 9 m with the aid of extension poles) and quickly closed the mouth of the bag tightly around the branch with a drawstring. Then we clipped the branch free with a telescoping tree pruner, lowered the bag and visually inspected the bag and clipped branch for arthropods (Schowalter 1994; Johnson 2000; Johnson & Sherry 2001). All arthropods were categorized immediately by 1 mm size intervals and identified to order, except for Hymenoptera [separated into Formicidae or non-Formicidae (mostly parasitic wasps)]. Members of Phasmida (e.g. walkingsticks), Mantodea (e.g. mantids) and Blattaria (e.g. cockroaches) were rare and therefore combined with Orthoptera (e.g. crickets), because members of these orders tend to be large and relatively soft-bodied. Abundances per sample were converted to biomass using length–weight regressions generated from voucher specimens collected at the study sites (Johnson & Strong 2000). We obtained two branch clip

samples at each study point, one from the subcanopy (mean height 5.5 m  $\pm$  2.2 m SE) and one from the understorey (mean height 1.2 m  $\pm$  0.3 m SE). The exact positions of samples were chosen to represent where insectivorous birds typically forage (Johnson 2000; generally toward the outer edges of branches), and diverse plant species were sampled; we did not stratify the sampling by branch position. Non-breeding season samples were from 1995 to 1997 concurrent with the bird surveys; all breeding season samples were collected from the same locations (different branches) in June 1998. The breeding season for Jamaican residents varies among taxa, but peak breeding activity occurs April–June (Downer & Sutton 1990; MDJ personal observation). We chose the end of this period to emphasize the nestling stage, when breeding currency is hypothesized to be the most critical. Although the data come from various years, foliage arthropod samples from Jamaica showed little variation across years (within seasons) relative to between-season and spatial variation (Johnson & Sherry 2001).

We calculated the biomass of each sample as the total mg of arthropods per 100 g (wet mass) of clipped and inspected vegetation. Breeding currency biomass was calculated as the combined biomass of all arthropods > 5 mm in body length (excluding legs, wings and antennae), whereas total arthropod biomass (for the non-breeding season) was the sum of all trapped arthropods. Few data on prey sizes are available for wintering migrant and resident tropical birds. We chose a 5 mm cut-off based on Morton's (1980) and our (Medori and Sherry, unpublished data) findings that > 98% of all identified prey were < 5 mm in wintering warbler diet samples, and on Greenberg's (1981) observations that resident birds feed typically on prey larger than 5 mm in the breeding season. However, we emphasize that migrant birds wintering on Caribbean islands are mainly small-bodied warblers (Parulidae), which feed on especially small prey. Elsewhere in the Neotropics, where larger-billed migrants are more prevalent, a larger cut-off value may be more appropriate. We calculated the ratio of breeding currency biomass to non-breeding season total arthropod biomass, and log-transformed the ratios to normalize for analyses.

We used  $\chi^2$  analyses to examine the distribution of small ( $\leq$  5 mm) and large (> 5 mm) arthropods among various taxa, and we used an analysis of variance (ANOVA) to describe the variation in arthropod biomass among three factors: habitat (six types), season (breeding and non-breeding) and size (small and large). To test the principal prediction of the breeding currency hypothesis, we examined the correlation between the ratio of migrants to residents in the 19 sites and the ratio of breeding currency biomass to non-breeding season total arthropod biomass. The breeding currency hypothesis implies that resident birds are limited by breeding currency, so we evaluated the expectation that resident bird abundance is correlated positively with breeding currency biomass. Similarly, the hypothesis

implies that total bird abundance in the winter is limited by availability of arthropods suitable for adult bird self-maintenance, so we examined the correlation between total bird abundance and total non-breeding season arthropod biomass. To examine any differences in the use of habitats by migrants and residents after controlling for potential effects of the breeding currency hypothesis (the second prediction), we used an analysis of covariance (ANCOVA) with habitat as the grouping factor and the ratio of breeding currency to non-breeding currency arthropod biomass as the covariate. We also categorized the 19 sites as heavily human disturbed (which included all citrus, coffee and thorn scrub sites, plus site 8, the most disturbed wet limestone site; see Appendix S1) and minimally disturbed (remaining wet, dry and mangrove forest sites), and used disturbance class as the grouping factor in a second ANCOVA. For simplicity, hereafter we refer to these categories as 'disturbed' and 'undisturbed', respectively.

