Commentaries

Response to Latta and Baltz (1997)

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Latta and Baltz (1997) recently published a commentary on our paper, "Cause and effect in population declines of migratory birds" (Rappole and McDonald 1994) wherein we presented the following hypothesis for evaluation: "Populations of Nearctic avian migrants are declining as a result of breeding ground events." In our paper, we used our own data and available literature to evaluate 14 predictions deriving from this hypothesis, and concluded that "... populations of many species of Nearctic migrants appear to be controlled by wintering ground events" (Rappole and McDonald 1994:652). We welcome discussion on the critical issues involved in population changes in migratory birds. However, we prefer to defend only those positions that we actually took. In their opening statement, Latta and Baltz attribute the following conclusion to us: "They [Rappole and McDonald 1994] concluded that general declines of Neotropical migratory birds are a result of habitat alteration on the wintering grounds." We did not state, nor was it our intent to imply, that our conclusions applied to all migrants that winter in the Neotropics. Unquestionably, many migratory species' populations are controlled by breeding-ground events, including species dependent on ephemeral successional stages for breeding habitat, wetland birds, beach-nesting shorebirds, and raptors, to name only a few (Rappole 1995:141–144). However, populations of many species, mainly forest-breeding migrants, have been reported to be declining for reasons that are not understood (Morton and Greenberg 1989, Robbins et al. 1989b, Askins et al. 1990, Sauer and Droege 1992, DeGraaf and Rappole 1995). The causes for these declines have been the subject of debate, and were the impetus for our paper. We sought to emphasize that, contrary to the conclusions expressed in a number of papers on this topic (see Askins et al. 1990, Robinson et al. 1995, Sherry and Holmes 1995), events during the nonbreeding season can be *the principal factors* affecting population size for a migrant species. The bulk of the Latta and Baltz paper is devoted to a

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point-by-point rebuttal of their interpretation of our conclusions. We respond below.

1. *Several of the predictions (1, 5, 6, 10) are based on the assumption that we know which winter habitats are optimal for migrants.*—Perhaps the most commonly observed characteristic of many migrant species during migration and on the wintering grounds is their seeming lack of selectivity with regard to habitat. This phenomenon has been attributed to their status as marginal members of the tropical community (Karr 1976) or as habitat generalists (Petit et al. 1993). We suggest another possibility based on Fretwell's (1972) models on the sequence of habitat occupancy: "An alternative explanation is that more birds are present during the winter period than the declining amounts of optimal winter habitats can support ... forcing individuals to use suboptimal winter habitats" (Rappole and McDonald 1994:653). In the real world, however, "optimal habitat" cannot be identified because determination of what is optimal requires measurement of fitness for individuals simultaneously in all available habitat types. In practice, "optimal" is used as a relative term in comparing one habitat with another using one of three methods: (1) occurrence, (2) defense, or (3) survivorship. Occurrence is the crudest but most commonly used method, based on the assumption that a habitat in which a species actually occurs has higher value than one in which it does not. This reasoning often is extended to density measures (i.e. a habitat in which a species occurs at a higher density is more optimal than one in which it occurs at a lower density). However, density can be a function of social interaction so that higher densities can occur in habitats of lower quality because there is less competition (Van Horne 1983, Winker et al. 1995). Although more difficult to measure than occurrence, defense or selection of a particular piece of habitat also can be used as a measure of habitat quality. Hence, territoriality often is considered as prima facie evidence that a habitat containing territorial individuals is of greater value than one in which fewer or no territorial individuals occur.

Direct measures of fitness provide the best assessment of "optimal habitat." In one of the few long-

term studies of winter habitat use, movement, and survivorship, Rappole et al. (1989) used radio transmitters to study a Wood Thrush (*Hylocichla mustelina*) population in Veracruz, Mexico, over a five-year period. They found that territorial Wood Thrushes in rainforest habitat moved an average of less than 150 m from point of capture during the season, and showed greater survivorship (statistically significant) than nonterritorial wanderers. Wanderers moved longer distances and occupied a variety of different habitats including second growth, scrub, and agricultural sites. Latta and Baltz cite another effort (Conway et al. 1995) to measure relative winter survivorship; however, this paper reports the *failure* to determine a statistically significant difference between rainforest and second-growth habitats in terms of survivorship value for three wintering migrant species in Belize. Thus, we argue that in those few instances where evidence of occupation of suboptimal habitat by wintering migrants has been tested or examined (as in the case of the Wood Thrush and Hooded Warbler [*Wilsonia citrina*]; Rappole et al. 1989, Morton et al. 1993, Stutchbury 1994), the data indicate that some individuals are forced into lower-quality habitats. No one would disagree with Latta and Baltz in calling for more such studies.

