

31

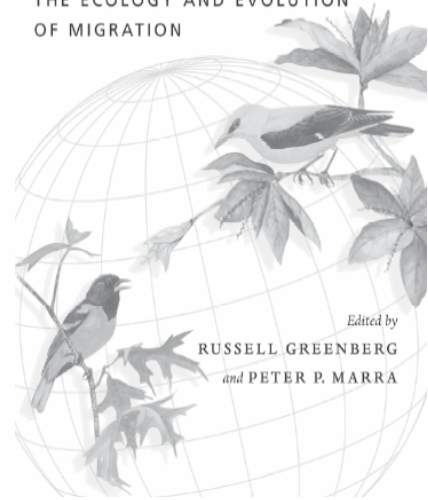
Does Winter Food Limit Populations of Migratory Birds?

THOMAS W. SHERRY,
MATTHEW D. JOHNSON,
AND ALLAN M. STRONG

Published in:

Birds of Two Worlds

THE ECOLOGY AND EVOLUTION
OF MIGRATION



Johns Hopkins Press, 2005

IN THEORY, WINTER HABITAT QUALITY, particularly food abundance, contributes to year-round population limitation in migratory birds, but this hypothesis has rarely been tested in the field. We hypothesize here that food availability in winter limits population size via winter habitat quality. From this Winter Food-Limitation Hypothesis (WFLH) we deduce and assess three testable predictions concerning winter populations in time and in space as well as delayed effects during and following migration. We find widespread support for the WFLH, involving diverse avian migratory taxa and geographic regions, although few studies have tested the strongest-inference prediction, namely that change in winter food affects survival and immediate winter population size. The lack of stronger support for the WFLH to date is primarily due to the expansive spatial scale of migration, the difficulty of distinguishing mortality from emigration, the paucity of dietary and available food data, and the multiple mechanisms by which food impacts populations. Further, the nearly complete lack of manipulative experiments makes it difficult to eliminate predators, parasites, diseases, and competitors as confounding factors that all potentially limit migratory bird populations. An important generalization emerging from many terrestrial studies is that prey abundance tends to track a late-winter dry season, causing decreased bird body condition, especially in some habitats and winters. This general response to decreased prey availability suggests that seasonal changes in food availability may have contributed to the evolution of migration. Although the frequently opportunistic response by migratory birds to variable prey availability

challenges our ability to document population responses, the mobility of these birds makes them useful indicators for conservation efforts.

INTRODUCTION

Population biologists are increasingly addressing the challenges presented by migratory animals, whose distribution, local abundance, and life history traits are influenced by ecological factors operating at different times and places. In the case of long-distance migrant birds, the ecological factors influencing reproductive success operate in different locations and times from nonbreeding-season factors that influence survival. These birds' life histories play out over spatial scales of continents and even different biogeographic regions. This scale of movement challenges scientists' ability to follow and study individuals throughout their lifetimes to address population questions, particularly in small-bodied species (Webster et al. 2002).

Understanding population dynamics of migratory animals is also daunting because of the range of possible influences operating at different temporal and spatial scales. Populations of migrant birds can in theory be limited during the reproductive period, the nonbreeding and nonmigratory phases of the life cycle ("winter"), or migration (Sherry and Holmes 1995). Moreover, ecological events in one season may carry over into, and interact with, demographic processes in a subsequent season (e.g., Marra et al. 1998; Sillett et al. 2000). Thus the question of when and how migratory bird populations are limited (or regulated), and by what resources, is still a challenge.

Abundant research supports the idea that breeding success in summer has an important impact on migrants' population sizes and dynamics (e.g., Robinson et al. 1995; Askins 2000). Although less studied, the winter period has also been postulated to limit migrant bird populations (e.g., Baillie and Peach 1992; Rappole and McDonald 1994; Sherry and Holmes 1995, 1996; Sillett et al. 2000); however, the causal mechanisms behind winter population limitation are largely untested. Assuming that aggressive (e.g., territorial) behavior is adaptive under conditions of limited resources, the widespread occurrence of such behavior in winter supports the idea that resources are limiting in this season (Morse 1980; Rappole and Warner 1980; Marra 2000). Both intraspecific and interspecific aggressive behavior are frequent in winter and often associated with local food resources (Greenberg 1986; Greenberg and Salgado-Ortiz 1994; Greenberg et al. 1994), implicating food as an important limiting factor. Furthermore, numerous authors have noted the association of migratory birds with particular kinds or concentrations of food in winter (e.g., Willis 1966; Sherry 1984; Lack 1986; Leisler 1990; Greenberg et al. 1993; Greenberg and Salgado Ortiz 1994). These observations suggest that food in winter is the most likely resource limiting populations—the "Winter Food-Limitation Hypothesis" (WFLH). Despite the likelihood that winter food con-

tributes to habitat quality, and ultimately to population limitation, the WFLH has rarely been tested, and when it has the evidence has been correlative and rarely considered in relation to factors other than food.

The purpose of the present review was to assess food in the nonbreeding season as a factor limiting migratory bird populations both in winter and in subsequent seasons. Here we deduce testable predictions from this WFLH, rank them in decreasing strength of inference, and assess them with available data. Considerable support for the predictions of the WFLH encourages discussion of several of its implications: How do food and other factors such as predators and parasites interact to limit migratory bird populations year-round? How does winter food limitation influence life history evolution? What are the major ecological factors that affect winter food availability? What are the conservation implications of the WFLH?

PREDICTIONS AND TESTS OF THE WINTER FOOD-LIMITATION HYPOTHESIS

The idea that winter habitat quality and availability limits bird populations on their wintering grounds is widely accepted (e.g., Baillie and Peach 1992; Rappole and McDonald 1994; Goss-Custard et al. 1995; Sherry and Holmes 1995, 1996; Newton 1998), but a mechanistic link between food and habitat use is not well established. By habitat quality we mean the survival or reproductive benefit a habitat confers upon its occupants (Hall et al. 1997). If food is the most important factor controlling winter habitat quality, then food controls the population size surviving the winter, because increases in food would increase habitat quality and thereby boost spring population size. Food can also cause delayed responses by a population, for example, influencing survival during migration or subsequent reproductive success. Unless an increase in winter survival is completely compensated by decreased migratory survival or breeding productivity, then winter food supply will help regulate migratory birds' overall population size (Sherry and Holmes 1995). With this background, we deduce three predictions from the WFLH, and we review evidence for these predictions primarily among long-distance migrants.

Prediction 1. Temporal change in winter food availability should affect winter population size proportionately. The simplest and most direct prediction of the WFLH is that a decrease in winter food supply should reduce the wintering population size and an increase in food should increase the population, up to the point permitted by the next most limiting factor. Support for this prediction provides the strongest evidence in favor of the hypothesis because it postulates a direct and immediate cause-effect link between food and wintering population size, N (fig. 31.1). Support of this prediction is both necessary and sufficient to demonstrate winter food limitation.

Evidence to support this prediction could be direct, via

Fig. 31.1. Schematic diagram of causation pathways by which food or food surrogates affect population size according to the Winter Food Limitation Hypothesis. Subscripts "t" and "s" represent time and space, respectively.

