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Population Limitation in Neotropical Migratory Birds: Comments on Rappole and McDonald (1994)

STEVEN C. LATTA¹ AND MICHAEL E. BALTZ

Division of Biological Sciences, University of Missouri, 110 Tucker Hall, Columbia, Missouri 65211, USA

The importance of breeding- and wintering-ground phenomena in population declines of Neotropical migratory birds is the topic of much debate and discussion (see Martin and Finch 1995, Sherry and Holmes 1995). Recently, Rappole and McDonald (1994) provided and evaluated 14 predictions that they argued should be supported if population declines in migrants are due to changes in North American breeding habitats. They concluded that general declines in Neotropical migrants have resulted from habitat alterations on the wintering grounds. Rappole and McDonald's conclusion is weakened, however, because they did not consider many relevant studies that contradict several of their predictions. In addition, they relied heavily on data from a few relatively unique, migratory species that are specialists on forest-interior habitats during the winter. In this commentary, we present alternative analyses that call into question the validity of some of Rappole and McDonald's (1994) predictions and their conclusion of population limitation on the wintering grounds. Our analyses often provide evidence in support of breeding-season limitation. Our intention is to emphasize the potential influence of events throughout the annual cycle on population trends (Morse 1980, Cox 1985, Sherry and Holmes 1995) and to point out the abundance of literature that supports the hypothesis that events on the breeding grounds are likely to influence population trends of Neotropical migrants. We also identify the need for additional data from wintering populations of many Neotropical migrants.

Optimal winter habitat.—Several of the predictions of Rappole and McDonald (i.e. nos. 1, 5, 6, and 10) are based on the assumption that we know which wintering habitats are optimal for a given species and that we can rank other habitat types in terms of optimality. Optimal breeding habitat has been identified for some species based on long-term studies and rates of survival and reproduction, but very little is known about habitat use and survival rates of birds on their wintering grounds (but see Conway et al. 1995, Sherry and Holmes 1996). Studies of win-

tering migrants generally have reported species distributions and estimated habitat suitability based on point counts, density, and other abundance indices (Hutto 1980, 1992; Waide et al. 1980; Wunderle and Waide 1993). But density and presence-absence data are not necessarily good indicators of habitat suitability or quality (Van Horne 1983). On North American breeding grounds, for example, sink populations can have equal or even greater densities than source populations (Donovan et al. 1995b). Thus, describing habitat quality based on density can be severely misleading (Donovan et al. 1995b, Brawn and Robinson 1996).

Direct measures of fitness components are needed to evaluate habitat quality. Fitness is expected to decline from optimal to suboptimal habitats (Fretwell 1972). Consequently, we believe that relative fitness indices of individuals associated with each habitat type need to be measured and compared before the quality of winter habitat can be assessed (see Martin 1992). Specific fitness indices such as home range or territory size (because fitness may vary with density of birds), site fidelity, overwinter turnover, overwinter survival probability, and annual return rates need to be compared within species across an array of habitats. Few demographic data of this sort have been available from wintering sites to assess habitat quality or factors affecting overwinter survival. Notable exceptions include studies by Martin and Karr (1986), Holmes et al. (1989), Lefebvre et al. (1992), Wunderle and Latta (1994), Conway et al. (1995), Wunderle (1995), and Sherry and Holmes (1996).

One result of using abundance indices to assess habitat quality is that many species appear to be widely dispersed in a variety of habitats on the wintering grounds, suggesting that they are generalists (Prediction no. 1). Although many migrant species use early successional or disturbed habitats disproportionately on their wintering grounds (Keast and Morton 1980, Terborgh 1989, Petit et al. 1995), numerous other species have been suggested to be habitat specialists in winter (Terborgh 1989, Hutto 1992, Sherry and Holmes 1995). Rappole and Morton (1985) and Rappole and McDonald (1994) suggested that the predominance of generalist species results

¹ E-mail: c675819@showme.missouri.edu

from winter habitat loss having forced migrants into a variety of suboptimal habitats. However, this turnover also may be strongly influenced by food abundance (Martin and Karr 1986; Loiselle and Blake 1991, 1992). Studies that compare species-specific fitness indices among habitats should clarify whether species are true generalists or have been forced into suboptimal habitats. Overwinter and annual turnover rates should be similar among habitats for habitat generalists, whereas marked differences would be expected in turnover rates among habitats for habitat specialists. However, in one study where these comparisons have been made (Conway et al. 1995), large differences in overwinter survival in mature and early-successional forest did not exist for three species considered to be habitat specialists: Wood Thrush (*Hylocichla mustelina*), Kentucky Warbler (*Oporornis formosus*), and Hooded Warbler (*Wilsonia citrina*).

