

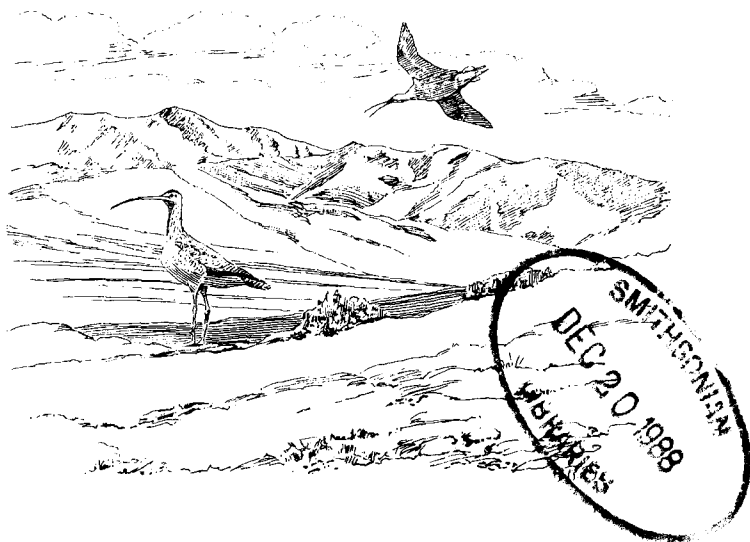
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CHAPTER 6

COMPETITION IN MIGRANT BIRDS IN THE NONBREEDING SEASON

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1. INTRODUCTION

Although it is widely recognized that migration is an adaptation that allows bird populations to exploit seasonal resources, the factors that underly the rich diversity of migration patterns is an area of active research. Predictably, the focus of much of the theory and most of the field work on migration has been the role of competition in shaping the timing and distribution of migration movements. In this review I will examine the theory and evidence for how competition affects the distribution and abundance of migrant birds during the nonbreeding season. I will focus the discussion on migrants that move from high to tropical latitudes, a distribution pattern that probably includes most of the migratory species. In the interest of economy of space, I will examine competition among and within migrant species and leave the overwhelming task of analyzing resident–migrant interactions to future reviewers.

The study of migrant birds in the nonbreeding season is a relatively recent endeavor. In the tropics, we have benefited from some pioneer studies and commentaries from veteran researchers (Eaton, 1953; Skutch, 1957; Bond, 1957; Miller, 1963; Willis, 1966; Brosset, 1968; Moreau, 1972). However, most research designed specifically to investigate mi-

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grant bird behavior has been conducted since 1970 (see papers in Keast and Morton, 1980). The youth of the study of migrant birds has profoundly affected the pattern of its development. Unlike the studies of temperate zone birds, which entered a more evolutionarily oriented phase in the 1950s and 1960s after a long period of basic natural history work, the explosion of interest in tropical migrant birds has occurred concurrently with the development of modern theoretical ecology. In fact, both Lack (1941, 1944) and MacArthur (1958, 1972) were early contributors to ideas concerning the evolution and ecology of migration systems. Because of this, little background information existed before questions of theoretical importance were addressed in the studies of tropical migrant birds in the nonbreeding season. We can therefore ask what influence has this sharp focus on community ecology and competitive interactions had on our understanding of migrant biology. Recent critiques of the empirical support for the efficacy of competition in bird communities in general (Wiens, 1983) also compel us to critically examine the evidence for competition among nonbreeding migrants.

1.1. Competition: Operational Definition

Competition is usually expressed as the reduction in fitness experienced by an individual in the presence of another individual (whether or not it is a conspecific). The ultimate effect of a particular interaction is difficult to measure in migrants since their movements bring them into different populations and communities throughout the year. Survivorship is the primary demographic feature that determines variation in fitness during the nonbreeding season. Competition in migrant birds can also influence the "decision" of where to spend the nonbreeding season to avoid the expected negative effects of potential competitors. As there are more data on distribution patterns than on the demography of migrants, the focus of most studies of competition has been on the potential geographic effects of intraspecific or interspecific competition. The focus of this review concerns the evidence on competition that is derived from the study of community or population composition and its inverse: geographic and habitat displacement of conspecifics or closely-related species.

1.2. The Role of Competition in Theories about Migratory Bird Distribution

A review of migration theory reveals an increasing emphasis on evolutionary arguments and the analysis of life history (Gauthreaux,

1982; Ketterson and Nolan, 1983). Gauthreaux (1982), for example, divided migration theories into those prior to the 1930s and 1940s, and those more evolutionarily oriented theories beginning in this period. Concomitant with the application of population biology principles to migration was the increased emphasis on competitive processes in the evolution of migration systems.

It has often been suggested that competition has been assigned an important primary role in the evolution of migration. Most of the arguments, however, even the influential model of Cox (1968), presuppose an increase in seasonality as the ultimate environmental force. Since the major temperate zone land masses experienced increased seasonality during the past 60 million years, it appears to be a likely force shaping the development of the major migration systems we see today.

Lack (1968) argued that movements allowed birds to spread out during the nonbreeding season to reduce the effects of competition. He also reasoned that the nonbreeding season represents a period of food shortage for many migrants, and as a result, less competition can be ameliorated through resource partitioning within a community. This basic view, that competition for food is particularly important during the nonbreeding season, has gained wide acceptance among students of migration (Pulliam and Parker, 1979; Fretwell, 1980; Gauthreaux, 1982; Ketterson and Nolan, 1983). Competition has two potential roles in affecting nonbreeding distributions: intraspecific competition will spread out species populations, and interspecific competition will restrict them with respect to potential competitors.

Salomonsen (1955) had earlier developed the idea that competition is important in shaping nonbreeding distributions. He used this concept to argue for the importance of winter isolation in the evolutionary divergence of populations of migrant birds.

Migratory behavior and the competition theories of community structure were first formally linked in a seminal paper by Cox (1968). He argued that competition was critical in shaping interspecific isolation of winter ranges. Since migrants separate geographically during the period of winter food shortage, more ecologically similar species can cooccur in breeding communities. This model has had much more influence on thinking about migration systems than on the equally relevant area of bird community ecology. The relationship between migration and bird species diversity has been explored recently by workers on tropical nectarivore communities (Colwell, 1973; Feinsinger, 1980). Feinsinger argued that movements to alternative habitats during resource-poor periods allows the larger island of Trinidad to support more hummingbird species than Tobago.

The most recent models of migration that incorporate competition have emphasized the role of social dominance (Fretwell, 1972, 1980; Gauthreaux, 1978, 1982). These theories focus on the problem of partial migration and similar migration patterns and suggest that either dominant individuals can secure enough resources to overwinter in seasonal habitats and thereby avoid migration mortality or dominant individuals overwinter to secure resources for breeding. These models are most readily applied to single species migration patterns but could be extended to interspecific differences in migration where behavioral competition for resources is important (e.g., Fretwell, 1980; Pulliam, 1983). They do not consider the effects of exploitation competition, which is at least of potential importance between demographic classes and species.

2. INTRASPECIFIC COMPETITION

2.1. Dominance

Direct behavioral competition has been implicated as being critical in determining which birds migrate and how far (Fretwell, 1972, 1980; Gauthreaux, 1982). While dominance hierarchies have been the subject of much study in birds, they can be shown to have ecological significance only when some aspect of the subordinate's biology that influences fitness has been adversely affected relative to dominants. Such factors include physical condition, the probability of survival, or the frequency of emigration from a more favorable area. The forced movement to more distant nonbreeding areas or to poorer habitats can only be linked to dominance by indirect reference, since the dominance status of a particular bird can only be expressed in the presence of other birds (Ketterson and Nolan, 1983). Dominance is often correlated with social asymmetries, such as age or sex of individuals (see Gauthreaux, 1982, for review), and the rank of an age or sex class can be compared with its geographical distribution. The relative dominance status of these demographic classes can be determined in areas where they co-occur (for social species) or by conducting removal experiments.