1. Changes in winter food availability affect winter population size proportionately:



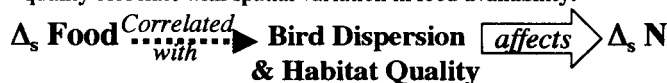
Corollary: Changes in food availability should affect demographic indicators of habitat quality accordingly:



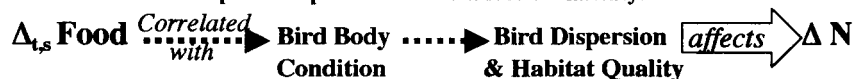
2. Spatial variation in population size (or density) correlates with spatial variation in food availability:



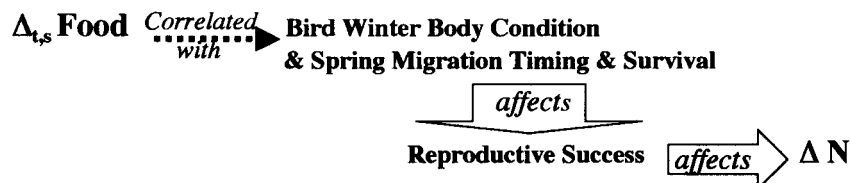
Corollary: Spatial variation in demographic parameters of habitat quality correlate with spatial variation in food availability:



Corollary: Temporal or spatial variation in indices of body condition (as a surrogate for demographic parameters) should correlate with temporal or spatial variation in food availability:



3. Winter food influences population size indirectly, via body condition and its effect on subsequent (migration, breeding season) survival and/or reproductive success:



experimental food manipulation, or correlational, via population response to extrinsic changes in food supply. Direct food manipulations have been conducted for wintering *resident* birds, and have generally been followed by enhanced survival, consistent with the hypothesis of food limitation (Berndt and Frantzen 1964; Watson and O'Hare 1979; Smith et al. 1980; Jansson et al. 1981). Strong (1999) reduced ant abundance in territories of the migratory Ovenbird (*Seiurus aurocapillus*) wintering in Jamaica, causing increased territory size. However, what effect this may have had on individual ovenbirds or their population is not known, and the experiment is being repeated on a larger spatial scale (D. R. Brown and T. W. Sherry, unpubl. data). We know of no other study that has manipulated winter food so as to assess its effect on a wintering migratory bird population.

Studies of diverse migratory taxa nonetheless provide correlational evidence for the first prediction of the WFLH by documenting changes in local density or population size immediately following natural changes in food availability (table 31.1). These taxa include perching birds, hummingbirds, ducks, shorebirds, and raptors. Although correla-

tional, the evidence reported by these studies provides some of the strongest support for the WFLH.

The interpretation of such changes in migrant numbers coincident with changing food is not always straightforward. First, unmeasured ecological conditions that change concomitantly with food supply could be responsible for any observed change in bird numbers. For example, drought depresses food supply and is correlated with dramatic declines in Palearctic migrants (Peach et al. 1991; Baillie and Peach 1992), but high mortality can also result from changes in temperature or other physiological stressors, not to mention predators or parasites. Nonetheless, without controlled experiments we can only speculate on the relative importance of factors other than food in governing population changes coincident with changing food supply. A second complication in interpreting temporal correlations between food and wintering migrant numbers is the temporal scale of observation. Short-term changes in migrant abundance over days or weeks may result simply from redistribution of birds without consequence to overall population size (Johnson and Sherry 2001). Thus, the strongest

evidence to date for the WFLH comes from the longer-term studies (see temporal scale in table 31.1).

If we assume that migrants' body condition and, ultimately, survival influence their overall population size, then a corollary of prediction 1 is that changes in food should affect these demographic parameters. However, support of this corollary alone is insufficient to support the WFLH because the assumption is invalidated when a change in one demographic parameter following a change in food availability is compensated by a change in another parameter, so that overall abundance remains stable. For example, a decrease in winter food availability could lower winter survival, consistent with this prediction, but the resulting smaller population could experience greater per capita reproduction, yielding an unchanged (regulated) population. Although partial compensation for winter events could occur during spring migration, complete compensation is unlikely because some migration mortality is likely independent of population size, as suggested by the effects of storms during migration (e.g., Zumeta and Holmes 1978; Sillett and Holmes 2002), and thus not regulatory. Food-mediated changes in demographic indicators are therefore likely to exert some influence on overall breeding population size.

Habitat-specific demography has received less attention in the winter than in the breeding season, perhaps because of

the long-term data required to quantify survival, the most relevant nonbreeding demographic trait. Of the few studies that have investigated nonbreeding season, habitat-specific survival for migrants (e.g., Conway et al. 1995; Marra and Holmes 2001; Brown et al. 2002), most have not simultaneously quantified food, so this corollary of the first prediction remains inadequately tested. Nonetheless, the studies that have measured food show a general tendency for survival to fluctuate in correspondence with variation in winter food availability. Latta and Faaborg (2001) and Johnson and Sherry (2001), working with wintering warblers, found that persistence over the winter (an indirect measure of survival, because survival is confounded with emigration) decreased following decreases in arthropod availability.

Prediction 1 involves changes in abundance that result from temporal changes in food supply. Where those changes are controlled and randomly assigned by experimentation, we can rule out most alternative factors; where those changes are natural, the inference that observed bird responses are due to food alone is weakened. With or without experimentation, however, prediction 1 provides some control of alternative factors because changes in population size follow changes in food supply in particular locations. In contrast, the following prediction is more poorly controlled because it relies on variation in food availability across space; that is, confounding factors in ecology are often bet-

Table 31.1 Evidence for the winter food limitation hypothesis based on temporal changes in bird abundance or density in correspondence with changes in food availability (tests of Prediction 1)

Species	Food	Temporal scale	Region	Reference
Various sparrows	Seeds	8–21 years	Arizona	Pulliam and Parker 1979 Dunning and Brown 1982
Rufous Hummingbird <i>Selasphorus rufus</i>	Nectar	Days–weeks	California	Gass et al. 1976
Various ducks	Mussels	Tens of years	Lake Erie	Wormington and Leach 1992
Various seaducks	Invertebrates	6 winters	Scotland	Campbell 1984
Dunlin	Invertebrates (inferred, not measured)	>3 years	Britain	Goss-Custard and Moser 1988
<i>Calidris alpina</i>				
Brant <i>Branta bernicla hrota</i>	Eel grass	~10 years	Svalbard	Clausen et al. 1998
Prairie Warblers	Insects	3 months	Dominican Republic	Latta and Faaborg 2001
<i>Dendroica discolor</i>				
Various frugivores-insectivores	Fruits and flowers	Monthly variation	Argentina	Malizia 2001
Northern Pintail	Seeds and invertebrates	2 winters	California	Miller and Newton 1999
<i>Anas acuta</i>				
Merlin	Rodents	16 years	Sweden	Wiklund 2001
<i>Falco columbarius</i>				
Various warblers	Insects	Weeks	Jamaica	Johnson and Sherry 2001
Various insectivores	Insects	3 years data but correlations within 1 year	Tanzania-Kenya	Sinclair 1978
Yellow Wagtail	Arthropods	5 months	West Africa	Wood 1979
<i>Motacilla flava</i>				

ter controlled over time than across space (Eberhardt and Thomas 1991; Manly 1992).

