FOOD AVAILABILITY, MIGRATORY BEHAVIOR, AND POPULATION DYNAMICS OF TERRESTRIAL BIRDS DURING THE NONREPRODUCTIVE SEASON

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Abstract. Migration is a phenomenon that has major implications for the spatial dynamics and organization of migrant populations and communities during the nonreproductive season, and food availability appears to be the major factor responsible for migratory behavior. The evolutionary relationship between spatial and temporal characteristics of resource availability and migratory behavior is briefly overviewed. Results of field work and laboratory experiments concerning the proximate relationship between food availability and migratory behavior indicate that some migrants extend autumn migration past the normal migratory period if food becomes scarce, and that some migrant populations can exhibit large-scale distributional shifts in winter in response to food availability. This is an important consideration when attempting to census and monitor wintering populations of migrants. More work is needed to clarify the role of food availability in regulating population size of migrants during the nonreproductive season and to assess the effects of differential migratory distance on individual fitness.

Key Words: Food availability; migration; population dynamics; warbler; *Dendroica*; *Sylvia*; *Junco*; nonreproductive season.

Bird migration comprises a movement from the breeding (natal) grounds followed by a subsequent return for the next reproductive effort. It has long been recognized that food availability probably plays a significant, if not dominant, role in the evolution of migratory behavior (see Gauthreaux 1982 for a recent review) and in the regulation of the distribution and dynamics of migrant populations. Few data, however, actually address this relationship empirically (e.g., Hutto 1980, Rappole and Warner 1980, Greenberg 1986).

I will briefly review and discuss food availability, migratory behavior, and migrant population-level phenomena during the nonreproductive period by: (1) reviewing the diversity of migratory behavior found in birds as a function of large-scale characteristics of resource availability; (2) considering the role of food availability in regulating dispersion, social behavior, and movements of nonbreeding migrants; and (3) outlining laboratory studies of the effect of food availability (including differential access to food as mediated through competition) on migratory behavior. Finally, I suggest how these results may be relevant to censusing and monitoring migrant populations.

RESOURCES AND THE REGULATION OF MIGRATORY BEHAVIOR

Bird migration is generally considered an adaptation that allows birds to exploit abundant food for reproduction in a region subject to harsh conditions between breeding seasons (e.g., Gauthreaux 1982, Cox 1985). Migratory behavior varies from strongly endogenously controlled, with high heritability values (e.g., Berthold 1988b), to environmentally stimulated (Berthold 1975; Gwinner and Czeschlik 1978; Gauthreaux 1982; Myers 1984; Terrill and Ohmart 1984; Terrill 1987, 1988, in press a, b; Gwinner et al. 1988). This variation parallels, and is probably an evolutionary response to, large-scale spatial and temporal characteristics of resource availability during the nonreproductive period.

Food availability is generally considered the fundamentally important determinant of migratory distance (e.g., Gauthreaux 1982). Some population-level trends indicate that birds migrate only as far as necessary to maximize the probability of obtaining adequate resources for survival between reproductive periods while minimizing the distance travelled to do so (e.g., Terborgh and Faaborg 1980, Terrill and Ohmart 1984, Terrill in press c). However, hypotheses concerning relationships between migratory distance, annual survivorship, and reproductive success remain largely untested.

When the probability of overwinter survival on the breeding grounds frequently approaches zero, natural selection has favored individuals (annual migrants) that leave the area *before* food becomes scarce (e.g., Farner 1955; Lack 1968a; Terrill 1987, 1988, in press a, b), an adaptation that enables them to accumulate and maintain substantial fat reserves for migration. Thus, this type of migratory behavior ("obligate" migra-

tion—see Terrill and Able 1988) is anticipatory in the sense that a decrease in food availability is ultimately responsible for its occurrence, but is not the proximate factor releasing the behavior (Lack 1968a). Obligate migratory behavior is apparently induced primarily by endogenous mechanisms (see Berthold 1975, 1988a, b, c; Gwinner 1986 for reviews). The duration and distance of obligate migration is theoretically related to the probability of overwinter survival along the migratory route (Terrill and Ohmart 1984; Terrill 1987, 1988, in press a, b). Presumably, individuals that spontaneously migrate across regions with very low probabilities of overwinter survival before resources become scarce for the winter are at an advantage relative to individuals that terminate their migration and attempt to overwinter in the region. Where food availability is more variable, selection has favored a more environmentally sensitive migratory system, "facultative migration," which appears to be a direct response to changes in environmental conditions and may, or may not, occur in any given year.