Dominance systems in otherwise social birds have been studied extensively in a few bird species (notably the Dark-eyed Junco, *Junco hyemalis*). There is almost no information on the role of dominance in the gregarious species of neotropical migrants. Supplantings and chases are often common in these species (personal observations) but few studies have individually marked birds. Of greater difficulty, many of these gregarious species, such as the Tennessee Warbler (*Vermivora*

peregrina) and the Eastern Kingbird (*Tyrannus tyrannus*) are quite mobile, if not nomadic, in the course of a winter (personal observations; Morton, 1971, 1980). For migrant shorebirds, Myers and McCaffrey (1984) report seeing higher levels of aggression in a number of species wintering in coastal Peru, but this preliminary study established no consistent dominance relationships between demographic classes. Aggression, however, short of demonstrable dominance hierarchies, was shown to confer some competitive advantage to some shorebirds wintering in Great Britain (Goss-Custard et al., 1982).

Results from studies on Dark-eyed Juncos have at least occasionally argued against any ecological effects: Sabine (1959) could not detect any reduction in feeding efficiency in subordinates, and Ketterson and Nolan (1982) did not detect any reduction in survivorship in subordinates during the most severe period of the winter. Ketterson and Nolan (1976a) and Fretwell (1969) reported that members of subordinate classes had reduced fat deposits, and Baker and Fox (1978) found that subordinates tended to be in poorer condition (although this may be an artifact of their classification system, according to Ketterson and Nolan [1983]). Given the difficulty of demonstrating an ecological effect of dominance systems in a bird facing dwindling nonrenewable resources under severe climatic conditions, it may be nearly impossible to detect such effects in insectivorous and frugivorous tropical species.

The second question is to what degree dominance systems within flocks regulate the habitat and geographic distribution of various demographic classes. Removal studies of gregarious sparrows (*Zonotrichia*, Mewaldt, 1964; *Junco*, Davis, 1973) suggest that flock size and composition may be socially regulated. Ketterson and Nolan (1983), however, argue that even if dominance systems affect the distribution of wintering birds, which class of birds is forced to emigrate is not intuitively obvious. Birds of intermediate rank may suffer greater harassment and be forced to move further than subordinates. Further, the prediction that subordinates should migrate further should only hold under conditions that the competition-free quality of the more distant wintering range is not more favorable than the more proximate areas. Dominants should gain access to the best, not necessarily the closest areas.

2.2. Territoriality

Territoriality or the aggressive defense of an area or resource is *prima facie* evidence for competition in migrant birds (MacArthur, 1972; Myers and McCaffrey, 1984; Rappole and Warner, 1980; Morton,

1980). Territorial systems have only recently been detected in wintering migrants; they were first described as anomalous behavior (Hamilton, 1959; Emlen, 1973) and more recently as an adaptive strategy (Myers et al., 1979a,b; Rappole and Warner, 1976, 1980; Mallory, 1981; Greenberg, 1984). Territoriality, however, appears to be quite common, probably occurring in a majority of neotropical migrant passerines (Rappole and Warner, 1980; Greenberg, 1985) and a number of shorebirds (Myers et al., 1979a).

Territorial systems are unified by the aggressive defense of a specific place. However, such systems can vary considerably in the type of resource defended, the range of species excluded, and the duration of the defense. In many migrant passerines, most individuals defend large, stable territories throughout the nonbreeding season, whereas in other species only a fraction of the individuals defend territories, and these are ephemeral (days or weeks) and associated with a specific localized resource.

Short-term site defense has been reported commonly in hummingbirds, shorebirds, and passerines that forage commonly on fruit or nectar (Kodric-Brown and Brown, 1978; Gass, 1979; Myers et al., 1979a; Tramer and Kemp, 1981; Morton, 1980). In shorebirds and passerines, territoriality often appears in species that are otherwise intraspecifically gregarious. Variation in social behavior has been related to the distribution of food for the individuals in question. For example, nectarivorous passerines (warblers and orioles) are more commonly observed in active territorial defense, and, within nectarivorous migrants, those feeding on discrete and productive flowers are more often territorial than those visiting mass floral displays. In Panama, Tennessee Warblers defend *Combretum* vines but are found in flowering *Trichospermum* trees in large flocks (Morton, 1980; personal observations). The resource defended need not be a nectar source; migrant warblers have been observed to defend localized sources of insects (e.g., ultraviolet lights) and fruiting trees (Morton, 1980; Greenberg, 1984).

It is tempting to suggest that the incidence of nonbreeding territoriality has a predictable economic basis (Brown, 1964; Gill and Wolf, 1975; Myers et al., 1979b). Few quantitative studies on the economics of territoriality in migrant birds have been conducted but they have shown that defense occurs only within certain predictable limits of resource abundance (Myers et al., 1979b; Gass, 1979; Kodric-Brown and Brown, 1981). In addition, these studies have established a strong negative correlation between food supply and intruder density and size of area defended. Zahavi (1971) was able to experimentally change social behavior of wintering White Wagtails (*Motacilla alba*) from gre-

gamous to territorial by manipulating the distribution of provisioned food on a field. An alternative hypothesis, that the territorial behavior of these birds is a nonadaptive carryover from behaviors selected for in other seasons (Hamilton, 1959; Emlen, 1973), loses some credibility since the defense often occurs in females and immatures (Myers *et al.*, 1979a). In Cape May Warblers (*Dendroica tigrina*), for example, the female is particularly aggressive and can exclude males from flowering plants (A. de Dod, personal communication).

The importance of long-term territorial defense of a habitat patch has taken longer for ornithologists to recognize. One of the earliest studies of such behavior was made for Northern Waterthrushes (*Seiurus noveboracensis*) wintering in Venezuela (Schwartz, 1964). Descriptions of the behavior of Kentucky Warblers (*Oporornis formosus*) on Barro Colorado Island, Panama, certainly suggested regular spacing of individuals by means of advertisement and aggression (Willis, 1966); the focus of Willis' studies, however, was on the opportunistic visitation to army ant swarms by migrants. Karr (1971) also reported long-term site tenacity of an individual Kentucky Warbler in a Panamanian forest. While a number of studies found high site tenacity of some neotropical bird species, it probably was not until the studies of Rappole and Warner (1980), using color-marked birds and various experimental procedures, that the preeminence of long-term territoriality was recognized for tropical forest wintering migrants.

Students of migratory bird ecology now face the seemingly intractable task of determining the importance of these territorial systems to population regulation. In addition, the factors underlying the decision of where and how big an area should be to defend do not seem to be readily inferable from studies of the economics of short-term territories.

Tropical habitats are usually distinctly seasonal during the period of occupation by migrant birds (Morton, 1980; Hespenheide, 1980; Greenberg, 1984). In addition, recent monitoring studies indicate that some tropical forests can vary considerably from year to year in rainfall and insect abundance, as well as flower and fruit abundance and phenology (Wolda, 1978; Foster, 1980). Any species' long-term territorial strategy must be viewed in terms of both predictable and unpredictable annual change. If direct cues indicating food abundance in the coming dry season are unavailable at the time of territorial establishment in the fall, then a migrant can affect its survivorship by using indirect cues or exercising a "conservative" territorial selection criterion, that is, defending an area and location that will provide sufficient resources for most years. Chestnut-sided Warblers (*D. pensylvanica*) on Barro Colorado Island, for example, defend territories that coincide with ex-

isting antwren territories (Greenberg, 1984). By defending an area occupied by resident foliage-gleaning birds, the warblers are more certain to occupy an area that is not seasonally unproductive, a problem that faces migrants wintering on the Isthmus of Panama (Morton, 1980). Morton (1980) suggested that many migrants exercise a fundamentally conservative strategy of defending territories in mesic sites, locations unlikely to dry out during the long Panamanian dry season.

The nature of competition over territories has also not been well established. Actual territorial disputes are often difficult to observe, particularly in small passerines living in dense tropical vegetation. Furthermore, few studies have focused on the early winter period of territorial establishment (but see Nisbet and Medway, 1972; Rappole and Warner, 1980; Price, 1981). Few studies have monitored marked or recognizable birds over entire winters (Schwartz, 1964; Myers *et al.*, 1979b; Rappole and Warner, 1980; Greenberg, 1984); only one study that I know of has removed territorial birds (Rappole and Warner, 1980); and only studies of migrant hummingbirds have used supplemented food or altered habitats (Gass, 1979; Kodric-Brown and Brown, 1978). Most importantly, no studies have monitored survivorship in relation to territorial status or habitat occupied.

