

# LEAP-FROG MIGRATION IN THE FOX SPARROW: MINIMIZING THE COST OF SPRING MIGRATION<sup>1</sup>

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**Abstract.** Leap-frog migration patterns are explicable in terms of the independent optimization of wintering location by different populations, without any need for assumptions concerning asymmetric competition between individuals from different breeding areas. The main factor influencing variation in choice of wintering site is the cost of spring migration in relation to its timing and the route taken. Among Fox Sparrows *Passerella iliaca* breeding on the west coast of Canada, later breeding northerly populations minimize the cost of spring migration by wintering in California, where food availability improves in early spring, enhancing conditions for premigratory fattening. This improvement occurs too late in the year for early breeding southerly populations which therefore truncate their migration. The southern wintering location of Alaskan populations is explicable if good conditions for premigratory fattening are particularly critical for populations undergoing a trans-oceanic migration.

**Key words:** time allocation, survival, migration route, seasonality, evapotranspiration, leap-frog migration, Fox Sparrow.

## INTRODUCTION

A central problem in the study of bird migration concerns the redistribution in winter of local breeding populations. In principle each individual or local population should choose the wintering site which confers the maximum rate of survival outside the breeding period, inclusive of the cost, if any, of getting there and back. The assumption is frequently made that, in terms of intrinsic qualities such as food supply, climate, security from predation, and accessibility, this optimal wintering location will be similar for populations originating across wide areas of the breeding range, especially those within a longitudinal corridor which share a migration route. Clearly, density-dependent factors will prohibit the use of the same site by all of these populations, a fact which drives the subsidiary assumption that the redistribution of breeding populations in winter is governed by the outcome of competitive interactions. In particular, patterns in which northern breeding populations leap-frog their southern neighbors to produce a mirror image of their respective breeding distributions in winter are attributed to asymmetric competition in which southern breeders have an advantage (Pienkowski et al. 1985, Wallin et al. 1987, Boland 1990, Drent and Piersma 1990).

Under this scenario, the extra mortality suffered by northern populations attributable to the extension of migration is less than would be suffered in competition with southern breeders in a shared wintering site, due to their relative disadvantage in competition.

There remain considerable doubts however, over whether such an asymmetry really exists and whether leap-frog patterns in general can be attributed to it. If southern breeders are generally larger than those in the north, body size related dominance could provide a rationale for asymmetric competition, but there appear to be many migratory patterns in which a leap-frogged population consists of smaller individuals (Salomonson 1955, Alerstam and Högstedt 1985). Alternatively, if southern populations are able to arrive first on wintering grounds because of their earlier breeding schedule, prior occupancy of sites could provide a competitive edge which could lead later arrivals to lengthen their migration (Holmgren and Lundberg 1993). However it is far from certain whether southern populations do in general arrive on wintering sites first, and in some species northern wintering populations are composed mainly of birds which arrive relatively late (Severinghaus 1996). There also is reason to doubt whether prior occupancy alone can confer a significant competitive advantage (Lindström et al. 1990).

Although density dependence and the result-

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ing competition are undoubtedly important in wintering populations, this does not necessarily mean that they cause observed patterns of migration. A different approach to the explanation of such patterns considers factors which cause populations to differ in their optimal wintering site, regardless of any interaction between them. One example of this alternative, generally referred to as the "arrival time" hypothesis, is based on von Haartman's (1968) observation that residency may be evolutionarily stable, even if it results in low over-winter survival, if the following spring it confers prior access to mates and breeding resources such as nest sites. Its potential to explain leap-frog patterns relies on the assumption that wintering nearer to the breeding site also confers the benefits of prior access (Alerstam and Högstedt 1980), but this becomes less likely as the distance between breeding and wintering areas increases, and is implausible for populations which migrate long distances between the Temperate Zone and the Tropics (Myers 1981).

Fewer assumptions are required by the "time allocation" hypothesis, which states that the optimal wintering latitude of a breeding population is determined by the length of its viable breeding season (Greenberg 1980). Among high latitude breeding populations with short breeding seasons (Baker 1938), the most important mortality factor is the rate of mortality experienced on the wintering site, because a large proportion of the year will be spent there. If this rate is high, the cumulative mortality experienced over the winter as a whole will be excessive, so there is a high priority on sites with low rates of mortality, which are frequently in areas with mild winter climates, distant from the breeding range. By contrast for low latitude populations with long breeding seasons, which spend only a short time on the wintering grounds, the most important mortality factor is that associated with migration. This is minimized by adopting a short-distance migration strategy, which is possible because the higher rate of mortality in closer wintering sites with harsher winters is suffered for only a short period. The independent optimization of migration strategy by each population therefore leads to a leap-frog pattern.