Obligate and facultative migration appear to represent two ends of a behavioral continuum (Gwinner and Czsechlik 1978). Not only are different species and populations represented along this continuum, but the behavior of even individual migrants can vary (e.g., Perdeck 1964; Terrill 1987, 1988, in press a, b, c; Gwinner et al. 1988). These studies indicate that as the endogenous drive to migrate wanes with time and distance, the stimulus to continue migrating becomes more directly dependent upon environmental conditions such as food availability and social environment (Terrill 1987, 1988; Gwinner et al. 1988; Terrill and Berthold in prep.). More specifically, at least some annual migrants are apparently capable of changing from an "obligate phase" (during which the fundamental stimulus for migration is endogenous) to a "facultative phase" (the stimulus to migrate is directly dependent upon immediate resource availability) with time and distance of autumnal migration. Theoretically, the obligate phase takes migrants across regions where the probability of overwinter survival is consistently very low. As the probability of survival increases, the birds switch to a facultative mode that enables them to track variations in resource distribution and minimize the total distance of migration during any given year. In a sense then, obligate migratory behavior might be considered as the coarse-grained determinant of migratory distance (an evolutionary result of long-term patterns of resource availability), while the facultative phase fine tunes migration during a given year (in response to short-term fluctuations in resources).

FOOD AVAILABILITY AND MIGRANT POPULATIONS DURING THE NONREPRODUCTIVE SEASON: A SURVEY

Nonbreeding migrant spacing behavior ranges from highly territorial to very social and apparently is correlated with a number of factors including habitat, distribution of resources, and predation (Gauthreaux 1982, Pulliam and Millikan 1982, Pulliam and Caraco 1984, Myers 1984). The dispersion and distribution of wintering migrants range from remaining essentially stable (between autumnal and vernal migration) to very dynamic, with movements continuing throughout much of the "wintering period" (e.g., Moreau 1972, Curry-Lindahl 1981, Lack 1983, Terrill 1988). It is often assumed that this behavioral continuum reflects a range in the distribution of resources on the wintering grounds from relatively stable to dynamic within and between winters (e.g., Gauthreaux 1982).

The potential importance of food availability during the nonreproductive period in regulating the overall size of migrant populations has not been ignored (e.g., Lack 1954, 1968a; Fretwell 1972; Schwartz 1980; Ketterson and Nolan 1982; Myers 1984; Berthold 1988b), and the degree to which migrant population size might be regulated during the nonbreeding periods is an important and generally open question.

Apparently, food can be limited during the nonreproductive period of migrants; evidence includes: defense of territories that play no role in reproduction (e.g., Rappole and Warner 1980); large-scale movements within and between winters (e.g., Terrill 1988, in press c); major population declines that appear to be occurring on the wintering grounds (e.g., Berthold 1988a); and differential movements by certain age or sex classes of the same populations (e.g., Kalela 1954; Lack 1954; Gauthreaux 1978, 1982). This last point has potential implications for differential access to food as mediated through competition, which, in turn, has relevance to the structure and dynamics of migrant populations. Theoretically, dominant individuals restrict access to food by subordinates, which forces subordinates to migrate farther to obtain resources. Distributional patterns often (but not always) support this concept; however, rigorous evaluations of the availability of resources per individual are generally lacking. Although it has been demonstrated that individuals migrating farther from the breeding grounds in winter have lower average reproductive success the following breeding season (e.g., Schwabl 1983), I know of no empirical information on the relationship between differential

migration, survival rates and *lifetime* reproductive success in any migrant.

During the nonreproductive period, migrants show the full spectrum of social behavior described for birds in the breeding season (see Pulliam and Millikan 1982). Although many migrants that are territorial during the reproductive season become gregarious during the nonreproductive season, others remain territorial throughout the year, establishing territories during migration and on the wintering grounds (e.g., Gauthreaux 1982). [The relationship between resource distribution and spacing and social behavior has been discussed in detail elsewhere, e.g., Brown 1969, Pulliam and Millikan 1982.]