2. *Predictions 2, 3, 4, and 9 are based on the assumption that we know something about optimal breeding habitat for migrants.*—"Optimal breeding habitat" for a species is that in which the largest number of quality offspring can be raised to maturity over the reproductive life of the adult. Because it is not feasible to measure reproductive success in all possible habitat types for even one species, the terms "optimal" versus "suboptimal" are always used as relative comparisons of two or more habitats for which the appropriate measures of reproductive success have been taken, or for which some other presumed measure of quality (e.g. breeding population size) has been assessed. Although, as Martin (1992) pointed out, many studies that purport to present this information actually do not, there are many studies in which the appropriate data have been collected (see Martin 1987, 1992; Askins et al. 1990). For several forest-related species, the results of a number of studies find that migrant population size is lower in disturbed or fragmented habitats (i.e. "suboptimal") than in larger fragments of mature ("optimal") habitats (Galli et al. 1976, Ambuel and Temple 1983, Askins et al. 1990, Freemark and Collins 1992). Curiously, several of these and other studies also find that fragmented habitats may not even be used, even when the only measurable difference between used and unused sites is size, a phenomenon referred to in the literature as the "area effect" (Galli et al. 1976, Robbins et al. 1989a). We offer a testable hypothesis to explain the area effect based on the reasoning in Fretwell's (1972) habitat use model, from which one would predict abandonment of lower-quality sites if higher-quality sites were available.

In our paper, we suggest that observed site-specific declines in breeding populations on sites at which no obvious structural change has occurred are potential indicators that nonbreeding-season factors are to blame. Latta and Baltz point out that other explanations for this occurrence are possible, citing McShea et al. (1995) in support of this position. They state that McShea et al. found that declines in a Virginia population of Kentucky Warblers (*Oporornis formosus*) resulted from browsing by white-tailed deer (*Odocoileus virginianus*). However, what McShea et al. actually reported was that Kentucky Warblers shifted *location* of their territories in apparent response to structural changes in understory vegetation caused by deer. They did not present their data as a cause of population change.

3. *Total amount of suitable breeding habitat is not necessarily an accurate predictor of population reproductive success.*—Several researchers have claimed that habitat fragmentation is a significant cause of decline in many forest-related migratory species (Lynch and Whitcomb 1978, Askins et al. 1990, Robinson et al. 1995). However, although fragmentation of forest habitats is an important conservation problem in some areas or regions, it may be less so in others. Thus, changes over the last half-century in total amounts of suitable forested breeding habitat are relevant to our understanding of migrant conservation. If one examines the entire range of forest-breeding migrants in the eastern United States, the total amount of mature forest habitat available within their range has increased significantly in the past half-century (Rappole and DeGraaf 1996). Entire regions of the country, such as much of the Appalachian chain, were in farmland as recently as the 1930s (Reeder and Reeder 1978). These areas are now large blocks of forest. Our point, in any case, is that the relative amounts of fragmented versus non-fragmented forest of all types are measurable, and not something about which we need to speculate.

4. *"Undisturbed" breeding habitat is not necessarily optimal.*—As pointed out in number 2 above, "optimal" (in the sense of being the best of all possible habitats) cannot be identified for any species because we cannot measure all possible habitats. Nevertheless, we can compare relative reproductive success, and designate one habitat as higher in value than another. This process has been done for a number of forest-related migrants, and for these species, the term "disturbance" has come to refer to a host of changes from fragmentation to clearcutting, many of which have obvious, measurable, negative effects on populations of certain forest-related species (Askins et al. 1990, Robinson et al. 1995). We argue that, in the absence of apparent change to mature, forested habitats ("optimal" in comparison with disturbed or fragmented habitats), populations of the forest-re-

lated species breeding in them should not change, unless the change is caused by factors during the nonbreeding season. The fact that few studies have recorded this phenomenon (e.g. Hall 1984, Marshall 1988, Baird 1990) is not surprising, considering that three special conditions must be met: (1) absence of any obvious change to the habitat as documented now and when the first breeding bird studies were performed; (2) existence of a thorough and reliable census of the breeding bird populations from several decades ago; and (3) performance of a new census using the procedures followed during the initial counts. The validity of the prediction, however, should not be diminished because of the lack of studies testing it. Rather, this lack should point to the need for additional work.