## Results

### ARTHROPOD DISTRIBUTION AND BIOMASS

The distribution of large (> 5 mm) and small ( $\leq$  5 mm) arthropods in branch clip samples was not uniform across all taxonomic groups ( $\chi^2 = 1516$ , d.f. = 10,  $P < 0.001$ ; Table 1). Among soft-bodied groups, 57% of all trapped orthopterans and lepidopterans (combined) were large, and together they contributed 158 of the 291 large insects trapped (54%). In contrast, in all the other soft-bodied groups combined, only 4% were large. Among hard-bodied groups, only 2% of all trapped arthropods were large, comprised mainly of Hemiptera (especially Pentatomidae and Berytidae) and Coleoptera. Large Formicidae were rare. These results are consistent with the assumption of the breeding currency hypothesis that large and small arthropods are taxonomically distinct.

The biomass of large and small arthropods showed marked variation by habitat and season (Table 2). The three-way interaction between season, habitat and size was significant, indicating that the seasonality of large and small arthropods differed from each other, and this difference varied among habitats. It is this variation in seasonality and size that Greenberg invoked as a potential explanation for variation in migrant to resident bird ratios in tropical habitats, for areas with a comparatively large breeding season increase in large arthropods should support a low migrant to resident bird abundance ratio. Overall, the biomass of large arthropods was more seasonal than that of small arthropods (season  $\times$  size,  $P < 0.001$ ), which is consistent with another assumption of the breeding currency hypothesis (see Introduction). Averaging all sites, large arthropod biomass increased 560% from the non-breeding to the breeding season, whereas small arthropod biomass increased only 10%.

**Table 1.** Percentages of small vs. large arthropods by taxonomic group trapped in 608 branch clip samples from 19 study sites in Jamaica during the avian non-breeding (January–March 1995–97) and breeding seasons (June 1998) combined. *n* = total number of arthropods in a group

	Small (≤ 5 mm)	Large (> 5 mm)	<i>n</i>
Soft-bodied groups			
Araneae	94	6	611
Orthoptera <sup>1</sup>	51	49	104
Homoptera	98	2	1085
Lepidoptera	38	62	172
Diptera	99	1	212
Hymenoptera (except Formicidae)	99	1	112
Other <sup>2</sup>	85	15	148
Orthoptera and Lepidoptera combined	43	57	276
All other soft-bodied groups combined	96	4	2168
Total (soft-bodied groups)	90	10	2444
Hard-bodied groups			
Hemiptera	91	9	172
Coleoptera	97	3	785
Formicidae	99	1	1520
Total (hard-bodied groups)	98	2	2477
Unknown			
Total arthropods captured	94	6	5034

<sup>1</sup>Includes Phasmida, Orthoptera, Mantodea, and Blattaria.

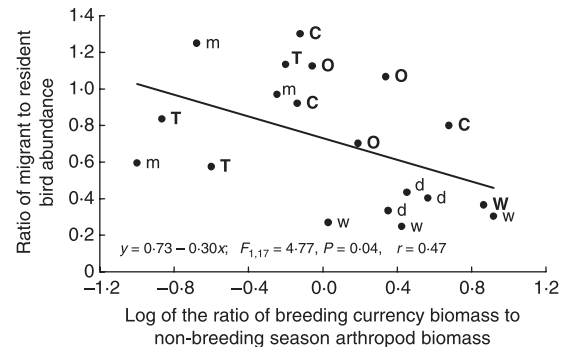
<sup>2</sup>Comprised largely (> 80%) of Psocoptera and Neuroptera.