Prediction 2. *Winter food availability should correlate spatially (e.g., by habitat) with winter population size.* This prediction rests explicitly on the links among bird dispersion, habitat quality, and population limitation (e.g., Sherry and Holmes 1995). As explained earlier, winter food limits migrant populations if it is the primary determinant of habitat quality, and animals should in theory disperse among habitats of different quality so as to match population size to food resources (Moreau 1972). The effect of food could be restricted to a simple redistribution of birds among habitats as food supply fluctuates, without any population consequences. This prediction is thus weaker than the previous one because it invokes a relatively indirect link between winter food and a migrant's population size (fig. 31.1), and support for this prediction is necessary, but not sufficient, to support the WFLH.

This prediction has received the most attention, with the majority of investigations showing a general spatial correspondence between bird distribution and food availability. The evidence is strongest for shorebirds, for which spatial correlation is documented between bird numbers and benthic macro-invertebrate density under diverse circumstances and scales (Goss-Custard 1970; Wolff and Smit 1990; Hockey et al. 1992; Yates et al. 1993). Although less well documented, migratory waterfowl and seabird abundance has also been found to vary in correspondence to their respective foods, including invertebrates (Yates et al. 1993), krill (Heinemann et al. 1989; Veit et al. 1993), and eel grass (Clausen et al. 1998).

Prediction 2 has received less attention for migratory landbirds, perhaps because of the comparative difficulty in quantifying resource availability in structurally complex habitats. Hutto (1980) and Johnson and Sherry (2001) found a positive correlation between migrant and insect numbers in the Neotropics, but Folse (1982) working in Africa did not. Price and Gross (Chap. 27, this volume) found correlations between food and *Phylloscopus* warbler abundance wintering in India. Studies with too few sites for correlation analysis corroborate the idea that wintering migrant landbirds tend to become more abundant in sites or habitats with more food (Sinclair 1978; Poulin et al. 1992; Lefebvre et al. 1994; Parrish and Sherry 1994; Katti and Price 1999; Latta and Faaborg 2001; 2002; Perez-Tris and Telleria 2002).

This second prediction invokes food as a proximate limiting factor via its effect on survival, a demographic indicator of habitat quality, which in turn drives population size (fig. 31.1). Like the corollary of prediction 1, this deduction therefore relies on the assumption that food's influence on survival is not compensated elsewhere in the birds' annual cycle. Few studies have examined a corollary of prediction 2, namely that the mechanism of food's effect on a population is via survival or other indicators of body condition, again because quantifying survival is difficult. Marra and Holmes (2001) found higher survival for American Red-

starts (*Setophaga ruticilla*) in mangrove swamp than in adjacent scrub forest, and Parrish and Sherry (1994) found correspondingly greater abundance of at least some insect taxa in mangroves, although this tendency may be restricted to old-growth mangrove swamps (Johnson and Sherry 2001). Working in three habitats, Johnson et al. (unpubl. data) found that apparent annual survival was highest in the food-rich and lowest in the food-poor habitat. Similarly, over-winter persistence was highest (among three habitats) in food-rich sites for both the insectivorous Prairie Warbler (*Dendroica striata* [Latta and Faaborg 2001]) and the omnivorous Cape May Warbler (*Dendroica tigrina* [Latta and Faaborg 2002]).

Thus far, we have reviewed evidence that links food to population size either directly or indirectly via demography, chiefly survival. If we assume that measures of individual birds' body condition determine or indicate survival, then a corollary of prediction 2 is that surrogate variables for survival should vary spatially with variation in food availability. Marra and Holmes (2001) showed that this assumption was valid for wintering American Redstarts, but because the assumption has been inadequately tested for other taxa, we have ranked evidence involving variability in body condition lower in strength of inference than variability in survival.

Several studies of terrestrial migrants in winter have documented temporal or spatial variation in body condition, but as before, few have done so concurrently with measures of food availability. Those studies that have examined body condition have focused on surrogates for fitness, including change in body mass (Marra et al. 1998; Johnson et al., unpubl. data), rate of feather regrowth (e.g., Strong and Sherry 2000), stress hormones (Marra and Holberton 1998), subcutaneous fat (Katti and Price 1999), and pectoral muscle mass (Latta and Faaborg 2002). Insectivorous Ovenbirds varied in maintenance of body mass and feather regrowth rate both spatially (among territories) and temporally with ant biomass, their primary winter food (Strong and Sherry 2000).

Measures of body mass have generally varied as predicted with measures of food availability. Copious data obtained from winter-harvested waterfowl indicate a clear correlation between food availability and body mass (e.g., Hobaugh 1985; Miller and Newton 1999), and nonharvested species appear to exhibit similar patterns (e.g., Nariko et al. 1999). Studies of shorebirds also suggest a positive correlation between variation in food across time and/or space and variation in body mass (Tsipoura and Burger 1999; Mitchell et al. 2000). An important caveat here is that body mass is composed of separate components (e.g., body fat, overall body size in relation to skeletal characters, and pectoral muscle mass) that may respond independently over space and time to various ecological circumstances; moreover, predation risk and food predictability likely affect body lipids and pectoral body mass (Rogers, Chap. 9, this volume). Thus body mass likely does not depend simply on overall food abundance.

In a variety of studies foraging behavior has been used as a surrogate for measurements of food (e.g., Lovette and Holmes 1995; Wunderle and Latta 1998). When behavior is used to estimate food availability, the linkage between the predictor variable (e.g., foraging) and the population response is even more indirect than the pathways in fig. 31.1, and thus more tenuous. Better understanding of the link between foraging behavior and food availability is necessary to justify the use of foraging behavior as a surrogate for food availability.

Prediction 3. Winter food influences population size indirectly, via body condition and its effect on subsequent (migration, breeding season) survival and/or reproductive success. Because food abundance influences body condition in winter as reviewed above, winter food can therefore exert delayed, indirect effects on populations that ecologists have only begun to suspect (e.g., Marra et al. 1998; Sillett et al. 2000). Support of this third prediction is sufficient, but not necessary, to support the WFLH, because a particular species could in theory respond immediately in winter to concurrent changes in food abundance (in support of predictions 1 and 2), but show no delayed responses (prediction 3). We also rank evidence in support of this third prediction of WFLH as weaker than that for prediction 1 because the delay between winter food abundance and subsequent population responses allows the possibility that ecological conditions subsequent to winter can intervene and modify the population's response to winter food (fig. 31.1). The "carry-over effects" implicit in prediction 3 are poorly understood, in part because of the challenge of linking migratory populations spatially during their annual travels (Webster et al. 2002). Nonetheless, these delayed population effects may be widespread (e.g., Sillett et al. 2000; Møller and Hobson 2004; Norris et al. 2004; Saino et al. 2004, and they certainly increase the range of population responses to winter food (Marra et al. 1998), and thus the challenge of testing such food impacts.

Our third prediction of the WFLH converges with a deduction from the idea of seasonal interactions in migratory birds (Webster et al. 2002), which in general predicts delayed effects of ecological conditions in one season on migrants' population and individual responses in subsequent phases of the annual cycle (winter to summer, summer to winter, migration to summer, and so on). The WFLH differs from seasonal interaction predictions in specifying food as the dominant ecological factor and in focusing on impacts of ecological conditions arising solely in winter.

Our review of data relevant to the three predictions of the WFLH suggests that food can be an important factor limiting migratory bird populations, affecting their distribution, year-round abundance, survival, and even reproduction following a migration away from the winter range. These data come from a variety of species on most continents, and they represent different temporal and spatial scales of study. Nonetheless, strong direct support of the hypothesis (prediction 1) is infrequent.