Extended use of resources in the same locality throughout the winter (site tenacity) should occur when food is available for an extended period (throughout a particular winter), and between-year faithfulness to the same wintering site (site fidelity) should occur when food availability is relatively constant between years. Examples of migrants that are often territorial during the winter and frequently exhibit both nonbreeding site tenacity and fidelity include a group of parulid warblers that breed in temperate North America and winter in dense understory in tropical and subtropical regions (Schwartz 1964, Rappole and Warner 1980). This habitat is apparently buffered from the extreme fluctuations in food availability found in higher vegetational strata and in other regional habitats between the wet and dry seasons. Nonbreeding site tenacity and fidelity are not restricted to territorial migrants, but appear in gregarious species as well. For example, there are numerous reports of banded sparrows (that readily associate in flocks during winter) returning to the same wintering sites (e.g., Ketterson and Nolan 1985), especially at feeders. Cases of winter site tenacity and fidelity by migrants are numerous (for example, see Curry-Lindahl 1981 and Gauthreaux 1982) and they indicate (as do some studies on wintering migrant communities, e.g., see Keast and Morton 1980) that migrant assemblages are often stable throughout the wintering period. Alternatively, some studies indicate that movements by migrants can occur throughout the nonbreeding season and that individuals (even large numbers) may occupy different regions within and between winters. These studies indicate a much higher potential for extensive winter movement by migrants than has generally been considered to be the case (cf. Curry-Lindahl 1981, Terrill in press a).

The presence of both winter-site faithfulness and tenacity and winter-site plasticity within the same species provides opportunities to test assumptions about both proximate and ultimate

factors responsible for this variation (Ketterson and Nolan 1985). There exists a growing list of species that appear to exhibit the full spectrum of behavior (Curry-Lindahl 1981). One such species is the Yellow-rumped Warbler (*Dendroica coronata*). Some annual migrant populations of this species winter in the Sonoran desert of the southwestern United States and northwestern Mexico. These populations comprise good systems for testing hypotheses concerning the relationship between food availability and winter population dynamics for several reasons. First, these birds are highly restricted to insular patches of lush habitat surrounded by desert, which facilitates accurate censusing of local populations (and greatly decreases the possibility that birds disappearing from a site are dispersing locally rather than actually migrating). Second, numbers of wintering warblers at particular sites (and even within regions) vary greatly within and between winters. Third, there is a general correlation between severity of weather conditions and numbers of overwintering birds in a particular area (the colder the winter the fewer the overwintering warblers), implying either large-scale mortality or changes in winter distribution.

Terrill and Ohmart (1984) found that numbers of Yellow-rumped Warblers were positively correlated with food availability at a series of sites from the northern edge of the winter distribution in Arizona south into northern Mexico (Fig. 1). Transects were established at each site, birds were censused, and insect sweep samples were used to measure food availability throughout two winters. There was a strong positive association between the dominance of certain insect groups in the sweep samples and in the stomach contents of warblers collected at the same sites, indicating that sweep samples adequately reflected warbler diets (Terrill and Ohmart 1984). Changes in insect populations appeared to be strongly influenced by climatic conditions with numbers crashing with the occurrence of relatively severe cold fronts.

The dynamic state of the wintering warbler population was reflected in numerical changes along the north–south transect during two different winters (Fig. 2). Decreases at northerly sites corresponded to increases at southerly sites, suggesting movement, and the magnitude of change was correlated with the availability of insects (Terrill and Ohmart 1984). These population shifts occurred in January, even though these birds were considered winter residents. A subsequent analysis of tower kills of nocturnally migrating Yellow-rumped Warblers in Florida demonstrated that they are capable of migrating throughout the entire winter, although numbers are highly variable between years and large num-
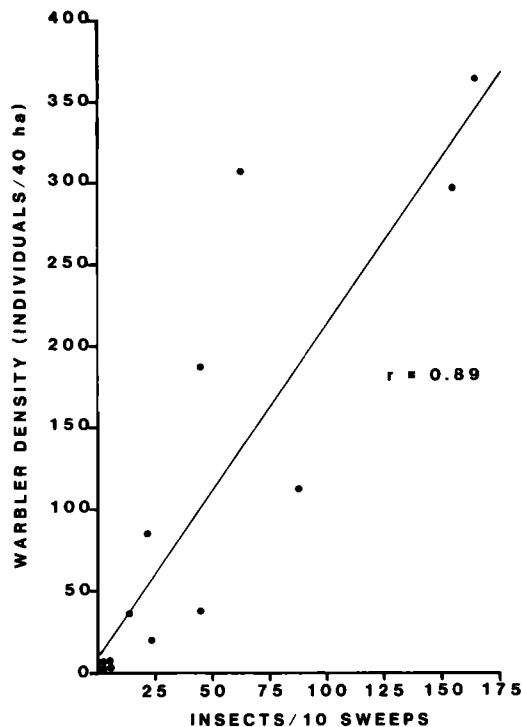
FIGURE 1. Significant (P < 0.001) correlation between numbers of insects and numbers of Yellow-rumped Warblers at Arizona riparian sites from October through early February for two years (from Terrill and Ohmart 1984).