The measurable effects of a territorial system will depend on the type (especially the duration) of the territorial system. For territories held at ephemeral resources or during periods of actual migration, we might expect to detect differences in weight gain between territorial and nonterritorial birds; this was demonstrated for migrating waterthrushes (Rappole and Warner, 1976). Carpenter *et al.* (1983) argued that migratory hummingbirds adjusted their territorial behavior to increase their rate of weight gain. Long-term territoriality might additionally result in differences in survivorship across habitats (Fretwell, 1972) or between territorial and nonterritorial birds. So far, few studies have attempted to study the demographic consequences of different territorial strategies.

2.3. Age- and Sex-Related Geographic Separation

Age and sex classes within a species often winter in areas that differ in habitat quality or in proximity to the breeding grounds. Such patterns (for reviews see Myers, 1981b; Gauthreaux, 1982; Ketterson and Nolan, 1983) are sometimes considered evidence for the role of intraspecific competition since it is assumed that morphology and be-

havior of conspecifics, even those in different demographic classes, are usually sufficiently similar to reduce the possibility that winter range differences relate to intrinsic biology. In addition, asymmetries in dominance are often detectable along sex and age lines. Furthermore, certain generalities in the distribution of age and sex classes are at least consistent with models involving intraspecific competition. For example, young-of-the-year and females often migrate further than adults and males (Gauthreaux, 1982), a pattern often consistent with relative social dominance. Even these generalities however, have been questioned (Ketterson and Nolan, 1982, 1983).

Among tropical migrants, such patterns of age and sex separation are poorly known. Pearson (1980) noted a possible latitudinal gradient in the relative abundance of adult male Summer Tanagers (*Piranga rubra*) between Central and South America and attributed this to adults or males wintering further north than other Summer Tanagers. This is the only proposed case that I know of for a Neotropical landbird migrant. In several species of calidridine sandpiper, however, males winter further north (on the average) than females (see references in Myers, 1981b). As I will discuss in Section 2.4, competition is not the only factor that could explain latitudinal differences in winter distribution (Myers, 1981b; Ketterson and Nolan, 1983).

Any pattern of geographic displacement along a latitudinal transect could probably be explained either by competition or differences in other life history parameters of the sex and age classes. Males, for example, might benefit from wintering closer to the breeding grounds by gaining access to territories earlier in the spring (Ketterson and Nolan, 1976b; Myers, 1981b). Age and sex classes that occur sympatrically but in different habitats could provide a clearer potential example of competition-induced winter displacement since access to breeding grounds would not differ. Unfortunately, few examples of such intersexual habitat segregation have been documented for migrants. Male and female Great Reed Warblers (*Acrocephalus orientalis*) occur in different habitats where they winter in Malaysia (Nisbet and Medway, 1972). Females occur more frequently in *Phragmites* swamps (similar to breeding habitat) and males tend to occur in a variety of scrub habitats (Nisbet and Medway, 1972). The authors suggest two possible explanations for this pattern. Competition between the sexes could be minimized; such a system could be maintained either through innate differences in habitat selection or enforced by male dominance over females during the establishment of winter residency. On the other hand, smaller females may be better adapted to foraging in swamp

vegetation than the larger males. Differences in size may be a result of sexual selection, which, as an evolutionary by-product, influences the displacement of males and females.

In the New World, only the Hooded Warbler (*Wilsonia citrina*) has so far been shown to have habitat separation of the sexes during the winter (Rappole and Warner, 1980; Lynch *et al.*, 1985). Males tend to occur in more mature forest and females are restricted to secondary scrub habitats. The mechanism accounting for this difference—aggressive exclusion or intrinsic differences in habitat preference—needs to be determined.

Most migrant species (excluding waterfowl) maintain no social bonds throughout both the breeding and nonbreeding seasons. Therefore, natural selection can favor the competitive dominance of individuals of one sex over all individuals of the other. If this dominance were severe enough, such as might occur in species with extreme sexual dimorphism, then it is conceivable that such intersexual competition could significantly reduce survival fitness of a large fraction of the species. It should be noted that some migrant species have been found to maintain male–female pairs during the nonbreeding season, and some of these species occur in pairs during migration as well (Zahavi, 1971; Leck, 1972; Morton, 1980; Greenberg and Gradwohl, 1980; Greenberg, 1985). It is not known whether this reflects permanent monogamy in these species or temporary winter consortships. The adaptive significance of these pairs is also unknown.

2.4. Latitudinal Separation of and Leap-Frog Migration between Geographic Races and Closely Related Species

In some species (and species groups) northern breeding forms migrate to and spend the winter in areas further south than more southerly breeding forms. This pattern, termed leap-frog migration, has been presented as a prime example of the influence of competition on migration systems (see Welty's, 1982, treatment of Swarth, 1920, on Fox Sparrows, *Passerella iliaca*). Other patterns of migration involving multiple geographic races have been enumerated by Salomonsen (1955), but it is the leap-frog migration pattern, that on the face of it, would argue most strongly for competition. This is because, intuitively, there should be a clear-cut cost associated with northerly birds overflying the winter ranges of more southerly breeders. The compensatory factor would be the reduction of competition that would be experienced by birds were they to winter in habitats already occupied. In addition, the northern

birds might migrate later and thus be subordinate to the southern breeders in the scramble for winter resources.

Leap-frog migrations are well documented in some taxonomic groups (Swarth, 1920; Stresemann, 1934; Salomonsen, 1955), although it appears to be relatively rare in its pure form (Salomonsen, 1955). Since most tropical migrant passerines and shorebirds have few geographic races, it has been frequently difficult to detect in tropical migrants. Most of the polytypic species, however, show great overlap in winter race distribution (for example, *Dendroica petechia* and *Vermivora celata*, American Ornithologists' Union, 1957; also see, Ramos and Warner, 1980). Leap-frog migration patterns probably do not involve highly discrete winter race distributions, but shifts in relative abundances with latitude; this sort of relative abundance data for different subspecies is generally not available, but badly needed.

Little direct evidence is available for the role of competition in shaping leap-frog migration patterns. We should find that individuals of southerly breeding races that arrive on the winter range earlier are in some way competitively dominant to northern birds. If this were not the case, northern races would rapidly evolve less lengthy and costly migrations. To my knowledge, this has not been examined in any of the classic cases of leap-frog migration. Morton (1976), however, suggested that members of northerly breeding subspecies of Yellow Warblers arrived in Panama later and were excluded from territories by members of southern subspecies.

As in other forms of latitudinal separation, the leap-frog distribution pattern can support other viable explanations based on considerations of other aspects of the life history of geographic races. For example, I elaborated a model whereby tradeoffs in time spent on breeding and nonbreeding ranges could determine migration distances independently of competitive effects (Greenberg, 1980). Northerly populations have more "nonbreeding" time available and can therefore compensate a greater migration mortality risk with increased winter survivorship.

Still other explanations excluding competition have been recently put forth. Alerstram and Hogstedt (1980), for example, suggested that northern breeding areas are more climatically predictable (at least for the timing of the onset of spring) than southern areas. Birds attempting to occupy territories as early as possible require less climatic information on breeding ground conditions and therefore can winter further south. Slagsvold (1982) demonstrated that the onset of spring was, if anything, less predictable further north. He argued that birds breeding further north are more sensitive to the risk of severe weather during

early arrivals and southern breeders are more vulnerable to competition and predation during later arrivals and nesting.

A fascinating example of how life history strategy and migration systems might interact was presented by Myers (1981a) for calidridine sandpipers. In this group, migration distance is correlated with mating and parental care systems. Longer-distance migrants tend to have non-monogamous mating systems and single-parent care. Species employing these more opportunistic breeding systems can probably spend less time on the breeding grounds and can afford longer migrations; this can result from a longer tenure on the nonbreeding range or the avoidance of poor fall migratory conditions (Myers, 1981a). This correlation does not clarify whether migration distance or breeding behavior is the prime mover in the evolution of this pattern. Competition could, therefore, still be important in shaping the system. It does alert us to the possibility that other aspects of the species' biology may well influence migration patterns.

