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CAUSE AND EFFECT IN POPULATION DECLINES OF MIGRATORY BIRDS

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ABSTRACT.—Population declines have been reported for nearly one-third of all Nearctic migrant birds that winter in the Neotropics. Speculative explanations for these reports have been presented emphasizing the importance of events occurring during one portion of the annual cycle versus another. These explanations are difficult to test directly. However, certain predictions can be made regarding the characteristics of populations controlled by breeding-ground factors as opposed to those associated with migration or wintering-ground phenomena. These characteristics can be measured for and tested experimentally on a species-by-species basis. We present 14 such predictions, and review data currently available to assess their relevance to observed declines. Based on these data, populations of many species of Nearctic migrants appear to be controlled by wintering-ground events. *Received 30 September 1993, accepted 5 January 1994.*

DECLINES IN AT LEAST 109 species of Nearctic migrants have been reported by one or more survey methods (Droege and Sauer 1989, Morton and Greenberg 1989, Terborgh 1989, Robbins et al. 1989a, Askins et al. 1990, DeGraaf and Rappole in press). These figures are cause for concern despite conflicting regional population trends (Sauer and Droege 1992), and despite arguments that at least some purported evidence of decline may be the result of procedural errors (e.g. survey design and analysis flaws; Hutto 1988, James et al. 1990, 1992, Rappole et al. 1993a). If the declines are real, what are the causes?

Measurement of mortality rates for different stages in the annual cycle and their relationship to reproductive rates is the key to determining when population regulation is taking place, and to understanding the origin of migratory-bird declines. However, this measurement is difficult enough for game species where a variety of natality and mortality data is available (Nichols 1991); such measurements are considerably more difficult or impossible to achieve for songbirds. Nevertheless, migratory-bird populations are likely to have different characteristics depending upon whether population regulation is a breeding versus a nonbreeding phenomenon. These characteristics can be measured.

In this paper, we do not evaluate the evidence for declines per se. Rather, we make several predictions regarding demographic aspects of migratory bird populations based on the assumption that these populations are declining as a result of breeding-ground factors. Available information from our own work or the literature is presented to aid in evaluation of each prediction. In the interest of conciseness, we do not attempt to provide a comprehensive literature review; instead, we refer the reader to reviews of the subject contained in Terborgh (1989), Hagan and Johnston (1992), Morton (1992), and DeGraaf and Rappole (in press).

After presenting our predictions and brief arguments, we conclude that wintering-ground habitat alteration, not breeding-ground factors, provides the best explanation for the observed declines in many Nearctic avian migrant species. Finally, we encourage critical reevaluation of our predictions and conclusions, and we provide some suggestions regarding further tests of the hypothesis.

HYPOTHESIS AND PREDICTIONS

The hypothesis to be evaluated is that populations of Nearctic avian migrants are declining as a result of breeding-ground events. We discuss 14 predictions based on this hypothesis.

Prediction 1. Wintering sites for migrants should not be limited. Migrants should have their choice of optimal winter habitat sites, and should not occupy suboptimal sites.—This prediction is derived from

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the population models of Fretwell (1972:89), which state that habitats of lower suitability will be occupied only when the "basic suitability" of optimal habitat declines due to overcrowding to the point where it equals the "basic suitability" of suboptimal habitat. If breeding habitat were limiting migrant populations, then more optimal winter habitat should be available than necessary, and individuals should be highly selective with regard to habitat on the wintering ground—avoiding suboptimal habitats (Brown 1969, Fretwell and Lucas 1970, Krohn 1992).

Several studies indicate that migrants, in fact, are not restricted to a few, apparently optimal habitats on the wintering ground (Karr 1976, Hutto 1980, Waide 1980, Greenberg 1992, Lynch 1992). Migrants are found in a wide variety of habitats, including those that are apparently suboptimal (see reviews and data in Rappole et al. 1983:7–14, Rappole et al. 1989, Askins et al. 1990).

Observation of this phenomenon has caused many observers to conclude that most migratory birds are habitat generalists capable of tolerating a wide range of winter habitats (e.g. Morse 1971, Petit et al. 1993). An alternative explanation is that more birds are present during the winter period than the declining amounts of optimal winter habitats can support (Rappole and Morton 1985), forcing individuals to use suboptimal winter habitats.