FIGURE 2. Mean densities of Yellow-rumped Warblers in highly isolated riparian habitats near Phoenix, Arizona (33°N) and to the south near Magdelena, Mexico (31°N). Note the dramatic decrease in numbers of birds in midwinter of 1979–80 in the Phoenix area (A) in the wake of a major cold front, relative to a much lesser decrease in 1980–81 (at the same sites) when no major fronts occurred (B). Numerical decreases in the north corresponded to increases to the south, at Magdelena, during 1979–80 (C) and 1980–81 (D).

bers migrate in winter only during, or after, unusually severe cold periods (Terrill and Crawford 1988).

Overall then, these results indicate that: (1) the number of individuals wintering at particular sites (and regions) is a function of food availability; (2) winter migrant communities can change substantially within and between winters; and (3) these dynamics are due, at least in part, to the presence of migratory behavior in response to changing resource availability in winter after the "normal" migration period has ended. Similar results have been found in other species including temperate migrants (e.g., Pulliam and Parker 1979, Niles et al. 1969) and tropical wintering migrants (e.g., Wood 1979). The Yellow Wagtail (*Motacilla flava*) provides a rather spectacular example of a situation similar to that found in Yellow-rumped Warblers. Wood (1979) found a progressive decline in numbers of wintering wagtails at an African study site from about 16,000 in November to 2000–3000 in March, and that food availability and numbers of wagtails in the study area declined concurrently. A southward
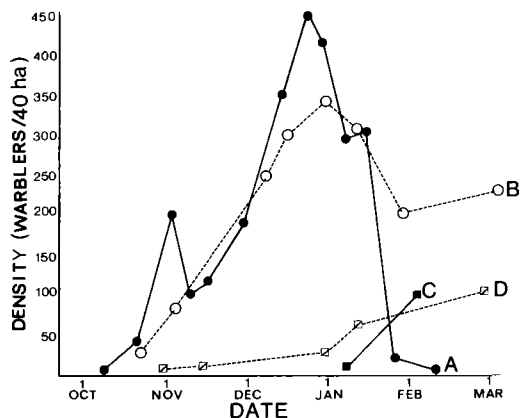
shift (i.e., extended migration) was supported by ringing recoveries.

FOOD AVAILABILITY AND INDIVIDUAL MIGRANT BEHAVIOR: AN EXPERIMENTAL APPROACH

The relationship between food availability and migratory behavior has been tested in the laboratory in several species, primarily during the autumn migration period. Most studies indicate that food deprivation heightens migratory activity at this time (e.g., Biebach 1985; Gwinner et al. 1985; Terrill in press b, c; Gwinner et al. 1988), especially if a migrant is unable to refuel during its diurnal rest (Gwinner et al. 1988). Several recent studies indicate that food deprivation may also inhibit fall migratory activity in some species, depending upon time of day food is restricted, severity of deprivation, and other factors (Terrill and Berthold in prep., Holberton pers. comm.).

Laboratory evidence for facultative migratory behavior in annual migrants during winter has recently been found in several species (Terrill 1987, Gwinner et al. 1988, Terrill and Berthold in prep.). These experiments have been carried out after the ending of spontaneous, autumnal, migratory activity associated with unlimited food (indicative of the obligate phase; see above).

One such species is the Dark-eyed Junco (*Junco hyemalis*). Juncos were used to test for pos-
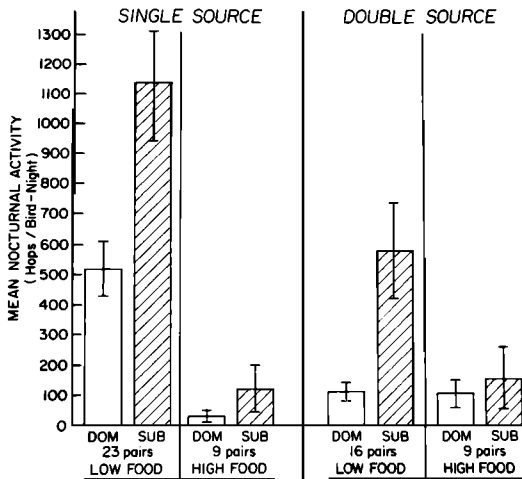
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FIGURE 3. The effects of manipulating social environment, food abundance, and number of food sources on migratory activity of Dark-eyed Juncos (from Terrill 1987; see text for details).

sible effects of restricted access to food, as mediated through social dominance, upon migratory behavior in winter. The potential role of social dominance in regulating demography and population dynamics in migrants is of considerable interest. Rigorously testing the effects of social dominance on migratory behavior in the field is difficult. Individual birds must be marked and tracked, dominance hierarchies determined, and access to food on an individual basis measured (Ketterson and Nolan 1985). Perhaps the most formidable aspect is determining whether the birds that disappear from a study site are actually migrating, dispersing locally, or dying.