While competition has always been a favored theory to explain geographic separation, particularly leap-frog migration, the number of alternative explanations having to do with factors intrinsic to different populations or species will doubtless increase. Unfortunately, the alternative explanations are rarely tested for their efficacy in explaining particular migration systems. If they were, it is unclear what observations would distinguish the different hypotheses. Ketterson and Nolan (1983) argued that several factors are probably shaping migration patterns simultaneously, so that a search for a unitary cause is unrealistic. Still, the recognition of the possibly complex sources of selection should not prevent us from attempting to evaluate the role of particular factors.

The theoretical work on habitat distribution of birds by Fretwell and Lucas (1970) may begin to provide the basis for evaluating the role of behavioral competition in shaping winter distributions. As suggested by Greenberg (1980) and Ketterson and Nolan (1983), competition should produce a pattern of equal survivorship along a latitudinal gradient. This distribution would correspond to the "ideal free distribution" of Fretwell and Lucas; the distribution results when habitat quality varies both intrinsically and with the density of occupants. Individuals will distribute themselves between habitats to equalize fitness. In migrant birds, for example, an individual might increase its expected mortality from increased migration distance until it balances the expected decrease in survivorship associated with crowded conditions close to the breeding range. Of course, in the real world, many factors other than proximity to breeding range could affect the intrinsic quality of a winter habitat. In the absence of dominance, birds should still distribute them-

selves so that the average survivorship between locations is equal. Pulliam and Parker (1979) have argued that sparrows may actually assess the food abundance and amount of aggression encountered as rules of thumb to determine how far to migrate before settling.

Conformance to an ideal free distribution would tend to argue against the importance of other demographic tradeoffs in determining migration distance, such as those suggested by Von Haartmann (1968) or Greenberg (1980), since in these models different populations should be increasing reproduction at the cost of survivorship and thus should produce a gradient in winter survivorship. Unfortunately, testing for competition using this distribution will place the worker in the uncomfortable position of supporting and not rejecting a null hypothesis; i.e., at what point can we declare that the correlation between survivorship and latitude is zero and hence competition is important? Conversely, in situations where different populations show significant differences in survivorship it may not be easy to distinguish whether competition mediated by dominance is occurring or variations in tradeoff between reproduction and survival are driving the system.

The only data pertaining to gradients in survivorship once again come from the temperate zone migrant, the Dark-eyed Junco (Ketterson and Nolan, 1982, 1983). Since the source of the wintering birds is unknown, it cannot be determined whether we are dealing with a leap-frog migration pattern. Nonetheless, it will give us an idea of what the data from leap-frog migrants might look like, if and when they are gathered. Based on U.S. Fish and Wildlife Service data and their own banding program, Ketterson and Nolan suggested that the survivorship of juncos does not vary significantly between the sexes or within one sex on the basis of latitude. Since overwinter survivorship is higher in more southerly wintering populations, they concluded that the increased cost of migration balances the increase in expected overwinter survivorship. If this result can be generalized, it suggests that competition is important. If competition were not important, then we would have to posit that the gradient of increased expected survivorship with latitude is precisely correlated with the gradient of increased migration-related mortality.

We lack information on the distribution patterns of sex and age classes and different breeding populations of most migrant birds, and so we need more descriptive biogeographic work. It should be clear, however, that continued cataloging of nonbreeding isolation between sex and age classes and subspecies will not alone determine the importance of competition within species of migrant birds. The detailed work on juncos and other temperate zone migrants suggests ways that

life history competition can be studied based on combining distributional and demographic data. Similar studies focusing on particular tropical species would complement the temperate studies.

3. INTERSPECIFIC COMPETITION

3.1. Dominance and Interspecific Territoriality

The frequency and significance of interspecific aggression is poorly documented for Neotropical migrant birds. Interspecific territoriality has been described in several published notes (e.g., Kale, 1967; Emlen, 1973; Tramer and Kemp, 1981); however, these have nearly always involved short-term defense of a specific food resource. Myers and McCaffrey (1984) found evidence of interspecific territoriality among several shorebird species in Peru, but the duration of the phenomena deserves further study.

Long-term territorial defense between migrant species has rarely been reported. Leck (1972) suggested that the two species of waterthrushes defend intra- and interspecific territories at ecotones between the fast-moving rocky streams preferred by Louisiana Waterthrushes (*Seiurus motacilla*) smaller and slower streams occupied by Northern Waterthrushes (*Seiurus noveboracensis*). This presumed interaction requires more documentation. While it is possible that other species of tropical migrants, such as in *Empidonax*, may defend interspecific territories at areas of habitat and range overlap, interspecific territoriality is unimportant in the winter distribution of migrant birds.

The role of interspecific aggression, short of exclusive territoriality, is even less clear. Aggression between species of migrants can be consistent, so that interspecific dominance hierarchies can be determined (for example, see Greenberg, 1984). Aggressive acts usually consist of supplantings in the context of mixed species flocks and are usually much less common than during the breeding season (compare Rappole and Warner, 1980, Chipley, 1980, and Greenberg, 1984, with Morse, 1970). Morse (1974) argued that, in general, interspecific dominance can influence resource use. However, the significance of these dominance relationships among nonbreeding migrants remains obscure. For a temperate area, Davis (1973) showed through removal experiments that Golden-crowned Sparrows (*Zonotrichia atricapillus*) excluded juncos from a riparian area. He related this to access to water and cover rather than food competition. Pulliam (1983) has argued that behavioral

competition for access to cover could be important for wintering finch assemblages.

3.2. Feeding Specialization

The investigation of the role of interspecific competition among wintering migrants has often focused on the mode of resource partitioning between species occurring together. The nearly universal conclusion of these studies is that migrants do forage sufficiently differently from each other (and resident species) to reduce competition (but see Post, 1978). One of the earliest and most comprehensive studies of feeding and habitat differences in sympatric migrant passerines was conducted by Lack and Lack (1972) on Jamaica. Based on a few, standard variables, they were able to account for ecological segregation among a large number of wintering warblers (and a smaller number of resident warblers and vireos). Their analysis included data on their use of different habitats, foraging attack methods, foraging strata, foods (insect versus fruit or nectar), and foraging substrate. Since this analysis, several other papers have presented data on entire "migrant communities." Since little had been published on the foraging ecology of wintering migrants, these papers summarize data gathered with variable rigor. Several studies consist of qualitative description of how migrants or residents segregate ecologically (Rappole and Warner, 1980; Willis, 1980; Terborgh and Faaborg, 1980). None of the quantitative (Chiple, 1977; Tramer and Kemp, 1980; Hutto, 1981; Waide, 1981) studies have reached the degree of sophistication found in recent works on temperate zone communities (for example, see Robinson and Holmes, 1982). These shortcomings are not surprising; gathering foraging data on birds in tropical habitats is demanding work, and the number of migrant and resident species can often be overwhelming.

Community studies of foraging behavior of migrants cannot alone provide evidence for or against the importance of interspecific competition. The most interesting result of these preliminary studies of foraging in migrant birds is the degree to which certain species show ecological specialization. Often, the subjective impression of observers is that the niche gestalt of a species during the nonbreeding season closely resembles that of the breeding season. Some striking exceptions occur: the Worm-eating Warbler (*Helmitheros vermivorus*), for example, is a fairly typical foliage-gleaning bird during most of the breeding season (Bennett, 1980) but becomes highly specialized on foraging from the aerial leaf litter of tropical forests in the nonbreeding season (Willis,

1980). Although in hindsight such ecological stereotypy in nonbreeding migrants seems natural, it was at least conceivable that most migrants show a high degree of foraging plasticity to allow them to exploit ephemeral and underused resources (Willis, 1966; Morse, 1971). In fact, some migrants seem to show such behavioral plasticity; for example, the Yellow-rumped Warbler (*Dendroica coronata*) is highly generalized during the nonbreeding season (MacArthur, 1958; personal observations).