ALTERNATIVE MECHANISMS OF POPULATION LIMITATION IN WINTER

Despite the foregoing evidence supporting the WFLH, we still understand only sketchily the mechanisms by which food limits populations, for a variety of reasons. First, food abundance influences populations in diverse and often indirect ways, including socially constrained dispersion of individuals among habitats (Marra and Holmes 2001), interaction with predators and parasites, and time delays. For example, resource distribution patterns can influence bird dispersion among habitats, which can in turn differentially influence survival and body condition via predation, parasitism, and other factors that vary by habitat. Another consideration is that food availability is influenced not only by prey abundance (i.e., "standing crop"), but also by resource productivity (i.e., turnover rate), and standing crop alone may be a poor estimate of food supply for highly renewable foods. The abundance of migratory shorebirds supported by high tropical marine productivity in the Banc d'Arguin (Zwarts et al. 1990) exemplifies how low arthropod standing crop of small-bodied prey may not predict abundance as well as prey population productivity—a circumstance that may apply to "terrestrial" habitats such as mangroves.

The relationship between food and population size can also be obscured by competitors, including other bird species (Greenberg 1986), other vertebrates such as lizards and frogs, and potentially even invertebrates such as ants and spiders (Van Bael et al. 2003). A variety of recent studies document effects of migratory species on the feeding success and habitat choice of other migrants (Greenberg et al. 1993; Greenberg and Salgado-Ortiz 1994; Greenberg et al. 1994; Latta and Faaborg 2002). Resident tropical birds can also be important competitors (e.g., Lack 1976; Greenberg 1986). Greenberg's (1995) Breeding Currency Hypothesis (BCH) formalizes a general mechanism of competition between migrant and resident insectivorous birds. Johnson et al. (in press) found support for the primary prediction of the BCH, namely that large arthropods ("breeding currency") most suitable for the reproductive success of resident birds tended to be proportionately more abundant in Jamaican resident-dominated habitats, whereas smaller arthropods in winter tended to be most abundant in the habitats with proportionately more wintering migrants. The implication of this relationship is that wintering terrestrial migrant birds compete diffusely with resident birds for subsistence or survival food, and resident species displace migrants from the best local breeding habitats. This example of migrant-resident avian niche partitioning is a special case of resource partitioning among consumers in the Tropics (e.g., Lack 1976), an appealing, if still inadequately understood phenomenon. An important implication of our review for studies of competition is that the diverse pathways by which winter food can influence a population (fig. 31.1)

should lead to similarly diverse ways that competitors can influence a population.

Predators and parasites can also obscure the relationship of the winter population response to food both directly through mortality and indirectly by influencing feeding behavior and habitat choice. For example, animals in poor body condition, which can be the result of food shortages, may be more susceptible to predators, as illustrated by young Dunlin (*Calidris alpina*) wintering on the Banc D'Arguin, Mauritania (Bijlsma 1990). Expanded home range size and dispersal movements of animals, which can be precipitated by low food abundance, should also put individuals at greater risk of both predation (Hubbard et al. 1999) and parasitism. Both predators and parasites cause mortality in wintering migrants. Scaley-leg mite infests migrant and resident birds wintering in the Caribbean region and it affects both body condition and survival (e.g., Latta and Faaborg 2001; Latta 2003), but the quantitative impact on populations remains poorly understood. Rogers (Chap. 9, this volume) emphasizes the importance of predators to wintering migrants by illustrating the complex ways in which predators can shape adaptive patterns of body mass variation.

Our ability to test the relationship between available food and population responses also depends on methodological challenges, some of which have been mentioned already, including problems of establishing population connectivity (Webster et al. 2002) and quantifying resource abundance. In addition, food resources are filtered by consumers—depending on their searching, handling, and digestive adaptations—which makes it challenging to quantify what foods are effectively available to a particular population (Hutto 1990; Strong 2000). Predation and disease can also be difficult to measure because of their infrequent occurrence and indirect effects on survival and subsequent reproduction.

IMPLICATIONS OF WINTER FOOD LIMITATION FOR MIGRANT LIFE HISTORY EVOLUTION

One unifying pattern for both Old and New World terrestrial migratory systems is a decline in food resources in the late dry season (Katti and Price 1996; Rödl 1999; Strong and Sherry 2000; Johnson and Sherry 2001; Latta and Faaborg 2001, 2002), a simultaneous deterioration of body condition (Sherry and Holmes 1996; Marra and Holberton 1998; Marra et al. 1998; Strong and Sherry 2000; Latta and Faaborg 2002), and decreased survival or persistence both in drought-stressed habitats (Katti and Price 1996; Sherry and Holmes 1996; Marra et al. 1998; Rödl 1999; Strong and Sherry 2000; Latta and Faaborg 2001; Marra and Holmes 2001) and in relatively dry winters (Peach et al. 1991; Baillie and Peach 1992; Sillett et al. 2000). If ancestral, resident species/populations were constrained to occupy similarly seasonal, unbuffered habitats just before spring migration, then intra- or interspecific competition combined with em-

igration could be an intermediate step in the evolution of a long-distance migratory strategy.

Consider a hypothetical resident individual's annual cycle in an early successional habitat. If the lowest level of resource availability occurs at the end of the dry season, despotic interactions over the winter (e.g., Greenberg 1986; Greenberg and Salgado-Ortiz 1994; Marra 2000) may constrain individuals facing a negative energy balance either to starve or to emigrate just before the breeding season begins. If emigration leads to the location of increased food resources, then breeding may take place in areas with more favorable food resources. Although this hypothesis ignores many of the intermediate steps (e.g., physiological, anatomical, neurological) that are necessary for the evolution of a completely migratory life history, it is consistent with several of the evolutionary precursors that may have been responsible for migration: dry-season food limitation, despotic interactions, and increased emigration rates.

Studies of the migratory origins of parulid warblers support this hypothesis. Cox (1985) modeled the evolution of the Neotropical migration system in parulids and concluded that the Mexican Plateau, characterized by strong seasonality and interannual variation in rainfall, was the likely point of origin for many migratory taxa. Similar environmental conditions and subsequent forest fragmentation throughout North America during the Miocene-Pliocene boundary may have contributed to the rapid adaptive radiation of *Dendroica* (Lovette and Bermingham 1999). Thus, xeric conditions appear to be conducive to the proliferation of migratory species. Entomological studies corroborate the idea that drought reduces arthropod abundance (e.g., Wolda 1978; Levings 1983; Pearson and Derr 1986; Frith and Frith 1990), lending credence to dry-season declines in food availability as a driving mechanism for migration.

Chesser and Levey (1998) argued that habitats with poorly buffered resources in the nonbreeding season, rather than diet per se, are most likely to favor migratory behavior. They argued that although diet, specifically frugivory, was not supported as a precursor to migration, the use of ephemeral food resources might be a consequence of selection for poorly buffered habitats. There is strong empirical evidence that many (but not all) migrants use such disturbed, early successional habitats (Hutto 1980; Hagan and Johnston 1992; Petit et al. 1995; Johnson and Sherry 2001), and these species are generally "replaced" spatially by resident species in more buffered habitats (Keast and Morton 1980; Douglas 2002). This may occur because resident species are not as effective as migrants in tracking resources in space because of the constraint of defending suitable home ranges year round with sufficient breeding currency (sensu Greenberg 1995; Johnson et al. 2004). Many migrants, by contrast, appear to track ephemeral food resources spatially over the course of the nonbreeding season, as reviewed under hypothesis 2 above. Thus, ecological conditions typical of large parts of the Subtropics may have fa-

vored evolution of latitudinal migration, via patterns of food resource distribution and abundance.