The time allocation hypothesis has been criticized on the grounds that in some species, individuals which migrate to the southern end of the wintering range spend a shorter period on

their chosen wintering site than individuals wintering farther north (Myers et al. 1985, Hestbeck et al. 1992), although the examples cited are not generally leap-frog migrants. Another criticism has been that Greenberg's original presentation makes no provision for variation in mortality rates over the wintering period, or for variation in migration mortality according to the timing of migration to and from the wintering site (Pienkowski and Evans 1984). However, I recently have argued that an extension of the hypothesis which takes account of these factors provides a sufficient explanation of leap-frog migration patterns and of patterns of redistribution of populations in winter in general (Bell 1996). Here the model will be applied to the pattern generally considered to exemplify leap-frog migration, that of the winter distribution of the Pacific coast populations of the Fox Sparrow *Passerella iliaca* (Swarth 1920).

#### MODEL OF OPTIMAL WINTERING LATITUDE

The model assumes that optimal wintering latitude is determined primarily by the intrinsic relative suitabilities of the range of possible wintering sites, i.e., the relative probability of survival on a site when density-dependent effects are essentially nil. This is not the same as assuming an absence of density dependence, only that the patterns observed are the result of factors other than density dependence. As a first approximation, the migratory strategy adopted by each individual should maximize its probability of survival between the end of one breeding season and the beginning of another. Frequently there will be a trade-off between survival during migration and survival through the winter period, as longer migrations may result in better conditions for survival (Greenberg 1980). However, both the cost of migration and the rate of survival at any given wintering site will vary according to the time of year as availability of resources, such as food, varies in tandem with climate.

Ideally, variation in food availability across a range of wintering sites would be measured in the field by sampling components of a species' diet, such as arthropods or seeds. However in the absence of such data, a rough estimate of abundance of a range of potential food items can be derived from estimates of actual evapotranspiration (AE), which is thought to index primary

productivity (Rosenzweig 1968). Food availability for individual consumers depends both on productivity and the population density of consumers which share the food resource. Species of consumers which are resident at a site are thought to have their populations limited by the amount of food available at the time of year when productivity is lowest (Ashmole's hypothesis, Lack 1968). At other times therefore, an excess of food is available which can be used for breeding, and numbers of offspring produced have been found to correspond to the size of this excess (Ricklefs 1980, Koenig 1984, Møller 1986). Among bird communities which experience an influx of migrants at certain times of the year, clutch size is often higher than expected, as densities of residents are further restricted by inter-specific competition from migrants (Ricklefs 1980, Yom-Tov 1994). The corollary of this is that food availability for migrants is related to the density of residents, determined by the annual productivity minimum. The amount by which productivity exceeds this level (henceforth "excess AE") can therefore be used, in the absence of extensive field data, to provide a rough index of food availability for migrants.

For an individual, the relationship between food availability and survival should approximate a threshold response occurring at the point where weight can just be maintained, and probability of survival for a population can therefore be modeled using a sigmoid curve such as a logistic, whose inflexion occurs at the mean of the thresholds for all of the members of the population. If a period of winter residency is divided into half month periods, the probability of survival over the period as a whole is as follows:

$$S_w = \prod_{i=1}^n \frac{\exp(a + bV_i)}{1 + \exp(a + bV_i)} \quad (1)$$

where  $S_w$  is the probability of over-winter survival,  $n$  is the half month before spring migration, and  $V_i$  is excess AE during half month  $i$ . Cost of migration on the other hand is primarily determined by distance covered and can be modeled as follows:

$$S_m = \exp(-C_a[lat_s - lat_w]) \cdot \exp(-C_s[lat_s - lat_w]) \quad (2)$$

where  $S_m$  is the probability of surviving migration (both legs),  $C_a$  and  $C_s$  are the rate of mortality suffered per degree of latitude traversed in fall and spring migration, respectively, and  $lat_s$

and  $lat_w$  are breeding and wintering latitudes. Both  $C_a$  and  $C_s$  will be dependent on conditions at the time of migration, but conditions in spring are likely to be much more critical, as any delay to departure caused by food shortage before spring migration may reduce breeding success, adding to the cost of migration to a particular site. Moreover, conditions will tend to worsen in spring as migration progresses, whereas conditions will tend to improve in the fall as birds move southwards to more benign regions (Lindström and Alerstam 1992). Therefore, the success of migration may be most affected by conditions on the wintering ground immediately before spring migration, because under a time minimization strategy (Alerstam and Lindström 1990) most of the fattening required for the migratory journey should take place there, where it can be achieved most quickly. Assuming therefore that these migration costs are linearly dependent on  $V_n$  (excess AE during the half month prior to migration):