Habitat preferences and optimality also may be confounded by sex- and age-class segregation on the wintering grounds. Sex and age classes differ in their use of habitat types in many species, including Black-throated Blue Warbler (*Dendroica caerulescens*; Wunderle 1992), American Redstart (*Setophaga ruticilla*; Sherry and Holmes 1989, 1996; Parrish and Sherry 1994), Hooded Warbler (Lynch et al. 1985), and several other species (Lopez and Greenberg 1990). As a result, surveys of avian abundance may indicate a species occurs in a variety of habitats, suggesting it is a habitat generalist, when in fact different sex and age classes are occupying (and perhaps specializing in) unique habitat types.

Finally, optimal habitats often are assumed to be undisturbed or unaltered. However, disturbed winter habitats are suitable for use by some habitat specialists (Petit et al. 1995). Although habitat generalists may be expected to use such sites (Rappole and McDonald 1994), forest-dwelling migrants also use them. For example, forest-dwelling migrants have high annual return rates and overwinter survival in shade-coffee plantations in Hispaniola, the Caribbean, and Mexico (Wunderle and Waide 1993, Wunderle and Latta 1996, Greenberg et al. 1997).

Optimal breeding habitat.—Several of Rappole and McDonald's (1994) predictions (i.e. nos. 2, 3, 4, 9) assume that the suitability of breeding habitat for a given species is known. However, Martin (1992) has shown that in many cases the biologically significant variables that relate breeding habitat to reproductive success of migrants are not known or measured. As a result, statements about actual habitat suitability should be made with caution. In addition, Rappole and McDonald fail to consider relevant data that demonstrate that avian reproductive success can be significantly affected by many types of changes in habitat quality. For example, fragmentation of breeding habitat can have profound effects on reproductive success. Fragmentation can cause insularization

effects (Whitcomb et al. 1981, Lynch and Whigham 1984, Askins and Sugeno 1987, Blake and Karr 1987, Robbins et al. 1989), increased nest predation (Wilcove 1985, Yahner and Scott 1988, Paton 1994, Donovan et al. 1995b, Robinson et al. 1995b), increased nest parasitism by Brown-headed Cowbirds (*Molothrus ater*; Donovan et al. 1995b; Robinson et al. 1995a,b), and decreased pairing success (Gibbs and Faaborg 1990, Villard et al. 1993, Van Horn et al. 1995). In many cases, these effects may be sufficient to cause local declines in bird populations without invoking loss of habitat on the wintering grounds as a causal factor (e.g. Donovan et al. 1995a).

Several studies have revealed relationships between fragmentation effects on the breeding grounds and long-term population trends of birds. Bohning-Gaese et al. (1993) found that indices of predation susceptibility (which increases with fragmentation) were more strongly correlated with population trends detected by the North American Breeding Bird Survey than was migratory status (but see Sauer et al. 1996). Askins and Philbrick (1987) monitored bird populations on a forest plot for 32 years and found that changes in the abundance of long-distance migrants were positively related to the amount of forest within 2 km of their study site (i.e. insularization effect). Wilcove (1988) censused breeding birds in the Great Smoky Mountains National Park on plots that had been censused more than 35 years earlier. He found no significant declines in populations of Neotropical migrants and concluded that populations have remained stable in the absence of fragmentation in the park regardless of the species' winter habitat preferences. Studies documenting local and regional differences in population trends of migrants on the breeding grounds also suggest that land-use patterns on the breeding grounds are responsible for observed population trends (Holmes and Sherry 1988, Sauer and Droege 1992, James et al. 1992).

Rappole and McDonald (1994) emphasize that reproductive success is influenced by the absolute amount of available breeding habitat (Prediction no. 4). They conclude that migrants are unlikely to be limited by availability of breeding habitat because the absolute amount of forest habitat in the eastern United States is increasing. However, the amount of available breeding habitat is not necessarily an accurate predictor of reproductive success. Rather, reproductive success of forest-nesting birds is affected by the degree of habitat fragmentation and the shape and amount of core habitat remaining (Donovan et al. 1995b, Robinson et al. 1995b). Indeed, depending on fragment shape, many relatively large forested areas may offer little or no core area for nesting (Temple 1986, Faaborg et al. 1995). Attempts to quantify these variables (e.g. Robinson et al. 1995b) versus the absolute amount of breeding habitat are likely to be

more effective in explaining population trends of migrants.