CONSERVATION IMPLICATIONS OF WINTER FOOD LIMITATION

The mobility of migrant birds, their often opportunistic food habits as described above, and the lack of habitat-specific demographic data for most species make the conservation of migratory birds during the nonbreeding season challenging. The fact that individuals use multiple habitats outside the breeding season (e.g., Rappole et al. 1989; Wunderle and Latta 2000; Johnson and Sherry 2001) underscores the necessity of a landscape or regional approach in winter, just as in summer (Askins 2000). However, critical to any conservation strategy is the need to address issues of both habitat quantity and quality. Habitat quantity has long concerned avian conservationists (e.g., Keast and Morton 1980; Terborgh 1989). What we emphasize here is that conservation efforts need to increase consideration of habitat quality, including factors that maintain or degrade prey abundance. Increasing use of demographic data (birth and death rates) in assessing avian habitat quality is a positive development, but we nonetheless recommend greater effort to address the ecological determinants of habitat quality, and our review suggests that food availability merits more attention.

Humans can influence habitat quality to birds most obviously by influencing the kinds and abundance of resources (Greenberg 1992; Petit et al. 1995). For example, Johnson (2000) demonstrated that the species of shade trees used in coffee cultivation influenced the abundance of birds via foliage arthropods. Similarly, plant species influence the distributions of migrant and resident Jamaican birds via fruit and nectar resources (Douglas 2002). Anthropogenic habitat conversion and landscape changes (e.g., increased edge vegetation) will in general alter habitat quality for birds and other kinds of wildlife. Humans can also influence habitat quality for birds indirectly via weather patterns (Sillert et al. 2000), and potentially via effects on predators and pathogens (such as West Nile Virus).

Migratory birds may be useful indicator species in habitat restoration efforts because of their exceptional ability to discover and use resources opportunistically. Additionally, the ability of many migratory birds to track ephemeral resources (e.g., Sherry 1984; Johnson and Sherry 2001) makes them particularly effective consumers of some insect pests (Greenberg et al. 2000; Van Bael et al. 2003), because an increase in arthropods of the sizes and types consumed by these birds will result in a local increase in migratory bird populations. Such functional and numerical responses, coupled with birds' high metabolic rate, will increase consumption of these arthropods. Thus, our studies of the feeding behavior and food limitation underscore the potential of wintering migratory bird populations for arthropod control in tropical wintering areas.

FUTURE DIRECTIONS

Our inability to link winter food availability more strongly to changes in migratory bird population size, that is, to test the WFLH more rigorously, can be ascribed to several factors that indicate future research needs: paucity of dietary data for most species, prevalence of feeding opportunism and thus diet variability in space and time, large spatial scale necessary for manipulative experiments, unclear relationship between climate and food availability, difficulty in distinguishing between mortality and emigration as responses to food shortage, lack of understanding of population connectivity between breeding and wintering phases of the life cycle, the need to examine alternative hypotheses, and the need for a better understanding of the relationship between body condition and fitness. This review of winter food emphasizes diet as a logical link between the population dynamics, habitat-selection, life history evolution, and conservation needs of migratory birds. Future diet studies promise to advance our understanding of migratory birds in diverse ways, and such studies are feasible, if challenging, as reviewed above.

Dietary opportunism can both complicate and simplify our understanding of how food availability limits migratory bird populations in winter. The use of small, poorly digestible, abundant prey types—subsistence resources that are inadequate as breeding currency—have been documented as prey for arboreal species, ground foragers, and wetland species (Morton 1980; Zwarts et al. 1990; Poulin and Lefebvre 1996; Medori 1998; Strong 2000). Such breadth of prey types within species potentially complicates measurement of food availability, but recent studies have demonstrated the tendency for migrants to take prey in direct proportion to their abundance, an observation also consistent with dietary opportunism (Sherry 1984; Strong 2000). An opportunistic diet has the potential to simplify the daunting task of measuring food availability by using generalized sampling techniques. Although species-tailored food-sampling methods certainly provide better data for particular populations (e.g., Rödl 1999; Strong and Sherry 2000, 2001; Johnson and Sherry 2001), a sampling scheme with standard methodology used by collaborating researchers across a broad geographic scale should also help unravel the effects of climate, soils, and other factors influencing food availability. Moreover, more studies need to test simultaneously the impacts of food limitation in winter versus alternative factors (e.g., Johnson and Sherry 2001) and interacting factors.

Measuring a population's demographic response to resources is just as challenging as measuring the resources themselves, and this topic deserves a major review of its own. For example, distinguishing mortality from emigration remains one of the greatest challenges to studying these far-ranging animals (Webster et al. 2002). We need studies of the congruence and redundancy of different measures to assess body condition conducted under diverse ecological circumstances. A related need is the examination

of delayed responses of migrants to food conditions in winter, that is, seasonal interactions via body condition and demographic parameters. Such studies will be most feasible in species with limited geographical ranges or in those whose breeding and wintering population connectivity are known.

Two important conservation needs are to learn how to improve habitat quality for wintering migratory birds and to identify both the ecological and economic value of these birds. This review indicates that food abundance is an important determinant of habitat quality, which suggests that manipulating food abundance will be a fruitful experimental approach. Possible ways to do this include changing plant species (Johnson 2000) and more generally manipulating vegetation cover and habitat type. Future research should emphasize agricultural habitats such as irrigated and forest-based crops, because these are habitats in which humans and migratory birds potentially can coexist. Conversely, we need to quantify the value of the ecological and economic services provided by migratory birds, including their potential indirect beneficial effects on plants via the birds' consumption of insect herbivores (Marquis and Whelan 1994; Greenberg et al. 2000; Strong et al. 2000; Van Bael et al. 2003).

ACKNOWLEDGMENTS

We dedicate this chapter to the memory of Robert Sutton, passionate bird scientist, author, conservationist, and friend, who was instrumental in all phases of our research in Jamaica. Many other Jamaicans both facilitated our work and made it far more pleasurable: Anne Haynes-Sutton, Leo Douglas, Catherine Levy, the late Pamela Williams, Peter Vogel, Errol Ziadie of the Portland Ridge Hunting Club, and numerous field assistants.

We thank the National Science Foundation for continued financial support of our research in the Caribbean, and Dick Holmes and Pete Marra for constructive suggestions on the manuscript.