3.3. Testing Predictions of Community Theory

Few researchers have attempted to analyze the foraging resource partitioning of nonbreeding migrants beyond the merits of the qualitative argument: species forage differently from each other. Yet, the original intent of competition theory was to provide specific predictions on how communities would be "structured," based on knowledge of resource availability (MacArthur, 1972). By this theory, foraging could differ in variation in types of resources used (niche breadth), as well as the modal resource used (niche displacement) to reduce interspecific competition to some allowable level. The result would be tightly packed communities formed either by a filtering process (assembly rules) or actual shifts in the behavior of colonizers. Several authors have argued strongly for the action of competition in shaping nonbreeding migrant communities through the assembly rule mechanism (Lack and Lack, 1972; Pulliam, 1975; Terborgh and Faaborg, 1980).

Competition theory suggested some qualitative predictions concerning the relationship of niche overlap and the intensity of competition, and a few quantitative predictions concerning limiting similarity of coexisting species, expressed in terms of standard niche metrics. Although these models still have some heuristic value in exploring how species might respond to different competitive regimes, it is not surprising that few workers, particularly those working on migrant birds, have found much use for the specific predictions of competition theory.

Although numerous papers on migrant birds have used "niche metrics," few have used them in the way they were probably intended from a theoretical point of view. The application of competition theory, for example, demands that one knows much about the nature of the resources over which syntopic species might compete. Inclusion of some critical resources and exclusion of others will negate the value of the analyses. MacArthur (1972) argued, with some merit, that the behaviors and resources included in an analysis are best selected on the basis of the extensive natural history knowledge (and intuition) of

each worker. This presents a great problem when we turn to the study of alien and complex biological communities in the tropics. Few people have the kind of familiarity with birds, habitats, and potential food in tropical communities to devise legitimate sampling schemes for bird resource use.

Despite the possible pitfalls, some attempts have been made to analyze resource use by guilds of migrant birds. Bennett (1980) conducted an innovative analysis of foraging in the American Redstart (*Setophaga ruticilla*) on a number of breeding and wintering sites and in comparison with local potential competitors. She found that niche breadth of redstarts varied inversely with the number of species in her "redstart-like" guild. She also created random communities based on the niche characteristics of her entire species pool and found that the actual communities had niche overlaps consistently lower than the random communities. She concluded that the niches in this guild were generally hyperdispersed in niche space and implicated competition in structuring these guilds. The problem with this analysis is that the resource spectrum itself is not the same and may not be similar between communities. For example, the diversity, distribution, and abundance of foliage is difficult to compare between mangrove and upland tropical forests. The attributes of the arthropod faunas should also differ drastically. Niche breadth may decrease with increasing diversity as a response to increasing vegetation and prey diversity.

Bennett's study follows the approach of Baker and Baker (1973), who used interseasonal comparisons of niche breadth and overlap to assess the intensity of competition at various stages of the annual cycle in shorebirds. Bennett and Baker concluded redstarts and migrant shorebirds, respectively, were more specialized and had reduced foraging overlap with other species during the nonbreeding season. Once again, the resource spectrum is so drastically changed that the interseasonal comparison is weak. Capturing intertidal invertebrates may take greater foraging specialization than hunting crane flies on the tundra, irrespective of the competitive pressures.

Another interesting attempt at using competition theory to test the structure of wintering assemblages was conducted by Pulliam (1975, 1983); he compared sparrow communities in a series of habitats in southeastern Arizona. He argued that bill size correlates with mean seed size, that seeds are a nonrenewable resource on which birds depend throughout the winter, and that seed density contributes to local population regulation in migratory sparrows (Pulliam and Parker, 1979; Dunning and Brown, 1982). He was initially successful at predicting the array of sparrow bill sizes that should occur in various habitats

(Pulliam, 1975), although later studies (Pulliam, 1983) found that a random model predicted combinations as well as the community model. Pulliam suggested that certain variables, such as seed size distribution and seed size use, may not have been measured accurately enough to allow a precise quantitative test of community theory. It should be borne in mind that resources and resource use are probably more tractable to quantification in this granivore community than for insectivores and predators of intertidal organisms, which comprise the bulk of tropical migrants.

Duffy *et al.* (1981) assessed the efficacy of competition among tropical wintering shorebirds by comparing foraging behavior between wintering and oversummering individuals at mudflats of coastal Peru. They based their analysis on a qualitative prediction of competition theory: that as competition increases birds should shift their foraging to reduce resource-use overlap. They found no such systematic shifts, but, rather, a tendency of several species to converge on one habitat. Their conclusion, that competition is unimportant in this major wintering aggregation of shorebirds, is complicated by the fact that both interspecific and intraspecific competition increased between seasons, thus making any prediction on the direction of niche shifts difficult to make. In addition, resources were apparently increasing in the period of study (shorebirds were cropping the large increase to a constant level), and the resources were not compared between seasons. In addition, behavioral competition was not ruled out, and it may have been common at this site (Myers and McCaffrey, 1984).

Such detailed comparative work and experimental manipulations to test for competitive effects should be pursued wherever practical. The degree to which we should expect niche shifts or ecological release in response to such manipulations should vary with the proximate mechanisms that control foraging specialization. There needs to be considerably more study of the psychological aspects of foraging behavior (Klopfer, 1963; Greenberg, 1983). If foraging and habitat preferences are highly canalized, either through innate preferences or early learning, then it seems doubtful that individuals will show a rapid shift in foraging response to changes in competitor density, even when competition is important.

3.4. Interspecific Geographic Separation

Cox (1968) suggested that winter allopatry reduced competition between migrant bird species at the time of greatest food limitation. His hypothesis, in fact, has two important corollaries: winter distributions of closely related migrants tend to be hyperdispersed (Lack,

1944; Salomonsen, 1955); and second, the degree of allopatry is greater in the winter than in the breeding season. The logic underlying the analysis of congeneric distributions is that a high degree of morphological and locomotory similarity will require some sort of habitat or geographic displacement to be the critical mode of niche segregation.

Testing such a proposition requires working on a genus with a number of species, and it is not surprising that *Dendroica* has provided a focus. MacArthur (1958) first examined the possibility that winter distributions in *Dendroica* overlap less than expected in response to suggestions of Lack (1944) and Salomonsen (1955). He compared the degree of overlap in the AOU Check-lists' (American Ornithologists' Union, 1957) delineation of winter ranges of five "spruce woods" *Dendroica* against the frequency of overlap of randomly selected parulids (from species breeding in Maine). He found the frequency of range overlaps to be similar between the two species sets and concluded that congeneric warblers do not tend to winter apart to reduce nonbreeding competition.

This analysis was quite progressive, since it attempted to discern a biogeographic pattern through comparison with a null hypothesis. But it has some technical and analytical problems that prevent it from being the last word on the winter displacement hypothesis for *Dendroica*. The technical problems are based on the quality of distributional information used. Winter distributions of migrant birds are notoriously difficult to define in a biologically meaningful way. Such data cannot be handled like island biogeographic data where the presence or absence of a breeding pair has provided a minimal criterion for inclusion in an avifauna. Migrants, particularly young migrants, disperse over a much wider range than the area in which a species is truly common. It is likely that birds at the fringes of winter distributions will not form a viable population, and reach the fringes owing to navigational errors or behavioral displacements. In addition, some species move continuously throughout the "winter" and have no foci to their ranges. Winter ranges of tropical migrants are usually broad outlines of specimen records without any weighting by abundance or temporal differences. For example, several of the species that Lack and Lack (1972) analyzed ecologically on Jamaica are probably only of marginal abundance on the island. Since good census data are unavailable for many areas within the overall winter range of the genus *Dendroica*, the assignment of range overlaps must be done somewhat subjectively. This is what Chipley (1980) did to reevaluate MacArthur's analysis. His results suggest that the five sympatrically breeding *Dendroica* overlap in their winter distributions less than randomly selected warbler pairs.

The analytical problem with MacArthur's test is based on the spe-

cies used in the analysis. There is no apparent *a priori* reason for examining only syntopically breeding *Dendroica*, particularly if competition is important in determining the composition of breeding assemblages. According to the ideas of Lack (1944) and Salomonsen (1955), *Dendroica* species should migrate to reduce overlap with other *Dendroica*, not just the sympatrically breeding species.