Prediction 2. If breeding habitats are limiting, apparently suitable but marginal breeding habitats (i.e. lower in relative fitness than optimal breeding habitats) should appear filled with individuals of both sexes attempting to breed, regardless of the pressure from nest predation, parasitism, or similar fragmentation effects, since the principal alternative would be to forego breeding altogether (zero fitness).—Contrary to this prediction, abandonment rather than occupation of breeding habitat by Nearctic migrants has occurred. This abandonment has been identified as "the area effect" in which small or even medium-sized sites (up to 500 ha for some species) with apparently suitable breeding habitat are not occupied (Galli et al. 1976, Robbins et al. 1989b, Askins et al. 1990, Freemark and Collins 1992, McShea et al. unpubl. manuscript).

An explanation, based on the assumption that populations are controlled by wintering-ground events, would be that the "area effect" results from the fact that too few breeding adults are returning to fill all available breeding sites (Wilcove and Terborgh 1984, Askins et al. 1990: 26, DeGraaf and Rappole in press). If this were the case (i.e. if fewer birds were returning than necessary to fill all available breeding space), one would predict that breeding habitats would be abandoned in a regular, predictable fashion from least to most favorable, as suggested by the Brown-Fretwell-Lucas model of habitat use (Brown 1969, Fretwell and Lucas 1970, Krohn 1992). In other words, the "area effect" would be the result of fewer birds returning to breed than the habitat can support.

Prediction 3. Migratory bird declines should not be observed in breeding habitats that are undisturbed, and presumably optimal.—Contrary to this prediction, long-term studies have been performed in apparently undisturbed breeding habitats that have found declines in Nearctic migrants (e.g. Hall 1984, Marshall 1988, Holmes and Sherry 1988). These studies are based on counts of singing males, a number that can vary markedly depending on the number of unpaired males in the population (Rappole and Waggerman 1986, Rappole et al. 1993a, Gibbs and Wenny 1993). If wintering-ground factors cause a large reduction in number of adults returning to breeding territories, this decline should cause a reduction in number of unpaired males (since more breeding territories would be open to them), resulting in decline of the amount of song, and a concomitant decline in the population estimates based on song counts.

A 15-year study of a banded population of Kentucky Warblers (*Oporornis formosus*) in mature oak forest, initiated by E. S. Morton in Virginia, has assessed territory occupancy and singing behavior (McDonald and Morton unpubl. manuscript). Attributes of optimal Kentucky Warbler territories have been characterized (McShea et al. unpubl. manuscript), and the proportions of available optimal versus occupied areas noted for each year. In 1979, the first year of the study, 60 (89%) of the 73 territories used at one time or another during the 15-year period were occupied. By 1993, only 36 (45%) of the apparently suitable territories were occupied. This decline is highly significant ($r^2 = 0.81$). Yet, rates of predation, brood parasitism, and number of young successfully fledged per pair have remained unchanged over the years.

Prediction 4. Declines should not occur in species where no apparent change has occurred in breeding *habitat.*—Use of remote sensing eventually will make the comparative assessment of absolute amount of breeding versus wintering habitats possible (Green et al. 1987, Powell et al. 1992, Homer et al. 1993, Rappole et al. in press). Lacking the information necessary to complete such a comparison at present, researchers have examined subsets of Nearctic migrants for which declines have been recorded and which winter in lowland wet forest, one of the most threatened tropical habitats. These comparisons show a strong correlation, not with loss or degradation of breeding habitat, but between observed declines and loss of winter habitat (Robbins et al. 1989a, Askins et al. 1990:41–44).

In fact, there is debate over whether or not breeding habitat has declined at all for many forest-related migrants in recent decades. Available data indicate that breeding habitat for a number of forest-related species has increased during this period in many parts of North America (Birch and Wharton 1982, Powell and Rappole 1986). In contrast, wintering habitat for the Wood Thrush (*Hylocichla mustelina*) has declined by 23% in southern Belize, 73% in northeastern Costa Rica, and 95% in southern Mexico since pre-Columbian times (Rappole et al. in press). Even for those species for which scrub or second-growth habitats are optimal, habitat availability in many parts of the tropics is becoming increasingly difficult. Shade coffee and cacao plantations and shifting agriculture, which once provided considerable habitat for these birds, have given way in many areas to monocultures (G. Stiles pers. comm.).