**Table 2.** ANOVA of arthropod biomass, measured as mg of arthropods per 100 g clipped vegetation, for 19 sites in Jamaica, West Indies (data were arcsine-transformed to normalize). Habitat = wet limestone forest, dry limestone forest, thorn scrub, mangrove swamp, coffee plantation, and citrus orchard. Season = non-breeding season (January–March 1995–97) and breeding season (June 1998). Size = small arthropods (≤ 5 mm) and large arthropods (> 5 mm)

Source	d.f.	Mean squares	<i>F</i> -statistic	<i>P</i>
Habitat	5	3.06	6.13	< 0.001
Season	1	9.12	18.28	< 0.001
Size	1	0.29	0.58	0.452
Habitat × season	5	2.17	4.36	0.002
Habitat × size	5	1.24	2.48	0.044
Season × size	1	6.77	13.58	< 0.001
Habitat × season × size	5	1.49	2.98	0.019
Error	52	0.50		

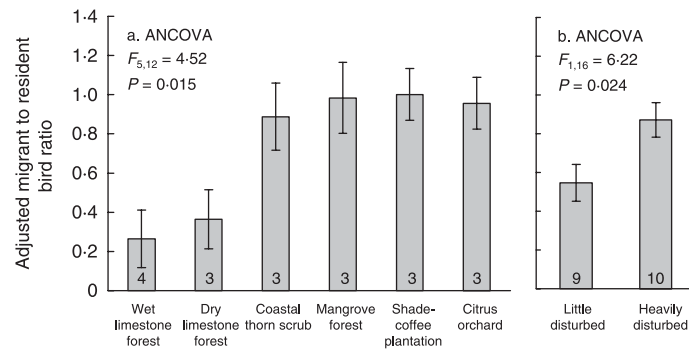
#### ASSESSMENT OF BREEDING CURRENCY HYPOTHESIS PREDICTIONS

The ratio of migrant to resident birds was significantly negatively correlated with the ratio of breeding currency to non-breeding season total arthropod biomass (Fig. 1). In other words, proportionally more wintering migrants resided in habitats with proportionally less breeding currency for resident birds, which supports the first prediction of the breeding currency hypothesis. Consistent with the implication of the hypothesis that residents are limited by arthropods suitable for reproduction, the abundance of resident birds was significantly positively correlated with breeding currency biomass

**Fig. 1.** Inverse relationship between the ratio of migrant to resident birds and the log of the ratio of large arthropod biomass in the breeding season (breeding currency) to total arthropod biomass in the non-breeding season among 19 study sites. Letters next to data points indicate habitat type: w = wet limestone forest, d = dry limestone forest, t = thorn scrub, m = mangrove, c = shade-coffee plantation, o = citrus orchard. Capital bold letters indicate sites that were heavily human disturbed.

( $y = 1.21x + 5.12$ ,  $F_{1,17} = 9.81$ ,  $P < 0.01$ ,  $r = 0.60$ ). Similarly, the total abundance of birds (migrant + resident) was correlated positively with total non-breeding season arthropod biomass ( $y = 2.47x + 9.07$ ,  $F_{1,17} = 9.81$ ,  $P < 0.05$ ,  $r = 0.57$ ).

The results of the ANCOVA failed to support the second prediction of the breeding currency hypothesis. After controlling for the effects of differences in the ratio of large to total arthropod biomass (i.e. effects of the breeding currency hypothesis), habitat types differed significantly in the proportion of migrants they supported (Fig. 2a). This analysis evaluated each habitat at a large



**Fig. 2.** Ratio of migrant to resident bird abundance ( $\pm 1$  SE) after adjusting for effects of the relationship in Fig. 1 among six habitat types (a) and between heavily disturbed vs. little disturbed sites (b). Bird ratio is evaluated at a (log) breeding currency to total arthropod biomass ratio of 0.047.