LITERATURE CITED

- Askins, R. 2000. Restoring North America's birds: lessons from landscape ecology. Yale University Press, New Haven.
- Baillie, S. R., and W. J. Peach. 1992. Population limitation in Palaearctic-African migrant passerines. *Ibis* 134:120-132.
- Berndt, R., and M. Franzen. 1964. The influence of the severe winter of 1962/63 on the breeding status of hole nesting birds in Braunschweig. *Ornithologische Mitteilungen* 16: 126-130.
- Bijlsma, R. G. 1990. Predation by large falcons on wintering waders on the Banc D'Arguin, Mauritania. Pages 75-82 in *Homeward Bound: Problems Waders Face When Migrating from the Banc D'Arguin, Mauritania, to Their Northern Breeding Grounds in Spring* (B. J. Ens, T. Piersma, W. J. Wolff, and L. Zwarts, eds.). Special edition of *Ardea* 78(1/2).
- Brown, D. R., C. M. Strong, and P. C. Stouffer. 2002. Demographic effects of habitat selection by hermit thrushes wintering in a pine plantation landscape. *Journal of Wildlife Management* 66:407-416.
- Campbell, L. H. 1984. The impact of changes in sewage treatment on seaducks wintering in the Firth of Forth, Scotland. *Biological Conservation* 28:173-180.
- Chesser, R. T., and D. J. Levey. 1998. Austral migrants and the evolution of migration in New World birds: diet, habitat, and migration revisited. *American Naturalist* 152:311-319.
- Clausen, P., J. Madsen, S. M. Percival, D. O'Connor, and G. Q. Anderson. 1998. Population development and changes in winter site use by the Svalbard light-bellied brant goose, *Branta bernicla hrota* 1980-1994. *Biological Conservation* 84:157-165.
- Conway, C. J., G. V. N. Powell, and J. D. Nichols. 1995. Overwinter survival of Neotropical migratory birds in early-successional and mature tropical forests. *Conservation Biology* 9:855-864.
- Cox, G. W. 1985. The evolution of avian migration systems between temperate and tropical regions of the New World. *American Naturalist* 126:451-474.
- Douglas, L. 2002. Impact of human habitat degradation on resident and Neotropical migratory birds occupying the Tropical Dry Forest Life Zone of southern Jamaica. M.S. thesis, University of the West Indies, Mona Campus, Jamaica.
- Dunning, J. B., and J. H. Brown. 1982. Summer rainfall and winter sparrow densities—a test of the food limitation hypothesis. *Auk* 99:123-129.
- Eberhardt, L. L., and J. M. Thomas. 1991. Designing environmental field studies. *Ecological Monographs* 61:53-73.
- Folse, L. J., Jr. 1982. An analysis of avifauna-resource relationships on the Serengeti Plains. *Ecological Monographs* 52: 111-127.
- Frith, D., and C. Frith. 1990. Seasonality of litter invertebrate populations in an Australian upland tropical rain forest. *Biotropica* 22:181-190.
- Gass, C. L., G. Angehr, and J. Centa. 1976. Regulation of food supply by breeding territoriality in the Rufous Hummingbird. *Canadian Journal of Zoology* 54:2046-2054.
- Goss-Custard, J. D. 1970. The response of Redshank (*Tringa totanus* (L.)) to spatial variations in the density of their prey. *Journal of Animal Ecology* 39:91-113.
- Goss-Custard, J. D., R. T. Clarke, K. B. Briggs, B. J. Ens, K.-M. Exo, C. Smit, A. J. Beintema, R. W. G. Caldow, D. C. Catt, N. A. Clark, S. E. A. Le V. dit. Durell, M. P. Harris, J. B. Hulscher, P. L. Meininger, N. Picozzi, R. Prys-Jones, U. N. Safriel, and A. D. West. 1995. Population consequences of winter habitat loss in a migrating shorebird: Pt. 1. Estimating model parameters. *Journal of Applied Ecology* 32:320-336.
- Goss-Custard, J. D., and M. E. Moser. 1988. Rates of change in the numbers of Dunlin wintering in British estuaries in relation to the spread of *Spartina anglica*. *Journal of Applied Ecology* 25:95-109.
- Greenberg, R. 1986. Competition in migrant birds in the non-breeding season. *Current Ornithology* 3:281-307.
- Greenberg, R. 1992. Forest migrants in non-forest habitats on the Yucatan Peninsula. Pages 273-286 in *Ecology and Conservation of Neotropical Migrant Landbirds* (J. M. Hagan III and D. W. Johnston, eds.). Smithsonian Institution Press, Washington, D.C.

- Greenberg, R. 1995. Insectivorous migratory birds in tropical ecosystems: the breeding currency hypothesis. *Journal of Avian Biology* 26:260–264.
- Greenberg, R., P. Bichier, A. Cruz Angon, C. MacVean, R. Perez, and E. Cano. 2000. The impact of avian insectivory on arthropods and leaf damage in some Guatemalan coffee plantations. *Ecology* 81:1750–1755.
- Greenberg, R., C. Macias Caballero, and P. Bichier. 1993. Defense of homopteran honeydew by birds in the Mexican highlands and other warm temperate forests. *Oikos* 68:519–524.
- Greenberg, R., and J. Salgado-Ortiz. 1994. Interspecific defense of pasture trees by wintering Yellow Warblers. *Auk* 111: 672–682.
- Greenberg, R., J. Salgado Ortiz, and C. Macias Caballero. 1994. Aggressive competition for critical resources among migratory birds in the Neotropics. *Bird Conservation International* 4:115–127.
- Hagan, J. M., III, and D. W. Johnston (eds.). 1992. *Ecology and Conservation of Neotropical Migrant Landbirds*. Smithsonian Institution Press, Washington, D.C.
- Hall, L. S., P. R. Krausman, and M. L. Morrison. 1997. The habitat concept and a plea for standard terminology. *Wildlife Society Bulletin* 25:171–182.
- Heinemann, D., G. Hunt, and I. Eversson. 1989. The distribution of marine avian predators and their prey, *Euphausia superba*, in Bransfield Strait, Southern Drake Passage, Antarctica. *Marine Ecology Progress Series* 58:3–16.
- Hobaugh, W. C. 1985. Body condition and nutrition of snow geese wintering in southeastern Texas. *Journal of Wildlife Management* 49:1028–1037.
- Hockey, P. A. R., R. A. Navarro, B. Kalejta, and C. R. Velasquez. 1992. The riddle of the sands: why are shorebird densities so high in southern estuaries? *American Naturalist* 140: 961–979.
- Hubbard, M. W., D. L. Garner, and E. E. Klaas. 1999. Factors influencing Wild Turkey hen survival in south-central Iowa. *Journal Wildlife Management* 63:731–738.
- Hutto, R. L. 1980. Winter habitat distribution of migratory land birds in western Mexico with special reference to small foliage gleaning insectivores. Pages 181–203 in *Migrant Birds in the Neotropics: Ecology, Behavior, Distribution, and Conservation* (A. Keast and E. S. Morton, eds.). Smithsonian Institution Press, Washington, D.C.
- Hutto, R. L. 1990. Measuring the availability of food resources. *Studies in Avian Biology* 13:20–28.
- Jansson, C., J. Ekman, and A. von Brömssen. 1981. Winter mortality and food supply in tits (*Parus* spp.). *Oikos* 37: 313–322.
- Johnson, M. D. 2000. Effects of shade-tree species and crop structure on the winter arthropod and bird communities in a Jamaican shade coffee plantation. *Biotropica* 32:133–145.
- Johnson, M. D., and T. W. Sherry. 2001. Effects of food availability on the distribution of migratory warblers among habitats in Jamaica. *Journal of Animal Ecology* 70:546–560.
- Johnson, M. D., T. W. Sherry, and R. T. Holmes. Manuscript. Measuring habitat quality for a migratory songbird wintering in natural and agricultural habitats. Submitted to *Conservation Biology*.
- Johnson, M. D., T. W. Sherry, A. M. Strong, and A. Medori. In Press. Migrants in Neotropical bird communities: an assessment of the breeding currency hypothesis. *Journal of Animal Ecology*.
- Katti, M., and T. Price. 1996. Effects of climate on Palaearctic warblers over-wintering in India. *Journal of the Bombay Natural History Society* 93:411–427.
- Katti, M., and T. Price. 1999. Annual variation in fat storage by a migrant warbler overwintering in the Indian tropics. *Journal of Animal Ecology* 68:815–823.
- Keast, A., and E. S. Morton, eds. 1980. *Migrant Birds in the Neotropics: Ecology, Behavior, Distribution, and Conservation*. Smithsonian Institution Press, Washington, D.C.
- Lack, D. 1976. *Island Biology: Illustrated by the Land Birds of Jamaica*. University of California Press, Berkeley and Los Angeles.
- Lack, P. R. 1986. Ecological correlates of migrants and residents in a tropical African savanna. *Ardea* 74:111–119.
- Latta, S. C. 2003. Effects of scaley-leg mite infestations on body condition and site fidelity of migratory warblers in the Dominican Republic. *Auk* 120:730–743.
- Latta, S. C., and J. Faaborg. 2001. Winter site fidelity of Prairie Warblers in the Dominican Republic. *Condor* 103:455–468.
- Latta, S. C., and J. Faaborg. 2002. Demographic and population responses of Cape May Warblers wintering in multiple habitats. *Ecology* 83:2502–2515.
- Lefebvre, G., B. Poulin, and R. McNeil. 1994. Temporal dynamics of mangrove bird communities in Venezuela with special reference to migrant warblers. *Auk* 111:405–415.
- Leisler, B. 1990. Selection and use of habitat of wintering migrants. Pages 156–174 in *Bird Migration* (E. Gwinner, ed.). Springer-Verlag, Berlin.
- Levings, S. C. 1983. Seasonal, annual, and among-site variation in the ground ant community of a deciduous tropical forest: some causes of patchy species distributions. *Ecological Monographs* 53:435–455.
- Lovette, I. J., and E. Bermingham. 1999. Explosive speciation in the New World *Dendroica* warblers. *Proceedings of the Royal Society of London, Series B, Biological Sciences* 266:1629–1637.
- Lovette, I. J., and R. T. Holmes. 1995. Foraging behavior of American redstarts in breeding and wintering habitats: implications for relative food availability. *Condor* 97:782–791.
- Malizia, L. R. 2001. Seasonal fluctuations of birds, fruits, and flowers in a subtropical forest of Argentina. *Condor* 103: 45–61.
- Manly, B. F. J. 1992. *The Design and Analysis of Research Studies*. Cambridge University Press, Cambridge.
- Marquis, R. J., and C. J. Whelan. 1994. Insectivorous birds increase growth of white oak through consumption of leaf-chewing insects. *Ecology* 75:2007–2014.
- Marra, P. P. 2000. The role of behavioral dominance in structuring patterns of habitat occupancy in a migrant bird during the nonbreeding season. *Behavioral Ecology* 11:299–308.
- Marra, P. P., K. A. Hobson, and R. T. Holmes. 1998. Linking winter and summer events in a migratory bird by using stable-carbon isotopes. *Science* 282:1884–1886.
- Marra, P. P., and R. L. Holberton. 1998. Corticosterone levels as indicators of habitat quality: effects of habitat segregation in a migratory bird during the non-breeding season. *Oecologia* 116:284–292.
- Marra, P. P., and R. T. Holmes. 2001. Consequences of dominance-mediated habitat segregation in American Redstarts during the nonbreeding season. *Auk* 118:92–104.
- Medori, A. 1998. Seasonal and habitat changes in the diet of a Neotropical migrant warbler, with special emphasis on the