Prediction 5. Spring return rates by adults to unaltered, optimal breeding sites should be higher than return rates by adults to unaltered winter sites in optimal habitat.—If adult birds are equally faithful to both destinations of the migratory journey, lower return rates would be expected from birds returning from the site most likely to have been altered; that is, if breeding-site quality has been reduced (reducing survivorship), birds should show a relatively lower rate of return to winter site (than breeding site) and, if the wintering site has been altered, there should be lower return rates to the breeding site.

Site fidelity has been documented for many species of migrants for both the breeding and winter seasons (Rappole et al. 1983, Mabey and Morton 1992), but seldom has this phenomenon been examined during the same time period for both breeding and wintering populations of a species. Holmes and Sherry (1992) performed such a study and found that American Redstarts (*Setophaga ruticilla*) and Black-throated Blue Warblers (*Dendroica caerulescens*) showed a higher degree of site fidelity to the wintering ground than to the breeding ground, contrary to Prediction 5. However, they provide an alternative explanation, maintaining that breeding-ground habitats vary markedly in quality from year to year, and low return rates reflect movements of competitive individuals to higher-quality sites.

We disagree with this explanation for higher return rates to wintering than to breeding grounds for the following reasons: First, there is no evidence to indicate that the missing birds have moved to "higher-quality" sites. The birds are simply not present. Second, if breeding habitat were limiting, individuals would not have the option of moving to higher-quality sites, since these likely would already be occupied. Third, there is no reason to believe, *a priori*, that breeding habitats are any more or less variable on an annual basis than wintering habitats.

Prediction 6. The proportion of young birds allowed to enter the breeding population should decrease as the amount of quality breeding habitat decreases relative to quality winter habitat.—If breeding habitat were limiting, one would predict that available breeding sites would be occupied mainly by older, experienced individuals. Older birds would return to successful wintering sites and show higher survival and return rates, due to experience and site dominance, than younger birds. However, if winter habitat were limiting, both older and younger birds would be forced into lower-quality winter habitats where age and experience would provide less of a competitive edge because density-independent factors would more likely be operative. Indeed, if winter habitats were declining rapidly, then the experience of older birds in sites formerly optimal but now degraded would be nullified and might even be disadvantageous. This negative effect on older birds would result in an overall decrease in the age of the population, an outcome that has been observed by Sherry and Holmes (1992, 1993). However, they explain this phenomenon as the result of cyclic variation in production of offspring from year to year based on food availability and on other breeding-ground phenomena.

Prediction 7. The number of nonbreeding males in *the breeding population should be high.*—Nonpaired males have long been recognized as a characteristic aspect of breeding populations for many species of birds (Hensley and Cope 1951, von Haartman 1971, Rappole et al. 1977). These males fall into four categories: males holding territory in apparently optimal habitat; males holding territory in suboptimal habitat; wanderers (floaters) moving over large distances in search of unoccupied territories; and "lurkers" (McDonald et al. unpubl. manuscript), unpaired males that do not move over large areas, but stay on or near the territories of one or two paired males. If breeding habitat is limiting, there should be large numbers of individuals in the latter three categories. However, if winter habitat is limiting, fewer individuals should return north to breed than the available breeding habitat could accommodate, and a decline should be observed in the number of nonbreeders in the population because an abundance of breeding habitat is available in which they can settle and establish territories.

This phenomenon has been observed in the aforementioned Kentucky Warbler study in Virginia. The total number of male Kentucky Warblers (both territorial and nonterritorial) captured on the study site annually declined from 80 to 50 individuals between 1980 and 1993 (McDonald et al. unpubl. manuscript); over the same time span, the number of individuals occupying suboptimal sites declined from an estimated 20 individuals to 0, and the total number of lurkers declined from about 10 to 5 individuals (based on intensive multiyear investigation of a breeding population of color-banded birds using netting, playback, and observation).

Comparing DNA-based markers or using other molecular-genetic techniques could provide additional information on this phenomenon. If populations are declining below the carrying capacity of optimal breeding habitat, then rates of extrapair fertilization not attributable to neighbors should decline as well.