As pointed out by Chipley (1980), migrant *Dendroica* tend to winter commonly in small geographic areas, and usually only one, or at most a few, common species co-occur. Although the distributional data are probably not sufficient to formally test this idea, I will briefly examine the hypothesis for its heuristic value. I have taken a template the size of Hispaniola and placed it over various areas of topical and temperate America to determine the number of co-occurring common species of *Dendroica*. I found that as many as eight to 11 species can occur together on the breeding range, along the Appalachians and states bordering Canada. During the non-breeding season, however, no more than five to seven species co-occur. Despite the relatively small area in which most of the *Dendroica* species winter, the various species tend to separate sufficiently to reduce the number of sympatric species when compared to the much larger breeding area. Needless to say, these crude analyses should be repeated if and when more precise distributional data (weighted by abundance) are available. I include them here simply to point out that the issue of winter segregation of *Dendroica* species is worth further investigation.

The *Empidonax* flycatchers provide another striking example of winter range separation (Fitzpatrick, 1980). Few species winter together in the same area and almost none winters in the same habitat within a region. Winter displacements often reflect different habitat preferences that are similar to habitats occupied during the breeding season (Fitzpatrick, 1980; Hespenheide, 1980). In some cases, however, species winter allopatrically without there being any obvious difference in habitat used; Yellow-bellied (*E. flavescens*) and Acadian (*E. virens*) flycatchers occupy lowland tropical forest at different latitudes. Since Yellow-bellied Flycatchers are common breeders in coniferous habitats, the correspondence between breeding and winter habitat is insufficient to explain the winter range separation. The strong winter segregation found in wintering *Empidonax* is similar to the situation in the breeding season, when one is generally able to find one species in a particular habitat. The strong habitat association coupled with interspecific territoriality between some species pairs has caused Johnson (1980) to argue that competitive exclusion is important in determining the breeding distributions in this group.

Geographic segregation, such as found in *Dendroica*, *Empidonax*, *Vireo*, and other genera of tropical migrant species, offers compelling, but not necessarily convincing evidence for interspecific competition. An alternative explanation is that these species show strong habitat associations that are independent of competitive interactions (see James et al., 1984). Many of the species of *Dendroica* and *Vireo* are quite generalized in the habitats they use within a region in the tropics, occurring from scrubby second-growth to mature forests (Rappole and Warner, 1980; Morton, 1980; Greenberg, 1984). On the other hand, our perception of variation in tropical habitats is poor. Perhaps birds are responding to fundamental differences in forest phenology found in different areas (Morton, 1980). Forests and scrub that appear similar may in fact be quite distinct in their rainfall regimes.

To simply assert, however, that birds winter in different areas as a result of habitat preferences uninfluenced by competition seems to beg the question of how diversity in habitat specialization may have arisen. It is at least reasonable to hypothesize that interspecific competition is an ultimate factor underlying divergence in foraging ecology of different bird species. It might be a difficult proposition to falsify, since habitat preferences may well be behaviorally stereotypic and therefore difficult to manipulate in experiments. Nonetheless, simply because an hypothesis is difficult to falsify does not mean that it could not be true.

In the interest of economy of space I have limited the discussion to interactions among migrant birds. However, this arbitrary decision should be borne in mind when considering interspecific segregation among migrant bird species. The arguments of MacArthur (1958), Lack and Lack (1972), and Terborgh and Faaborg (1980) depend heavily on the assumption that migrants, or at least closely related migrants, form discrete ecological units that encompass most of the potential competitive interactions. This assumption may be true for small foliage gleaning warblers wintering in the Antilles but almost certainly is not true for similar birds wintering in species-rich Central American and South American woodlands. Several authors have argued that some migrant species are more similar in their foraging ecology to resident species than to other migrants (Willis, 1980; Rappole and Warner, 1980; Morton, 1980; Greenberg, 1984).

Ecologically similar migrants, of course, may be those species that tend not to winter together. This argument, however, should be employed with great care. Chestnut-sided and Bay-breasted (*D. castanea*) warblers tend to winter allopatrically in lowland forests of Central America and South America, respectively. This might be seen as a good

example of ecologically similar species segregating geographically. However, both Morton (1980) and Greenberg (1979, 1984) have shown that the two species are distinctly different ecologically where they winter together in central Panama. Both are more similar to a variety of resident birds than they are to each other.

4. CONCLUSIONS

Competition theories have provided some elegant and exciting mechanisms for explaining variation in migratory strategies and non-breeding distributions of birds. It should be clear that evidence suggesting that competition is important in shaping winter distributions within or among species is tentative at best. This is not surprising, because our knowledge of the distribution, resource and habitat use, and population dynamics of migrant species is still primitive. The importance of competition in research on migrant birds has proven to be a mixed blessing; on one hand, it has inspired and conceptually armed a large number of ornithologists to go to tropical wintering grounds of migrant species; on the other hand, it has narrowed the focus of such studies to relatively short-term foraging behavior studies. In fact, a majority of recent studies have attempted to resolve the seemingly less tractable question of how "migrants" as a whole interact with residents.

The evaluation of possible effects of competition on migrants demands a pluralistic research approach. Of primary importance is an improved understanding of the distribution of migrant birds, beginning with an abundance-weighted geographic analysis and proceeding to a quantitative survey of habitat relations of individual migrant species. In addition, the natural history and ecology of individual species of migrants should be studied in detail, with particular attention paid to responses to seasonal and annual variation in resource abundance. The demography of migrant populations based on studies of color-marked birds should be examined in light of current theories of the habitat distribution of birds. Finally, modern studies of such behavioral mechanisms of competition such as dominance and territoriality should be undertaken.

I am suggesting that the serious study of the ecology of migrant birds in tropical areas has barely begun. The preliminary investigations conducted over the past 20 years, however, suggest a wealth of problems related to competition and other mechanisms of population regulation that require more work. Unfortunately, the opportunities to examine these topics under reasonably unaltered conditions are rapidly disap-

pearing. Like so many other tropical phenomena, these questions require patient and long-term studies, but demand immediate attention.

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REFERENCES

- Alerstram, T., and Hogstedt, G., 1980, Spring predictability and leap-frog migration, *Ornis. Scand.* **11**:196–200.
- American Ornithologists' Union Checklist Committee, 1957, A Checklist of North American Birds, American Ornithologists' Union.
- Baker, M. C., and Baker, E. M., 1973, Niche relationships among six species of shorebirds on their wintering and breeding ranges, *Ecol. Monogr.* **43**:193–212.
- Baker, M. C., and Fox, S. F., 1978, Dominance, survival and enzyme polymorphisms in dark-eyed juncos, *Evolution* **32**:697–711.
- Bennett, S. E., 1980, Interspecific competition and the niche of the American Redstart (*Setophago ruticilla*) in wintering and breeding communities, in: *Migrant Birds in the Neotropics: Ecology, Behavior, Distribution, and Conservation* (A. Keast and E. S. Morton, eds.), Smithsonian Inst. Press, Washington, D.C., pp. 319–332.
- Bond, J., 1957, North American warblers in the West Indies, in: *The Warblers of North America* (L. Griscom and A. Sprunt, eds.), Devin Adair, New York, pp. 257–263.
- Brosset, A., 1968, Localizations ecologiques des oiseaux migrateurs dans la forêt équatoriale du Gabon, *Biol. Gabonica* **4**:211–216.
- Brown, J. L., 1964, The evolution of diversity in avian territorial systems, *Wilson Bull.* **76**:160–169.
- Carpenter, F. L., Paton, D. C., and Hixon, M. A., 1983, Weight gain and adjustment of feeding territory size in migrant hummingbirds, *Proc. Natl. Acad. Sci. (USA)* **80**:7259–7263.
- Chiple, R., 1977, The impact of wintering migrant wood warblers on resident insectivorous passerines in a subtropical Colombian oak forest, *Living Bird* **15**:119–141.
- Chiple, R., 1980, Nonbreeding ecology of the Blackburnian Warbler, in: *Migrant Birds in the Neotropics: Ecology, Behavior, Distribution, and Conservation* (A. Keast and E. S. Morton, eds.), Smithsonian Inst. Press, Washington, D.C., pp. 309–319.
- Colwell, R. K., 1973, Competition and coexistence in a simple tropical community, *Am. Not.* **107**:737–760.
- Cox, G. W., 1968, The role of competition in the evolution of migration, *Evolution* **22**:180–189.
- Davis, J., 1973, Habitat preferences and competition of wintering juncos and Golden-crowned Sparrows, *Ecology* **54**:174–180.
- Duffy, D., Atkins, N., and Schneider, D., 1981, Do shorebirds compete on their wintering grounds?, *Auk* **98**:215–219.
- Dunning, J. B., and Brown, J. H., 1982, Summer rainfall and winter sparrow densities: a test of the food limitation hypothesis, *Auk* **99**:123–129.
- Eaton, S. W., 1953, Wood warblers wintering in Cuba, *Wilson Bull.* **65**:169–174.