5. *Rappole and McDonald fail to acknowledge population-level phenomena that may be affecting migrant populations on the breeding grounds irrespective of events on the wintering grounds. "In general, information on population trends, in the absence of data on reproductive success or survival, is of limited value in determining the cause(s) of population changes."*—Our main purpose in writing Rappole and McDonald (1994) was because data on reproductive success and survival to time of migration at specific breeding-ground study sites *do not* appear to provide insights into causes of migratory bird population changes. This point has been demonstrated by Robinson (1992), who documented the maintenance of substantial breeding populations for several migrant species in Illinois despite extremely low annual productivity. Sherry and Holmes (1992) perhaps have been the strongest proponents of the view that regional breeding "population-level phenomena" control size of regional breeding populations in subsequent years. Their data on American Redstarts (*Setophaga ruticilla*) indicate that productivity on their New Hampshire study sites in one year is strongly correlated with the number of individuals in the breeding population in the next breeding season. A demonstration of correlation, however, does not constitute a demonstration of cause and effect. For their interpretation of the correlation to be true, there should be evidence that young from breeding populations of migratory species migrate and winter as recognizable and definable regional units (presumably suffering similar survival probability), as well as evidence that these young also return to join the same breeding population from which they were derived. To our knowledge, there are no data supporting either of these points. Several studies have documented differential winter distribution of migrants by sex or age (Ramos 1988:266), but none has shown that individuals that breed in a given region migrate together to a specific winter region (Salomonsen 1955, Lack 1968). Nor is there evidence to document that young birds, returning to the breeding ground for the first time, settle within the "regional population" from which they originat-

ed. Banding studies generally find that return rates of young to their natal area are less than 5% (Nolan 1978:463). Furthermore, a recent study by Graves (1997) found that young Black-throated Blue Warblers (*Dendroica caerulescens*) show range-wide age- and sex-specific distribution, with young males returning to the breeding ground for the first time at much higher ratios at the periphery of the species' range. If birds that breed in a specific area do not winter together, and the birds raised at a site do not return to breed there, it is difficult to define what sort of "population level" phenomena might exist below the level of the species, or in some cases, the subspecies (Salomonsen 1955).

6. *The presence of floaters does not provide information on population status of birds on either their breeding or wintering sites.*—Floaters are "Individuals unable to claim a territory and hence forced to wander through less suitable surrounding areas" (Wilson 1975:584). Their presence can be documented by banding and observation, radio-tracking, or removal experiments. The existence of floaters has been documented in a large number of studies on the breeding grounds (Brown 1964, von Haartman 1971), and in studies of at least three species on the wintering grounds (Hooded Warbler, American Redstart, and Wood Thrush; Rappole et al. 1989, Marra et al. 1993, Stutchbury 1994). Latta and Baltz claim that because floaters have been documented in both breeding and wintering populations, they cannot be used as evidence to indicate which portion of the annual cycle is more critical in terms of competition for space. However, the fact that there were Hooded Warbler floaters in Veracruz in 1987 and Bay-breasted Warbler (*Dendroica castanea*) floaters in Maine in 1950 is not relevant. The species and time chosen are critical, particularly when one considers the rate of change in winter habitats that has occurred within the past two decades in many parts of Middle America. We argue that testing for the presence of floaters can be highly instructive (when measured on breeding and wintering areas for the same species, in the same annual cycle, and for known populations across years) because the presence of these floaters may indicate that preferred habitat is limited, whereas their absence may indicate that habitat is not limited. Of course, this type of analysis would be valid only for species that tend to be territorial and site-specific on the wintering grounds. Nearly all individuals of species that depend on food resources that are temporally variable, e.g. fruits or seeds, could be classified as floaters on the basis of their movement patterns (Rappole and Warner 1980:383, Martin and Karr 1986).