arthropod to total arthropod biomass (log) ratio of 0.047, effectively documenting patterns in the residuals of Fig. 1 for habitat groups. Migrants comprised a disproportionately high fraction of the bird community in citrus and coffee sites, whereas residents comprised a disproportionately high percentage of the birds in wet limestone forest (citrus and coffee adjusted bird ratios > wet limestone forest ratio based on Tukey's *post-hoc* comparisons;  $P < 0.05$ ). Moreover, adjusted migrant to resident ratios were significantly higher in disturbed sites than in undisturbed sites (Fig. 2b). When the agricultural citrus and coffee sites were excluded from this analysis, the proportion of migrants was no longer significantly different between disturbed and undisturbed sites ( $F_{1,10} = 0.3$ ,  $P > 0.5$ ; adjusted proportions 0.66 and 0.56, respectively).

## Discussion

Our results supported the principal prediction of the breeding currency hypothesis for the integration of migratory birds in tropical communities (Greenberg 1995; Fig. 1). Moreover, resident abundance was correlated positively with breeding currency biomass as predicted, and total bird abundance (migrant + resident) was correlated positively with total arthropod biomass in the non-breeding season. These findings are consistent with the implications of the hypothesis that resident and total bird abundances are limited by the availability of arthropods suitable for reproduction and adult bird self-maintenance, respectively. However, our data failed to support a second prediction of the hypothesis; once we controlled statistically the effects of insect seasonality, the proportion of migrants remained significantly higher in disturbed than in undisturbed sites (Fig. 2).

These findings indicate that while the breeding currency hypothesis partially explains migrant to resident ratios in tropical habitats, other factors are also operating. We suggest that processes other than the availability of large arthropods suitable for reproduction may limit the abundance of breeding residents in some areas, which could create vacancies occupied by migrants during the non-breeding season. For example, safe-nesting sites may be scarce in human disturbed habitats, particularly

in agricultural plantations. The resulting hyper-dispersion of nests and high rates of nest predation may limit resident populations to levels well below those set by the availability of breeding currency (Hutto 1980; Gibbs 1991; Telleria & Diaz 1995; but see Oniki 1979; Laurance, Garesche & Payne 1993). This reasoning provides an *ad hoc* explanation for our observation that migrant to resident ratios were similar among disturbed and undisturbed sites once we excluded agricultural sites from our analysis. However, any mechanism for low resident numbers in plantations could explain this observation. For example, structural simplicity may make nests more conspicuous, but it could also increase detectability and predation risk for adult birds (Lima & Dill 1990), reduce thermal cover (Lustick 1983) or limit exposed perch availability for sally flycatchers (Greig-Smith 1983). All these processes could conceivably affect residents more than migrant birds, because the former are generally larger and occur in the tropics during the hottest seasons. Thus, spatial variation in any ecological factor that acts in concert with food availability to limit breeding resident abundance could operate along with the availability of breeding currency to account fully for migrant to resident ratios in the tropics.

An inadequacy of both Greenberg's breeding currency hypothesis and any hypothesis invoking additional possible factors is the oversimplification of avian life histories as 'migrant and resident'. These hypotheses account poorly for the integration of intratropical migrants into northern tropical avian communities. In Jamaica, the gray kingbird (*Tyrannus dominicensis*) and the black-whiskered vireo (*Vireo altiloquus*) breed on the island in the summer months, then migrate in autumn to northern South America before returning to Jamaica in the spring (Lack 1976; Downer & Sutton 1990). Other intratropical migrant species exist, often with these two, at comparable latitudes. Hypotheses invoking breeding season limitation offer no obvious reason for these species to migrate from the northern Neotropics during the winter months. If there are more small arthropods in the winter than residents can consume (thereby supporting a winter influx of migrants from the Nearctic), why do these species leave their breeding sites and risk migration mortality? One