- Emlen, J. T., 1973, Territorial aggression in wintering warblers of Bahama agave blossoms, *Wilson Bull.* **85**:71-74.
- Feinsinger, P., 1980, Asynchronous migration patterns and the coexistence of tropical hummingbirds, in: *Migrant Birds in the Neotropics: Ecology, Behavior, Distribution, and Conservation* (A. Keast and E. S. Morton, eds.), Smithsonian Inst. Press, Washington, D.C., pp. 411-419.
- Fitzpatrick, J., 1980, Wintering of North American tyrant flycatchers in the Neotropics, in: *Migrant Birds in the Neotropics: Ecology, Behavior, Distribution, and Conservation* (A. Keast and E. S. Morton, eds.), Smithsonian Inst. Press, Washington, D.C., pp. 67-79.
- Foster, R. B., 1980, The seasonal rhythms in fruit fall on Barro Colorado Island, in: *Ecology of a Tropical Forest: Seasonal Rhythms and Long-term Changes* (E. G. Leigh, A. S. Rand, D. Windsor, eds.), Smithsonian Inst. Press, Washington, D.C., pp. 151-173.
- Fretwell, S., 1969, Dominance behavior and winter habitat distribution in juncos (*Junco hyemalis*), *Bird-Bonding* **40**:1-25.
- Fretwell, S., 1972, *Populations in a Seasonal Environment*, Princeton University Press, Princeton, New Jersey.
- Fretwell, S., 1980, Evolution of migration in relation to factors regulating bird numbers, in: *Migrant Birds in the Neotropics: Ecology, Behavior, Distribution, and Conservation* (A. Keast and E. S. Morton, eds.), Smithsonian Inst. Press, Washington, D.C., pp. 517-529.
- Fretwell, S., and Lucas, H. L. 1970, On territorial behavior and other factors influencing habitat distribution in birds, *Acta Biotheor.* **19**:16-36.
- Gass, C. L., 1979, Territory regulation, tenure, and migration in Rufous Hummingbirds, *Can. J. Zool.* **56**:1535-1539.
- Gauthreaux, S., 1978, The ecological significance of behavioral dominance, in: *Perspectives in Ornithology* (P. P. G. Bateson and P. H. Klopfer, eds.), Plenum, New York, pp. 17-54.
- Gauthreaux, S., 1982, The ecology and evolution of avian migration systems, in: *Avian Biology*, Volume 6 (D. S. Farner and J. R. King, eds.), Academic Press, New York and London, pp. 93-167.
- Gill, F., and Wolf, L. L., 1975, Economics of feeding territoriality in the Golden-winged Sunbird, *Ecology* **56**:333-345.
- Goss-Custard, J. D., Lek, S. E. A., Durrel, D., and Ens, B. J., 1982, Individual differences in aggressiveness and food stealing among wintering oystercatchers, *Hoematopus ostrolegus* L., *Anim. Behav.* **30**:917-928.
- Greenberg, R., 1979, Body size, breeding habitat, and winter exploitation systems in Dendroico, *Auk* **96**:756-766.
- Greenberg, R., 1980, Demographic aspects of long distance migration in birds, in: *Migrant Birds in the Neotropics: Ecology, Behavior, Distribution, and Conservation* (A. Keast and E. S. Morton, eds.), Smithsonian Inst. Press, Washington, D.C., pp. 493-504.
- Greenberg, R., 1983, The role of neophobia in determining the degree of foraging specialization in some migrant warblers, *Am. Nat.* **122**:444-453.
- Greenberg, R., 1984, The winter exploitation systems of Bay-breasted and Chestnut-sided Warblers in Panama, *Univ. Calif. Publ. Zool.* **116**:1-107.
- Greenberg, R., 1985, The social behavior and feeding ecology of neotropical migrants in the non-breeding season, *Proc. XVII Ornith. Congr., Moscow* (in press).
- Greenberg, R., and Gradwohl, J., 1980, Observations of paired Canada Warblers *Wilsonia canadensis* during migration in Panama, *Ibis* **122**:509-512.

- Hamilton, W. S., 1959, Aggressive behavior in migrant Pectoral Sandpipers, *Condor* **61**:161-179.
- Hespenheide, H. A., 1980, Bird community structure in two Panamanian forests: residents, migrants, and seasonality during the non-breeding season, in: *Migrant Birds in the Neotropics: Ecology, Behavior, Distribution, and Conservation* (A. Keast and E. S. Morton, eds.), Smithsonian Inst. Press, Washington, D.C., pp. 227-237.
- Hutto, R. B., 1981, Seasonal variation in the foraging behavior of some migratory western wood warblers, *Auk* **98**:765-777.
- James, F. C., Johnston, R. F., Wamer, N. O., Niemi, G. J., and Boecklen, W. J., 1984, The Grinnellian niche of the Wood Thrush, *Am. Not.* **124**:17-30.
- Johnson, N. K., 1980, Character variation and the evolution of sibling species in the *Empidonox difficilis-flovescens* complex, *Univ. Calif. Publ. Zool.* **112**:1-151.
- Kale, H., 1967, Aggressive behavior by a migrating Cape May Warbler, *Auk* **84**:120-121.
- Karr, J. R., 1971, A wintering Kentucky Warbler, *Bird-Banding* **42**:299.
- Keast, A., and Morton, E. S., 1980, *Migrant Birds in the Neotropics: Ecology, Behavior, Distribution, and Conservation*, Smithsonian Inst. Press, Washington.
- Ketterson, E. D., and Nolan, V., 1976a, Aggressive behavior in wintering Dark-eyed Juncos: determinants of dominance and their possible relation to geographic variation in sex ratio, *Wilson Bull.* **91**:371-383.
- Ketterson, E. D., and Nolan, V., Jr., 1976b, Geographic variation and its climatic correlates in the sex ratio of eastern-wintering Dark-eyed Juncos (*Junco hyemalis hyemalis*), *Ecology* **57**:679-693.
- Ketterson, E. D., and Nolan, V., Jr., 1982, The role of migration and winter mortality in the life history of a temperate-zone migrant, the Dark-eyed Junco, as determined from demographic analysis of winter populations, *Auk* **99**:243-259.
- Ketterson, E. D., and Nolan, V., Jr., 1983, The evolution of differential migration, in *Current Ornithology* Vol. 1, (R. F. Johnston, ed.), Plenum Press, New York. pp. 357-402.
- Klopfer, P. H., 1963, Behavioral stereotypy in birds, *Wilson Bull.* **79**:290-300.
- Kodric-Brown, A., and Brown, J. H., 1978, Influences of economics, interspecific competition, and sexual dimorphism on territoriality in migrant Rufous Hummingbirds, *Ecology* **51**:285-296.
- Lack, D., 1941, The problem of partial migration, *Br. Birds* **37**:122-133, 143-150.
- Lack, D., 1944, Ecological aspects of species-formation in passerine birds, *Ibis* **86**:260-286.
- Lack, D., 1968, Bird migration and natural selection, *Oikos* **19**:1-9.
- Lack, D., and Lack, P., 1972, Wintering warblers of Jamaica, *Living Bird* **11**:129-153.
- Leck, C. F., 1972, The impact of some North American migrants at fruiting trees in Panama, *Auk* **89**:842-850.
- Lynch, J. F., Morton, E. S., and Van der Voort, M., 1985, Habitat segregation between the sexes of wintering Hooded Warblers (*Wilsonia citreina*), *Auk* (in press).
- MacArthur, R., 1958, Population ecology of some warblers of Northeastern coniferous forests, *Ecology* **39**:599-619.
- MacArthur, R., 1972, *Geographical Ecology*, Harper and Row, New York.
- Mallory, E. P., 1981, Ecological behavioral and morphological adaptations of a migratory shorebird, the Whimbrel (*Numenius phaeopus*) in its different environments, Unpublished doctoral dissertation, Dartmouth College, Hanover, New Hampshire.
- Mewaldt, L. R., 1964, Effects of bird removal on winter populations of sparrows, *Bird-Banding* **35**:184-195.
- Miller, A. H., 1963, Avifauna of an american equatorial cloud forest, *Univ. Calif. Publ. Zool.* **66**:1-72.