Rappole and McDonald (1994) point to declines of migrants in "undisturbed" breeding habitats as evidence that migrants are limited by changes on the wintering grounds (Prediction no. 3). However, studies cited in support of this conclusion (e.g. Hall 1984, Holmes and Sherry 1988, and unpublished data from a long-term study of Kentucky Warblers) are open to alternative interpretations. For example, McShea et al. (1995) attributed declines in Kentucky Warblers in Virginia to changes in breeding habitat resulting from browsing by white-tailed deer (*Odocoileus virginianus*). In assessing population trends of forest birds in New Hampshire, Holmes and Sherry (1988) concluded that most of the declines were consistent with the hypothesis that the main cause was successional changes in breeding habitat.

In all of their predictions, Rappole and McDonald (1994) fail to acknowledge population-level phenomena that may affect migrants on the breeding grounds irrespective of events on the wintering grounds. For example, several studies have shown a correlation between productivity in one year and population size in the next (Sherry and Holmes 1992, Johnson and Geupel 1996, McCleery et al. 1996). Additionally, source-sink dynamics may affect local populations of migrants. Population changes (positive or negative) at a particular site may be due to immigration or emigration rather than to conditions at the site or on the wintering grounds (Brawn and Robinson 1996). In general, information on population trends, in the absence of data on reproductive success or survival, is of limited value in determining the cause of population changes.

Floating or wandering individuals.—Rappole and McDonald (1994) predict that if populations of migrants are declining because of events on the wintering grounds, then winter populations would be larger than the habitat could support, resulting in the presence of many floaters (or "wanderers" sensu Wunderle 1992; Prediction no. 8). These nonterritorial birds are thought to be individuals that adopt a wandering strategy because territorial conspecifics occupy all suitable habitats (Rappole and McDonald 1994). Although a number of studies have suggested the presence of wanderers (Rappole et al. 1992, Stai- cer 1992, Wunderle 1992), removal experiments are the only true test to determine whether wanderers actually seek to settle in territories (in presumably optimal habitat) that become vacant. Removal experiments during the winter have been performed only at small scales and on only two species, the Hooded Warbler (Rappole and Warner 1980, Morton et al. 1987, Stutchbury 1994) and the American Redstart (Marra et al. 1993). These studies did indeed find that vacant territories were filled, suggesting that wanderers exist. Nonetheless, removal studies on the breeding grounds also indicate that wander-

ers are present (Hensley and Cope 1951, Stewart and Aldrich 1951, Sherry and Holmes 1989). We believe that identifying wandering individuals and their position in the population is an important key to understanding the wintering ecology of migrants. Yet, given the occurrence of wanderers on the breeding grounds and the wintering grounds, it is difficult to use such information to conclude anything about the relative importance of habitat limitation. Beyond the studies cited above, no studies suggest that wanderers are searching for territories. Wandering may be a strategy that some species or sexes undertake depending on the reliability of food supplies; e.g. an individual may be territorial during part of the winter season and a wanderer when insects or fruit diminish within its territory (Morton 1980, Davies and Houston 1981, Martin and Karr 1986). Studies are needed that evaluate temporal changes in numbers of wanderers relative to changes in food availability.

Consideration also should be given to the significance of a third form of social organization: participation by migrants in mixed-species flocking during the winter. Migrants are an important component of mixed-species flocks in many areas (Greenberg 1984, Hutto 1994, Gram 1996, Latta and Wunderle 1996a). Fitness of individuals may be just as high in flocks as it is among territorial birds or wanderers. However, fitness indices have never been measured among migrants in mixed-species flocks, presumably because of the difficulty in banding and following individual flock participants. Moreover, flocking propensity varies by species and habitat, and species that are territorial in one habitat may be flock members in another (Gram 1996; Latta and Wunderle 1996a,b). Studies are needed that relate variation in foraging and social strategies among habitats to demographic measures of fitness.

Return rates.—Rappole and McDonald (1994) suggest that if populations are declining from breeding-ground factors, then return rates of adults to optimal breeding sites should be higher than those to optimal wintering sites (Prediction no. 5). But return rates generally may be poor estimators of annual survival (Martin et al. 1995). Moreover, this prediction ignores the probability that events during migration also affect return rates (Moore et al. 1995). Prediction no. 5 also includes an implicit assumption that breeding-ground problems affect adult survival (hence, lower return rates to wintering grounds). Yet, breeding-season effects on populations occur primarily through reproductive success rather than adult survival (Martin 1995). Finally, this prediction assumes that birds are "equally faithful to both destinations of the migratory journey." Data on return rates of American Redstarts and Black-throated Blue Warblers in summer and winter showed nearly equal site faithfulness in both seasons for both species (Holmes and Sherry 1992). These birds were not, however, the exact same individuals in winter and

summer. Although promising developments exist in the use of microsatellite techniques (Dias et al. 1996, Gibbs et al. 1996) and stable and radiogenic isotope ratios (Chamberlain et al. 1997) to identify regional differences in populations, an easily accessible and reliable means of identifying the origins of wintering or breeding populations of migrants is lacking. Therefore, we cannot pair breeding and wintering sites in order to distinguish the influence of seasonal events on bird populations. As a result, return rates (survival estimates) measure cumulative effects over the entire year, and it is difficult to separate winter versus summer effects.