Juncos were selected for this study for several reasons: (1) they exhibit both winter site fidelity and winter site plasticity (Ketterson and Nolan 1982, 1985); (2) they are highly social during the nonbreeding season and their social interactions have been extensively studied; (3) they are abundant and easily captured and maintained in captivity; (4) migratory juncos show nocturnal migratory activity (*Zugunruhe*) in the laboratory; and (5) females are generally subordinate to males during the nonbreeding season and on average migrate farther (Balph 1975; Ketterson and Nolan 1976, 1982, 1983).

Paired juncos (all but one bird were females) were kept indoors and their nocturnal activity was monitored from November through January 1983–84 and from December through May 1984–85. The dominant member of each of 23 pairs was determined. During the day members of each pair were allowed to interact. At night, a partition was used to divide each cage into two single-bird

activity cages, allowing the nocturnal activity of each individual to be measured. I compared migratory activity of dominants and subordinates subjected to several different treatments: (1) "low food" comprised approximately eight g of food per day per pair; (2) "high food" was 14 g; (3) "single source" indicates that the food (either high or low amounts) was placed into a single, centrally located source; and (4) "double-source" indicates that the food was evenly divided between two sources placed at opposite ends of each cage. Combining data from identical treatments over the two experimental periods, the following comparisons yielded significant (paired sample t-tests) differences in migratory activity (Fig. 3): (1) low single-source subordinates showed higher activity than dominants (t = 3.67; P < 0.01); (2) low double-source subordinates higher than dominants (t = 2.75; P < 0.05); (3) low single-source subordinates greater than low double-source subordinates (t = 2.17; P < 0.025); and (4) low single-source dominants greater than low double-source dominants (t = 3.34; P < 0.002). In general, birds (whether paired or solitary) showed little or no nocturnal activity when they had abundant food during the winter months. This lack of activity contrasts with the high activity in fall when birds have access to unlimited food during the fall migratory period. Although, on average, female juncos migrate farther than males, population-level studies (Ketterson and Nolan 1982, 1985) indicate that social dominance does not explain the differential migration of juncos in that immatures, which are normally thought to be subordinate, do not migrate as far as adults. Further, they consistently find no evidence of differential disappearance during the winter period of any age or sex class at their study sites (e.g., Rogers et al. 1988). Thus, they find conflicting patterns concerning the hypothesis that social dominance might be involved in differential migration in this species.

Experimental results very similar to those involving the juncos (Terrill 1987) have been found in a long-distance migrant, the Garden Warbler (*Sylvia borin*). This species shows spontaneous *Zugunruhe* during the autumnal migratory period (approximately September–December) with access to unlimited food and also shows enhanced migratory activity in response to food deprivation (Gwinner et al. 1985, 1988). In winter, these warblers are generally not active at night; however, nocturnal activity can be stimulated by food deprivation, indicating that migratory activity may be reactivated in birds that have settled for the winter in a certain area but are then confronted with a deteriorating food supply (Gwinner et al. 1988). In such situations further movement in the migratory direction may in-

crease the birds' probability of finding adequate food relative to local or random movements. Similar results have been reported in at least two other members of the Muscicapidae, the Blackcap, *Sylvia atricapilla* (Terrill and Berthold in prep.), and the Pied Flycatcher, *Ficedula hypoleuca* (Thalau and Wiltschko in prep.).

IMPLICATIONS FOR CENSUSING AND INTERPRETING DATA

Although more information is needed concerning resource availability, I conclude that food availability is potentially important in regulating the distribution and dynamics of wintering migrant populations. This general result has relevance to monitoring studies. First, a single winter census may not reflect the population size, or habitat utilization at a given site throughout the winter. Secondly, the possibility of large-scale geographic shifts of annual migrant populations within and between winters should be considered (this is especially important in terms of monitoring and interpreting data on absolute population size). Third, intraspecific competition may limit access to food during the nonreproductive period and be important in determining differential migration and population dynamics in some species of annual migrants.

The spatially complex life histories of migratory birds pose tremendous challenges to the analysis and understanding of avian populations and community dynamics (Bennett 1980). Although the challenge is substantial, the task is important in terms of accurately understanding migrant behavior and ecology, and is vital to proper conservation of migrant species.