Prediction 8. There should be little or no evidence of floaters (wanderers) in wintering populations.—In contrast to this prediction, those studies in which territorial competition for winter habitat has been studied in recent years have documented evidence of floaters (or "wanderers" sensu Wunderle 1992; Winker et al. 1990, Stacier 1992, Wunderle 1992). Rappole et al. (1989) measured mortality rates and movements of Wood Thrushes in Veracruz rain forest and second growth. They found that, while many Wood Thrushes occupied second growth habitats, they suffered higher mortality rates in these habitats and continually attempted to locate territories, moving as wanderers (floaters) through occupied territories. Rappole and Morton (1985) and Rappole et al. (1992) found that, while many species of forest-related migrants were found in low second growth, the turnover rates in these marginal habitats appeared to be much greater than in primary forest. Rappole and Warner (1980) performed removal experiments on Hooded Warblers (*Wilsonia citrina*) in Veracruz and found that removed territory holders were replaced by wanderers.

Prediction 9. The number of breeding individuals in populations of migrants in optimal habitats should not fluctuate appreciably with predator/prey and climatic cycles on the breeding ground because they will be buffered by the effect of having excess numbers of potential breeders in the population.—A consequence of having more winter habitat available than breeding habitat should result in having many more individuals in breeding condition than the breeding habitat can support. However, if winter habitat were limiting, one would predict that fewer breeders would be available than amount of breeding habitat, and droughts, cold snaps, and similar factors affecting mortality would translate into direct measurable effects on the number of breeding individuals. This phenomenon has been observed by Blake et al. (1992), who found that regional migratory-bird breeding abundances in the Midwest were affected negatively by drought. Rodenhouse (1992) constructed a model to demonstrate the potential effects of climatic change on warbler populations in which he predicted precise levels of population response to specific climatic fluctuations. This model presumes that the population is below breeding-habitat carrying capacity and, therefore, annual recruitment into the breeding population bears some direct relationship to fledging success. If breeding habitat were the critical factor limiting population size, this result would not be expected.

Prediction 10. The numbers of territorial individuals in optimal winter habitat should show sharp annual fluctuations.—If there were more optimal winter habitat available than necessary to support the population, there should be significant, observable changes in numbers of individuals in winter habitat as the numbers of migrants decline as a result of breeding-season phenomena. In fact, this effect has not been observed. Where studied, wintering migratory-bird densities in optimal habitats have remained remarkably stable across years and latitude (Rappole in press), indicating the presence of large buffer populations in suboptimal habitats.

Prediction 11. Alteration of breeding habitat could bring some species with similar ecological requirements into competition, forcing genetic or competitive replacement of one of the species.—Gill (1980) has documented evidence of increased interbreeding of populations of Golden-winged and Blue-winged warblers (*Vermivora chrysoptera* and *V. pinus*) over the past half century, resulting in gradual disappearance of the Golden-winged Warbler. This phenomenon has been explained as the result of recent breeding-ground contact between the two species. However, there is an alternative explanation. Interbreeding may have increased as an indirect result of the fact that these two species have very different winter-habitat use patterns. The Blue-winged Warbler winters "in a variety of brushy areas, scrub and open woodland" along the Gulf and Caribbean coasts of Middle America (AOU 1983:602), habitats that are not threatened in most parts of its range. In contrast, the Golden-winged Warbler winters in lowland wet tropical forests, a habitat that has undergone considerable alteration (Rappole et al. 1993b). If Golden-winged Warblers have been seriously reduced in numbers as a result of winter-habitat loss, they may have been forced to search for mates in the closely related Blue-winged Warbler population, a situation analogous to what has occurred between gray wolves (*Canis lupus*) and coyotes (*C. latrans*; Wayne et al. 1992).

Prediction 12. Declines in Nearctic migrants should be paralleled by changes in temperate, nonmigrant populations occupying the same breeding habitats.—If fragmentation causes severe degradation of breeding habitat as a result of loss of microhabitat or increased exposure to predation and cowbird parasitism (Askins et al. 1990), then resident species using these same habitats that have ecological requirements similar to those of migrants (e.g. open nesting birds) should decline in fragments in a manner similar to migratory species. Contrary to this prediction, most breeding-ground studies have found that, while migratory species declined on study sites, resident populations did not decline (Lynch and Whitcomb 1978, Briggs and Criswell 1979, Askins et al. 1990:2, Blake et al. 1992, Litwin and Smith 1992). However, Johnston and Hagan (1992) reported some instances in which temperate resident population changes were positively correlated with migrant trends.