In more general terms, we suggest that comparison of optimal winter and summer sites is insufficient to assess population trends because numerous regional influences potentially may affect one site and not another. Even within the breeding grounds, local and regional population trends may differ due to many environmental influences. As a result of these influences, local and regional differences in species population trends are clearly evident (Askins et al. 1990; Sauer and Droege 1992; James et al. 1992, 1996).

Genetic or competitive replacement.—Rappole and McDonald (1994) suggest that winter habitat changes that affect population sizes may alter interactions between species on the breeding grounds. As an example, they explain the increase in hybridization between Blue-winged (*Vermivora pinus*) and Golden-winged (*V. chrysoptera*) warblers by suggesting that alteration of winter habitat for the Golden-winged Warbler has resulted in severe population declines, forcing the species to look for mates in the closely related Blue-winged Warbler (Prediction no. 11). This hypothesis is contrary to the findings of Gill (1980) and Confer and Knapp (1981), who suggested that a fairly broad hybrid zone developed because of changes in breeding habitat and subsequent changes in the species' ranges. Studies indicate the more southerly Blue-winged Warbler is expanding its range northward, apparently displacing the Golden-winged Warbler northward in the process (Curson et al. 1994). Although numbers of Golden-winged Warblers have declined, they have not been expanding south into the Blue-winged Warbler populations (as would be expected if Rappole and McDonald's hypothesis were true). Instead, the Golden-winged population gradually has moved northward (Gill 1980, Confer and Knapp 1981). In this case, the prediction of Rappole and McDonald is interesting, but no evidence supports the prediction that winter habitat alteration alone is responsible for declines in Golden-winged Warblers.

Population changes in nonmigratory residents.—Rappole and McDonald (1994) conclude that migrants are not limited by the availability of breeding habitat because resident nonmigratory populations on both the breeding and wintering grounds have not

changed as expected (Prediction nos. 12 and 13). Rappole and McDonald (1994) predict that if populations are breeding-season limited, then changes in resident populations should parallel migrant declines in breeding-ground habitats that are degraded by fragmentation (Prediction no. 12). We suggest that this prediction is flawed, however, because it ignores fundamental differences in breeding biology between most Neotropical migrants and nonmigratory species. Due to the constraints of migration, migratory species generally lay smaller clutches and attempt fewer broods than do residents in the same habitat (Greenberg 1980, Whitcomb et al. 1981; but see Martin 1995). Resident species also generally have a longer breeding season, and because more resident than migratory species are cavity nesters (Haartman 1957), they may be less influenced by the effects of fragmentation (e.g. increased parasitism and predation; Sandstrom 1991). Migrants may thus be predisposed to suffer greater negative effects on reproduction due to events on the breeding grounds than are residents. In addition, increasing (and perhaps stable) populations of many permanent-resident species may be an artifact due to increased overwinter survival resulting from the availability of supplemental winter food (Brittingham and Temple 1988). Nevertheless, many resident species have shown national and regional declines that parallel declines in migrant populations (e.g. Geupel and Nur 1993).

Rappole and McDonald (1994) predict that if migrants are breeding-season limited, population trends of wintering migrants and tropical residents in the same habitat should not parallel each other (Prediction no. 13). They cite one study from Costa Rica (Stiles 1990) that refutes this prediction. We are aware of an important long-term study, however, that supports the prediction of breeding-season limitation. Faaborg and Arendt (1992) have documented declines to almost zero in captures of Northern Parulas (*Parula americana*) and Prairie Warblers (*Dendroica discolor*) overwintering in a Puerto Rican dry forest, while captures of resident insectivores showed no long-term negative trends. Clearly, more studies are needed before generalizations can be derived.