- conservation value of shade coffee plantations. Unpublished undergraduate thesis, Tulane University, New Orleans.
- Miller, M. R., and W. E. Newton. 1999. Population energetics of northern pintails wintering in the Sacramento Valley, California. *Journal of Wildlife Management* 63:1222–1238.
- Mitchell, P. I., I. Scott, and P. R. Evans. 2000. Vulnerability to severe weather and regulation of body mass of Icelandic and British redshank *Tringa totanus*. *Journal of Avian Biology* 31:511–521.
- Møller, A. P., and K. A. Hobson. 2004. Heterogeneity in stable isotope profiles predicts coexistence of two populations of barn swallows *Hirundo rustica* differing in morphology and reproductive performance. *Proceedings of the Royal Society of London, Series B, Biological Sciences* 271:1355–1362.
- Moreau, R. E. 1972. The Palearctic-African Bird Migration Systems. Academic Press, San Diego.
- Morse, D. H. 1980. Population limitation: breeding or wintering grounds? Pages 505–516 in *Migrant Birds in the Neotropics: Ecology, Behavior, Distribution, and Conservation* (A. Keast and E. S. Morton, eds.). Smithsonian Institution Press, Washington, D.C.
- Morton, E. S. 1980. Adaptations to seasonal changes by migrant land birds in the Panama Canal zone. Pages 437–453 in *Migrant Birds in the Neotropics: Ecology, Behavior, Distribution, and Conservation* (A. Keast and E. S. Morton, eds.). Smithsonian Institution Press, Washington, D.C.
- Nariko, O., M. Yamamuro, J. Hiratsuka, and H. Satoh. 1999. Habitat selection by wintering tufted ducks with special reference to their digestive organ and to possible segregation between neighboring populations. *Ecological Research* 14:303–315.
- Newton, I. 1998. *Population Limitation in Birds*. Academic Press, San Diego.
- Norris, D. R., P. P. Marra, T. K. Kyser, T. W. Sherry, and L. M. Ratcliffe. 2004. Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. *Proceedings of the Royal Society of London, Series B, Biological Sciences* 271:59–64.
- Parrish, J. D., and T. W. Sherry. 1994. Sexual habitat segregation by American Redstarts wintering in Jamaica: importance of resource seasonality. *Auk* 111:38–49.
- Peach, W. J., S. R. Baillie, and L. Underhill. 1991. Survival of sedge Warblers *Acrocephalus schoenobaenus* in relation to west African rainfall. *Ibis* 133:300–305.
- Pearson, D. L., and J. A. Derr. 1986. Seasonal patterns of lowland forest floor arthropod abundance in southeastern Peru. *Biotropica* 18:244–256.
- Perez-Tris, J., and J. L. Telleria. 2002. Migratory and sedentary blackcaps in sympatric non-breeding grounds: implications for the evolution of avian migration. *Journal of Animal Ecology* 71:211–224.
- Petit, D. R., J. F. Lynch, R. L. Hutto, J. G. Blake, and R. B. Waide. 1995. Habitat use and conservation in the Neotropics. Pages 145–197 in *Ecology and Management of Neotropical Migrant Birds: A Synthesis and Review of Critical Issues* (T. E. Martin and D. M. Finch, eds.). Oxford University Press, New York.
- Poulin, B., and G. Lefebvre. 1996. Dietary relationships of migrant and resident birds from a humid forest in central Panama. *Auk* 113:277–287.
- Poulin, B., G. Lefebvre, and R. McNeil. 1992. Tropical avian phenology in relation to abundance and exploitation of food resources. *Ecology* 73:2295–2309.
- Pulliam, H. R., and T. A. Parker. 1979. Population regulation of sparrows. *Fortschritte der Zoologie* 25:137–147.
- Rappole, J. H., and M. V. McDonald. 1994. Cause and effect in population declines of migratory birds. *Auk* 111:652–660.
- Rappole, J. H., M. A. Ramos, and K. Winker. 1989. Wintering Wood Thrush movements and mortality in southern Veracruz. *Auk* 106:402–410.
- Rappole, J. H., and D. W. Warner. 1980. Ecological aspects of migrant bird behavior in Veracruz, Mexico. Pages 353–393 in *Migrant Birds in the Neotropics: Ecology, Behavior, Distribution, and Conservation* (A. Keast and E. S. Morton, eds.). Smithsonian Institution Press, Washington, D.C.
- Robinson, S. K., F. R. Thompson III, T. M. Donovan, D. R. Whitehead, and J. Faaborg. 1995. Regional forest fragmentation and the nesting success of migratory songbirds. *Science* 267:1987–1990.
- Rödl, T. 1999. Environmental factors determine numbers of overwintering European stonechats *Saxicola rubicola*—a long-term study. *Ardea* 87:247–259.
- Saino, N., T. Szép, R. Ambrosini, M. Romano, and A. P. Møller. 2004. Ecological conditions during winter affect sexual selection and breeding in a migratory bird. *Proceedings of the Royal Society of London, Series B, Biological Sciences* 271:681–686.
- Sherry, T. W. 1984. Comparative dietary ecology of sympatric, insectivorous Neotropical flycatchers (Tyrannidae). *Ecological Monographs* 54:313–338.
- Sherry, T. W., and R. T. Holmes. 1995. Summer versus winter limitation of populations: issues and the evidence. Pages 85–120 in *Ecology and Management of Neotropical Migrant Birds* (T. M. Martin and D. Finch, eds.). Oxford University Press, Oxford.
- Sherry, T. W., and R. T. Holmes. 1996. Winter habitat limitation in Neotropical-Nearctic migrant birds: implications for population dynamics and conservation. *Ecology* 77:36–48.
- Sillett, T. S., and R. T. Holmes. 2002. Variation in survivorship of a migratory songbird throughout its annual cycle. *Journal of Animal Ecology* 71:296–308.
- Sillett, T. S., R. T. Holmes, and T. W. Sherry. 2000. The El Niño Southern Oscillation impacts population dynamics of a migratory songbird throughout its annual cycle. *Science* 288:2040–2042.
- Sinclair, A. R. E. 1978. Factors affecting the food supply and breeding season of resident birds and movements of Palearctic migrants in a tropical African savannah. *Ibis* 120:480–497.
- Smith, J. N. M., R. D. Montgomerie, M. J. Taitt, and Y. Yom-Tov. 1980. A winter feeding experiment on an island Song Sparrow population. *Oecologia* 47:164–170.
- Strong, A. M. 1999. Effects of prey abundance on winter habitat quality for two species of ground-foraging Neotropical migrant warblers. Ph.D. dissertation, Tulane University, New Orleans.
- Strong, A. M. 2000. Divergent foraging strategies of two Neotropical migrant warblers: implications for winter habitat use. *Auk* 117:381–392.
- Strong, A. M., and T. W. Sherry. 2000. Habitat-specific effects of food abundance on the condition of ovenbirds wintering in Jamaica. *Journal of Animal Ecology* 69:883–895.