- Moreau, R. E., 1972, *The Palearctic-African Migration Systems*, Academic Press, London.
- Morse, D. H., 1970, Ecological aspects of some mixed species foraging flocks, *Ecol. Monogr.* **40**:119-168.
- Morse, D. H., 1971, The insectivorous bird as an adaptive strategy, *Annu. Rev. Ecol. Syst.* **2**:177-200.
- Morse, D. H., 1974, Niche breadth as a function of social dominance, *Am. Not.* **108**:818-830.
- Morton, E. S., 1971, Food and migration habits of the Eastern Kingbird in Panama, *Auk* **88**:925-926.
- Morton, E. S., 1976, The adaptive significance of dull coloration in Yellow Warblers, *Condor* **78**:423.
- Morton, E. S., 1980, Adaptations to seasonal changes by migrant landbirds in the Panama Canal Zone, in: *Migrant Birds in the Neotropics: Ecology, Behavior, Distribution, and Conservation* (A. Keast and E. S. Morton, eds.), Smithsonian Inst. Press, Washington, D.C., pp. 437-457.
- Myers, J. P., 1981a, Cross-seasonal interactions in the evolution of sandpiper social systems, *Behav. Ecol. Sociobiol.* **8**:195-202.
- Myers, J. P., 1981b, A test of three hypotheses for latitudinal segregation of the sexes in wintering birds, *Can. J. Zool.* **59**:1527-1534.
- Myers, J. P., and McCaffrey, B., 1984, Paracas revisited: do shorebirds compete on their wintering grounds? *Auk* **101**:197-199.
- Myers, J. P., Connors, P. G., and Pitelka, F. A., 1979a, Territoriality in non-breeding shorebirds, *Studies in Avian Biol.* **2**:231-246.
- Myers, J. P., Connors, P. G., and Pitelka, F. A., 1979b, Territory size in wintering sand-erlings: the effects of prey abundance and intruder density, *Auk* **96**:551-561.
- Nisbet, I. C. T., and Medway, Lord, 1972, Dispersion, population ecology, and migration of the Eastern Great Reed Warbler (*Acrocephalus orientalis*) wintering in Malaysia, *Ibis* **114**:451-494.
- Pearson, D., 1980, Bird migration in Amazonian Ecuador, Peru and Bolivia, in: *Migrant Birds in the Neotropics: Ecology, Behavior, Distribution, and Conservation* (A. Keast and E. S. Morton, eds.), Smithsonian Inst. Press, Washington, D.C., pp. 273-285.
- Post, W., 1978, Social and foraging behavior of warblers wintering in Puerto Rican scrub, *Wilson Bull.* **90**:197-214.
- Price, T., 1981, The ecology of the Greenish Warbler (*Phylloscopus trochiloides*) in its winter quarters, *Ibis* **123**:131-144.
- Pulliam, H. R., 1975, Coexistence of sparrows: a test of community theory, *Science* **189**:474-476.
- Pulliam, H. R., 1983, Ecological community theory and the coexistence of sparrows, *Ecology* **64**:45-52.
- Pulliam, H. R., and Parker, T. A. III, 1979, Population regulation of sparrows, *Fortschr. Zool.* **25**:137-147.
- Ramos, M., and Warner, D., 1980, Analysis of North American subspecies of migrant birds wintering in Las Tuxtlas, Southern Veracruz, Mexico, in: *Migrant Birds in the Neotropics: Ecology, Behavior, Distribution, and Conservation* (A. Keast and E. S. Morton, eds.), Smithsonian Inst. Press, Washington, D.C., pp. 173-181.
- Rappole, J. H., and Warner, D. W., 1976, Relationships between behavior, physiology, and weather in avian transients at a migration stopover site, *Oecologia* **26**:193-212.
- Rappole, J. H., and Warner, D., 1980, Ecological aspects of migrant bird behavior in Veracruz, Mexico, in: *Migrant Birds in the Neotropics: Ecology, Behavior, Distri-*

- buton, and Conservation (A. Keast and E. S. Morton, eds.), Smithsonian Inst. Press, Washington, D.C., pp. 353–395.
- Robinson, S., and Holmes, R. T., 1982, Foraging behavior of forest birds: the relationship among search tactics, diet, and habitat structure. *Ecology* **63**:1918–1931.
- Sabine, W. S., 1959, The winter society of the Oregon Junco: intolerance, dominance, and the pecking order, *Condor* **61**:110–135.
- Salomonsen, F., 1955, The evolutionary significance of bird-migration, *Dan. Biol. Medd.* **22**:1–61.
- Schwartz, P., 1964, The Northern Waterthrush in Venezuela, *Living Bird* **2**:169–184.
- Skutch, A. F., 1957, Migrant warblers in their North American home, in: *The Warblers of North America* (L. Griscom and A. Sprunt, eds.), Devin-Adair, New York.
- Slagsvold, T., 1982, Spring predictability and bird migration and breeding times: a comment on the phenomena of leap-frog migration, *Ornis. Scand.* **13**:145–148.
- Stresemann, E., 1934, Aves, in: *Hondbuch der Zoologie*, Band 7, Pt. 2, Berlin and Leipzig, 899 pp.
- Swarth, H. S., 1920, Revisions of the genus *Posserella* with special reference to the distribution and migration of the races of California, *Univ. Calif. Publ. Zool.* **21**:75–224.
- Terborgh, J., and Faaborg, J. R., 1980, Factors affecting the distribution and abundance of North American migrants in the eastern Caribbean region, in: *Migrant Birds in the Neotropics: Ecology, Behavior, Distribution, and Conservation* (A. Keast and E. S. Morton, eds.), Smithsonian Inst. Press, Washington, D.C., pp. 157–165.
- Tramer, E., and Kemp, T. A., 1980, Foraging ecology of migrant and resident warblers and vireos in the highlands of Costa Rica, in: *Migrant Birds in the Neotropics: Ecology, Behavior, Distribution, and Conservation* (A. Keast and E. S. Morton, eds.), Smithsonian Inst. Press, Washington, D.C., pp. 285–297.
- Tramer, E., and Kemp, T. R., 1981, Diet-correlated variation in social behavior of wintering Tennessee Warblers. *Auk* **98**:263–264.
- Von Haartmann, L., 1968, The evolution of resident versus migratory habit in birds. some considerations, *Ornis Fennica* **45**:1–7.
- Waide, R. B., 1981, Interactions between resident and migrant birds in Campeche, Mexico, *Trop. Ecol.* **22**:134–154.
- Welty, J. C., 1982, *The Life of Birds*, 3rd ed., W. B. Saunders Co., Philadelphia.
- Wiens, J. A., 1983, Avian community ecology: an iconoclastic point of view, in: *Perspectives in Ornithology* (A. Brush and G. Clark, eds.), Cambridge University Press, London, pp. 355–403.
- Willis, E. O., 1966, The role of migrant birds at swarms of army ants, *Living Bird* **5**:187–231.
- Willis, E. O., 1980, Ecological roles of migratory and resident birds of Barro Colorado Island, Panama, in: *Migrant Birds in the Neotropics: Ecology, Behavior, Distribution, and Conservation* (A. Keast and E. S. Morton, eds.), Smithsonian Inst. Press, Washington, D.C., pp. 205–225.
- Wolda, H., 1978, Fluctuations in abundance of tropical insects, *Am. Not.* **112**:1017–1045.
- Zahavi, A., 1971, The social behavior of the White Wagtail *Motacilla alba alba* wintering in Israel, *Ibis* **113**:203–212.