Conclusions.—Rappole and McDonald (1994:657) conclude that for Neotropical migrants, "alteration of wintering-ground habitat provides the most parsimonious explanation for the observed demographic trends." Although habitat loss or alteration on tropical wintering grounds clearly can have significant implications for overwinter survival of many migratory species, the extent to which most Neotropical migrants currently are limited by events on the wintering grounds remains unclear. We have shown that it is difficult to assign causation to either breeding- or wintering-ground events to explain observed population trends in Neotropical migrants

because of: (1) limited knowledge of the wintering ecology of many migrant species (especially the lack of direct measures of fitness components to evaluate habitat suitability), (2) the current inability to link breeding and wintering populations, and (3) the inability to separate the effects of concurrent events on both the breeding and wintering grounds. We have also shown that abundant evidence suggests that breeding season events are likely to influence population trends of Neotropical migrants.

The stated aim of Rappole and McDonald (1994) is laudable; i.e. to move the study of migrant ecology in the direction of strong inference. Nonetheless, their main conclusion quoted above, and their suggestion that conservation activities be focused on the wintering grounds, are not supported by the data. Much of the research on migrants in the last 20 years (see Keast and Morton 1980, Hagan and Johnston 1992, Martin and Finch 1995) has revealed that species exhibit unique and diverse combinations of breeding and overwintering ecologies that make it difficult to generalize about the causes of population changes. Although we realize that conservation decisions cannot always wait for the results of dozens of autecological studies, we point out that inaccurate generalizations run the risk of sending the wrong messages to the public, to politicians, and to land managers. For example, if migrants are used as "indicator" taxa for guiding conservation decisions on tropical wintering grounds, then the unique habitat needs of far more sensitive year-round tropical residents and endemics may be overlooked. Additionally, a misguided emphasis on the importance of wintering-ground events may overshadow the need for habitat conservation on the breeding grounds. We suggest that conclusions regarding seasonal limitation of Neotropical migrants take into account the requirements of individual species on both the breeding and the wintering grounds, as well as in migration stopover habitats. Although there are many reasons to increase conservation efforts for migrants and other species in threatened habitats in the Neotropics, conservation of habitat on the breeding grounds and along migration routes also is of demonstrated importance to the conservation of Neotropical migrants.

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Estimating Lipid and Lean Masses in a Wintering Passerine: An Evaluation of TOBEC

MICHAEL F. BURGER¹

School of Natural Resources and Environment, University of Michigan, 430 East University, Ann Arbor, Michigan 48109, USA

Body composition is an important aspect of the energetic and ecological relationships between birds and their environments. Although lipid extraction with a solvent is widely regarded as the most accurate method of quantifying body fat (e.g. Johnson et al. 1985), it is time consuming and cannot be used for repeated measures on the same individual. Total body electrical conductivity, or TOBEC (Walsberg 1988), measured using the commercially available EM-SCAN Small Animal Body Composition Analyzer, is a recent tool that provides an alternative to solvent extraction. TOBEC is used as a variable in a regression model with or without body mass and morphometric variables to estimate either lean or lipid mass (Walsberg 1988, Castro et al. 1990, Morton et al. 1991, Roby 1991, Scott et al. 1991, Skagen et al. 1993, Conway et al. 1994, Asch and Roby 1995, Lyons and Haig 1995).

Use of TOBEC in these models has varied. In some models TOBEC has been used as the dependent variable, after which the equation is solved for lean mass (an independent variable). The resulting estimate of lean mass is then subtracted from body mass to yield an estimate of lipid mass (Walsberg 1988, Roby 1991, Skagen et al. 1993, Asch and Roby 1995). Morton et al. (1991) pointed out that this two-stage method produces the same absolute error (in grams) for estimates of lean mass and lipid mass, but because lipid mass makes up

a smaller proportion of body mass than does lean mass, the relative error for the lipid mass estimate is higher. They further suggested estimating lipid mass directly by fitting a regression model with lipid mass as the dependent variable and body mass and TOBEC as independent variables. Skagen et al. (1993) verified that this direct approach provides a more accurate estimate of lipid mass than the original two-stage method. Conway et al. (1994) and Lyons and Haig (1995), using a different approach, estimated both lean mass and lipid mass directly (as dependent variables) from body mass and TOBEC. Additionally, Lyons and Haig (1995) used a two-stage approach of estimating lipid mass by subtracting direct (rather than inverse) estimates of lean mass from body mass to compare with direct estimates of lipid mass.

The equipment for and application of this technology continue to evolve, and validation of the technique for individual species is recommended (Asch and Roby 1995). This report has two purposes. The first is to propose predictive equations from which lean mass and lipid mass can be estimated for Northern Cardinals (*Cardinalis cardinalis*). The data set used to construct this model includes cardinals from widely separated parts of the species' distribution, captured at different times of day, so as to maximize the ranges in body size and body fat included in the data set. In this manner I reduce the possibility that future uses of this equation will result in an extrapolation beyond the range of the model-building data

¹ E-mail: mburger@umich.edu