Prediction 13. Declines in Nearctic migrants should not be paralleled by changes in nonmigrant populations occupying the same wintering habitats.—If loss of breeding habitat is causing the decline in Nearctic migrants, then a comparison of regional population trends of wintering migrants and tropical residents occupying the same habitats should show declines in migrant populations while resident populations remain stable. However, if loss of wintering habitat is the cause of migrant declines, then populations of species in both groups should remain stable in optimal tropical habitats or, alternatively, migrants and residents requiring a given habitat should decline in parallel if that habitat is degraded. Evidence for the latter occurrence was found in a 21-year study in Costa Rica (Stiles 1990).

Prediction 14. The ratio of songbirds migrating in fall compared to spring should increase over time.—If carrying capacity of breeding versus wintering habitats were equal, the total number of birds in fall should be much larger than the number of birds in spring as a result of the large number of offspring added to the population during the breeding period because, by spring the number will have been reduced by six to eight months of mortality factors acting on the population. However, if overall bird populations are declining as a result of breeding-season phenomena, the number of birds heading south in fall should decline more sharply than the number of birds returning north in spring.

Measurement of these kinds of trends for migratory songbirds as a group would be difficult or impossible based on small samples at a few migration stopover sites due to the confounding effects of weather (Moore et al. 1993). However, it may be possible to assess trends in relative numbers of migrants using rigorous sampling protocols and censusing or netting for extended periods at several permanent sites throughout each migration season for a number of years. As yet, this has not been done.

Another technique that may prove to be a feasible method for assessing fall/spring population ratios for migrants would be to compare the volume of migrating birds near the Gulf Coast using weather-radar films, which record flocks of migrants in nocturnal flight. Changes in migration volume could be analyzed for a period covering several decades using this procedure, providing estimates of amounts of change in fall versus spring volume over time. Analyses to date provide evidence suggesting that absolute numbers of migrating birds had declined significantly between the years 1957 and 1990 (Gauthreaux 1992). This finding, of course, is not useful for determining when in the life cycle the declines are occurring. That determination will require long-term fall/spring ratio comparisons from specific sites.

Conclusions

Our chief aim is to move the debate on migratory-bird demographics and conservation from the realm of speculation based on inferences into one in which hypothetico-deductive principles can be applied. The formulation and examination of the predictions presented herein are meant as a step in this direction. Fourteen predictions have been made based on the hypothesis that Nearctic migrant population declines have occurred as a result of changes to breeding-habitat amount or quality. Examination of these predictions based on the literature does not support the hypothesis. Alteration of wintering-ground habitat provides the most-parsimonious explanation for the observed demographic characteristics. However, there is sure to be discussion over the appropriate predictions. Deduction of reasonable predictions that can be used to discriminate between the competing hypotheses should prove to be a fertile field for debate and experimentation.

For some of the above explanations, there are alternative explanations based on breeding-habitat limitation (e.g. Holmes and Sherry 1992, Sherry and Holmes 1992), or a combination of breeding/wintering population limitation (Sherry and Holmes 1993). In addition, it must be recognized that not all migratory species can be expected to respond in the same way, and that different factors may be at work in different regions of North America or in the Tropics (O'Connor 1992). For instance, trends are not always consistent (Hussell et al. 1992, Johnston and Hagan 1992, Witham and Hunter 1992), and what appears to be "disturbance" for one species may actually be beneficial for another (O'Connor 1991).

Several of the predictions made in this paper lend themselves well to further testing. Removal experiments can be used to test for the presence of wanderers (floaters) on both the breeding and wintering ground in habitats of different quality. Return rates can be calculated for banded birds at breeding and wintering sites. As valuable long-term and in-depth studies on breeding, stopover, and wintering-ground populations continue to accumulate data on reproductive success, return rates, and survivorship, it should be possible to construct meaningful and comprehensive life tables. Significant changes in recruitment rates or in proportions of different age classes should help to elucidate relevant demographic trends in these populations that mere counts cannot provide. Another use of life tables would be comparisons of demographic trends between breeding and wintering grounds for a given species, or among ecologically similar species (as in Robbins et al. 1989a). Further tests of the predictions made in this paper could involve comparison of temperate and tropical resident populations with those of migrants. Food supplements could be provided on breeding territories to test Sherry and Holmes' (1992) idea that food availability ("habitat quality") is the factor driving adult return rates, rather than decreased overwinter survival. With the increasing power of geographic information systems, it may even be possible before too long to calculate amounts of breeding and wintering habitat on a species-by-species basis (Homer et al. 1993, Rappole in press). Other tests will become obvious when the question is viewed from the perspective of testable predictions based on likely alternatives. 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.

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