7. *There is no evidence to support the contention by Rappole and McDonald that the subsuming of the population of the Golden-winged Warbler by the Blue-winged Warbler is anything other than a result of change in the breeding habitat of the Blue-winged Warbler.*—This statement is not true. Something quite radical is happen-

ing to the Golden-winged Warbler (*Vermivora chrysoptera*) above and beyond its disappearance from parts of its range and the apparent replacement by its closely related congener, the Blue-winged Warbler (*V. pinus*). The Golden-winged Warbler is being genetically swamped by the Blue-winged Warbler, a phenomenon that has been observed in other superspecies pairs where one member greatly outnumbers the other (e.g. *Canis lupus* and *C. latrans*; Wayne et al. 1992). "The composition of local populations changes from pure *chrysoptera* initially, to mixtures of both species with a variety of hybrid and backcross phenotypes, and then to introgressed *pinus*" (Gill 1987:444). In addition, Gill (1997) has found that a Golden-winged Warbler population composed of phenotypically pure and slightly introgressed *chrysoptera*, and located a considerable distance from historical golden-wing/blue-wing hybrid zones, shows a high rate of *pinus* mitochondrial DNA introgression, whereas reverse situations have not been found—further evidence of extensive breeding of Golden-winged Warblers with Blue-winged Warblers. These observations do not support a "habitat change" explanation for the disappearance of the Golden-winged Warbler. They indicate that golden-wings either *prefer* blue-wings as mates, which seems unlikely, or that they are unable to find conspecific mates and choose blue-wings as better than nothing. We believe that our "differential winter survival" hypothesis, in which blue-wings have higher survivorship than golden-wings because they winter in different habitats, provides a plausible explanation for the relative rarity and genetic compromising of golden-wings, whereas the "habitat replacement" hypothesis does not. There are, of course, other possible explanations for the phenomenon, e.g. interspecific competition and displacement. Further observation and experimentation will be required to understand the causes of golden-wing disappearance, but factors affecting these species during the nonbreeding portion of the life cycle should not be ruled out, *a priori*.

8. *The fact that intensive studies of temperate breeding communities have found long-term declines in migrant populations while residents have remained steady is not an indication that problems controlling migrant populations are occurring away from the breeding grounds.*—In several long-term, site-specific studies of breeding bird communities, the migrant species on the study sites have been reported as declining, while the resident species on these same sites are not (Askins et al. 1990). Latta and Baltz, using many of the arguments first presented by Lynch and Whitcomb (1978), suggest that compared with residents, migrants have: (1) smaller clutch sizes, (2) fewer broods per season, and (3) shorter breeding seasons. However, although these differences may explain why residents would not suffer to the same *degree* as migrants, they do not explain why residents should not suffer from the

same *kinds* of negative changes to breeding habitat (e.g. increased predation rates, decreased quality of feeding and nesting habitat, increased parasitism rates). Latta and Baltz also point out that many resident species are, in fact declining. This fact is irrelevant. The importance of data demonstrating migrant declines in the absence of resident population changes applies to migrant and resident populations occupying the same breeding communities, not to regional or national trends. In any event, it is not necessary to speculate about the possible effects of different life-history strategies when they can be tested directly in the field, for instance, by comparing the reproductive success and long-term population change for migrant and resident species with similar breeding life histories (e.g. Gray Catbird [*Dumetella carolinensis*] and Northern Cardinal [*Cardinalis cardinalis*]).

CONCLUSIONS

Throughout their critique of our paper, Latta and Baltz argue that we have taken the extreme position of claiming that the wintering ground is more important than the breeding ground for all Nearctic avian migrants. This was not our intent. Our approach was to present alternative explanations for observed phenomena that have been understood primarily as evidence supporting a breeding-ground interpretation for population control. Our paper suggested specific tests in which long-term studies of "reproductive success, return rates, and survivorship" (Rappole and McDonald 1994:657) could be used along with other demographic factors to evaluate the annual cycle of the migrant to determine where the most serious conservation problems occur. This process must be done on a species-by-species basis, although we may find patterns among similar species.

In their conclusion, Latta and Baltz take the position that an argument in favor of considering the conservation problems of migratory birds on the wintering ground poses a threat to conservation of resident tropical species. They state, ". . . if migrants are used as an 'indicator' taxon [*sic*] for guiding conservation decisions on tropical wintering grounds, the unique habitat needs of far more sensitive year-round tropical resident endemics may be overlooked." Besides being irrelevant, this statement sounds like a value judgement rather than a conclusion based on available data. Nowhere do we argue for consideration of migrants as "indicators." In fact, our only reference to the conservation implications of our work is in the final sentence of our paper: "If our tentative conclusions are correct, the focus of conservation activities for many species of migratory birds should be on factors affecting nonbreeding season survival." We believe that this statement reflects the sad reality of tropical conservation, and suggest

that more intensive consideration of the nonbreeding portion of the migrant life cycle will benefit all members of the tropical avifauna, not migrants alone.

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