possible explanation is that intratropical migrants have evolved larger bills to better exploit limiting large arthropods in the breeding season at the cost of reduced foraging efficiency for small insects (*sensu* Lack 1971; Grant 1986). This may have left them poorly adapted to compete with migrants for small insects in the winter, which they avoid by migrating to lower latitudes where large fruits are relatively abundant (Lack 1976). This argument predicts that intratropical migrants are larger-billed than wintering migrants, their diets are comprised of especially large prey while breeding, and their foraging on large arthropods in the breeding season is correspondingly more efficient than for small-billed wintering migrants. Lack (1976) provides support for the predicted bill differences and diets, but foraging efficiency data are lacking. Alternatively, migrants may 'force' their way into the tropical communities in the winter, reducing the potential carrying capacities of the local residents and driving some breeders to migrate as they deplete resources. This interaction could be reduced by the residents shifting their diets and distributional ranges away from migrants (Ricklefs 1992). Note, also, that Caribbean avifaunas differ from those on the mainland (e.g. fewer resident suboscines and migrants dominated by Parulidae on the islands, for example). It is unclear at this point whether our findings will be observable in other areas of the Neotropics. Further research on migrant and resident diets and abundance ratios could help illuminate the complexities of migrant–resident competition in the tropics.

Greenberg (1995) outlined and argued validity for the assumptions of the breeding currency hypothesis, and our results confirm some of his assertions (see Results). By generalizing the hypothesis to incorporate spatial variation in numerous other factors that could limit breeding residents, an additional assumption must be noted. For a winter surplus of arthropods to develop in habitats in which residents are limited in the breeding season, resident birds must not shift significantly among habitats between seasons. Seasonal site fidelity may confer evolutionary advantages on resident birds in the tropics, particularly when nest sites are limited (Switzer 1993), and evidence suggests that habitats little-used by residents remain so year-long (Hutto 1980; Gochfield 1985). Indeed, some tropical residents defend year-long territories (Greenberg & Gradwohl 1986). However, some 'resident' species do exhibit seasonal habitat shifts, including several in Jamaica (Lack & Lack 1972; M.D.J. & A.M.S., unpublished data; L. Douglas, personal communication). These species tend to be nectarivorous or frugivorous in the non-breeding season (Levey & Stiles 1992). Therefore, as with the intratropical migrants, these vagile species may switch from relying on large arthropods for breeding to frugivory during the non-breeding season. Unlike the intratropical migrants, however, these species have only moderate-sized bills (Lack 1976). Thus, they may have adopted a less extreme strategy than the intratropical migrants, compromising breeding currency foraging

efficiency (and hence productivity) for the survival advantages of avoiding migration. Indeed, seasonal dietary and habitat shifts may be intermediate points along a continuum of movement patterns from resident to migrant (Levey & Stiles 1992).

Our explanations for intratropical migrants and habitat-shifters draw from an inverse relationship between fecundity and survival (Lindon & Møller 1989; Martin 1995, 1996), and a demographic prediction is that intratropical migrants should have higher fecundity but lower survival rates than year-round tropical residents. Parallel predictions for temperate residents vs. Neotropical–Nearctic migrants have received some support (Greenberg 1980; Ricklefs 1992; Johnston *et al.* 1997; but see Karr *et al.* 1990). This implies that there exists a gradient of demographic parameters, from temperate residents to Neotropical–Nearctic and tropical breeding migrants to tropical residents. Elevational migrants and species that shift habitats and diets seasonally without migrating lie in intermediate zones of this gradient and illustrate what may have once been early evolutionary stages of both the Neotropical–Nearctic and intratropical migration systems (Levey & Stiles 1992). By suggesting that small-scale intratropical movements of partially frugivorous species can give rise to migrations both to and from Jamaica to breed, our arguments are consistent with theories for the origin of avian new world migration (Cox 1985; Levey & Stiles 1992; Rappole 1995). The assertion that various bird movement strategies manifest in different diets highlights that the breeding currency hypothesis is a special case of a more general theory of resource partitioning (Schoener 1974).

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### Supplementary material

The following material is available from <http://www.blackwellpublishing.com/products/journals/suppmat/JAE/JAE928/JAE928sm.htm>

**Appendix S1.** List and attributes of study sites used in analyses.

**Appendix S2.** List of migratory and non-migratory birds detected and used in analyses.

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