- Strong, A. M., and T. W. Sherry. 2001. Body condition of Swainson's Warblers wintering in Jamaica, with emphasis on the conservation value of Caribbean dry forests. *Wilson Bulletin* 113:410–418.
- Strong, A. M., T. W. Sherry, and R. T. Holmes. 2000. Bird predation on herbivorous insects: indirect effects on sugar maple saplings. *Oecologia* 125:370–379.
- Terborgh, J. 1989. *Where Have All the Birds Gone?* Princeton University Press, Princeton.
- Tsipoura, N., and J. Burger. 1999. Shorebird diet during spring migration stopover on Delaware Bay. *Condor* 101:635–644.
- Van Bael, S. A., J. D. Brawn, and S. K. Robinson. 2003. Birds defend trees from herbivores in a Neotropical forest canopy. *Proceedings of the National Academy of Sciences USA* 100:8304–8307.
- Veit, R. R., E. D. Silverman, and I. Everson. 1993. Aggregation patterns of pelagic predators and their principal prey, Antarctic krill, near South Georgia. *Journal of Animal Ecology* 62:551–564.
- Watson, A., and P. J. O'Hare. 1979. Red grouse populations on experimentally treated and untreated Irish bog. *Journal of Applied Ecology* 16:433–452.
- Webster, M. S., P. P. Marra, S. M. Haig, S. Bensch, and R. T. Holmes. 2002. Links between worlds: unraveling migratory connectivity. *Trends in Ecology and Evolution* 17:76–83.
- Wiklund, C. G. 2001. Food as a mechanism of density-dependent regulation of breeding numbers in the merlin, *Falco columbarius*. *Ecology* 82:860–867.
- Willis, E. O. 1966. The role of migrant birds at swarms of army ants. *Living Bird* 5:187–231.
- Wolda, H. 1978. Seasonal fluctuations in rainfall, food and abundance of tropical insects. *Journal of Animal Ecology* 47:369–381.
- Wolf, W. J., and C. J. Smit. 1990. The Banc d'Arguin, Mauritania, as an environment for coastal birds. Pages 17–37 in *Homeward Bound: Problems Waders Face When Migrating from the Banc D'Arguin, Mauritania, to Their Northern Breeding Grounds in Spring* (B. J. Ens, T. Piersma, W. J. Wolff, and L. Zwarts, eds.). Special edition of *Ardea* 78(1/2).
- Wood, B. 1979. Changes in numbers of overwintering Yellow Wagtails and their food supplies in a west Africa savannah. *Ibis* 121:228–231.
- Wormington, A., and J. H. Leach. 1992. Concentrations of migrant Diving Ducks at Point Pelee National Park, Ontario, in response to invasion of Zebra Mussels, *Dreissena polymorpha*. *Canadian Field Naturalist* 106:376–380.
- Wunderle, J. M., Jr., and S. C. Latta. 1998. Avian resource use in Dominican shade coffee plantations. *Wilson Bulletin* 110:255–265.
- Wunderle, J. M., Jr., and S. C. Latta. 2000. Winter site fidelity of Nearctic migrants in shade coffee plantations of different sizes in the Dominican Republic. *Auk* 117:596–614.
- Yates, M. G., J. D. Goss-Custard, S. McGrorty, K. H. Lakhani, S. E. A. Le V. dit Durell, R. T. Clarke, W. E. Rispin, I. Moy, T. Yates, R. A. Plant, and A. J. Frost. 1993. Sediment characteristics, invertebrate densities and shorebird densities on the inner banks of the Wash. *Journal of Applied Ecology* 30:599–614.
- Zumeta, D., and R. T. Holmes. 1978. Habitat shift and roadside mortality of Scarlet Tanagers during a cold, wet New England spring. *Wilson Bulletin* 90:575–586.
- Zwarts, L., A.-M. Blomert, B. J. Ens, R. Hupkes, and T. M. van Spanje. 1990. Why do waders reach high feeding densities on the intertidal flats of the Banc d'Arguin, Mauritania? Pages 39–52 in *Homeward Bound: Problems Waders Face When Migrating from the Banc D'Arguin, Mauritania, to Their Northern Breeding Grounds in Spring* (B. J. Ens, T. Piersma, W. J. Wolff, and L. Zwarts, eds.). Special edition of *Ardea* 78(1/2).