$$S_m^* = \exp(-C_a[lat_s - lat_w]) \cdot \exp(-[C_0 + dV_n][lat_s - lat_w]) \quad (3)$$

where  $S_m^*$  is the probability of surviving migration discounted by the effect of any delay in migration beyond the optimal time for breeding on subsequent breeding success,  $C_0$  is the cost of spring migration per degree of latitude traversed, in terms of mortality en route and loss of breeding success when  $V_n = 0$ , and  $d$  is the decrease in these costs per millimeter increase in  $V_n$ , i.e.,

$$S_m^* = \exp([-C + dV_n][lat_s - lat_w]) \quad (4)$$

where  $C = C_a + C_0$ . The optimal wintering latitude is that which maximizes the product of  $S_w$  and  $S_m^*$ .

#### LEAP-FROG MIGRATION IN THE FOX SPARROW

The instance of leap-frog migration generally considered the *sine qua non* of explanatory hypotheses is the winter distribution of the western races of the Fox Sparrow *Passerella iliaca* (Swarth 1920). The status of this distribution as the exemplar of leap-frog migration patterns is to some extent unfortunate because, although there are elements of a leap-frog pattern in this distribution, a number of factors confound both the leap-frog pattern and its interpretation. For instance, the breeding areas of populations

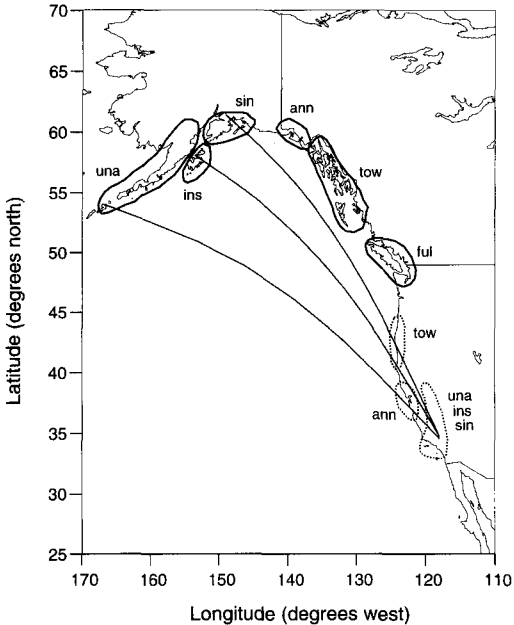


FIGURE 1. Distribution of the western races of the Fox Sparrow during breeding and the period of winter residency. Trans-oceanic great circle routes between breeding locations and the main wintering site of these populations in southern California are indicated. If great circle routes are indeed followed, then the migration of the population of Unalaska Island is a candidate for the longest ocean crossing undertaken by any landbird, exceeding the crossing of the Atlantic performed by nearctic breeding populations wintering in west Africa, and crossing of the Indian Ocean by Asian breeding populations wintering in east Africa. During fall migrations tailwinds can be expected for the entire migratory journey between the Aleutian Islands and California, whereas during spring crosswinds predominate during the early part of the journey, with tail winds towards the end (Bryson and Hare 1974). Labels: una = *Passerella iliaca unalaschensis*, ins = *P. i. insularis*, sin = *P. i. sinuosa*, ann = *P. i. annectens*, tow = *P. i. townsendi*, ful = *P. i. fuliginosa*. The latter subspecies is mainly resident.

which winter in southern California are only marginally the most distant from the wintering area, a fact which is not immediately obvious from the illustration used in Swarth's (1920) paper, and frequently reproduced elsewhere (e.g., Faaborg 1988, Welty and Baptista 1988), because of the orthographic projection used. One of these populations, *P. i. unalaschensis*, has a breeding distribution with a latitudinal range similar to that of *P. i. townsendi* which winters much further north, and *P. i. insularis* and most *P. i. unalaschensis* breed to the south of *P. i.*

*annectens* which also has a relatively northern wintering range (Fig. 1).

Ignoring the three western subspecies, a leap-frog pattern can be discerned among *P. i. annectens*, *P. i. townsendi* and *P. i. fuliginosa*. The latter population is primarily resident, so that its northern wintering latitude is readily explicable in terms of von Haartman's hypothesis. As *P. i. townsendi* is a relatively short distance migrant, the arrival time hypothesis cannot be entirely ruled out as an explanation for its wintering latitude. However, an alternative explanation is suggested by the application of the model described in the previous section. Figure 2 shows the trend in excess AE for the coastal region of western North America during the wintering period of the Fox Sparrow, derived as a polynomial approximation of monthly variation in excess AE for climatic stations covering a range of latitudes. During the spring migration period, a wave of productivity crosses the species' wintering range, starting in the south and moving

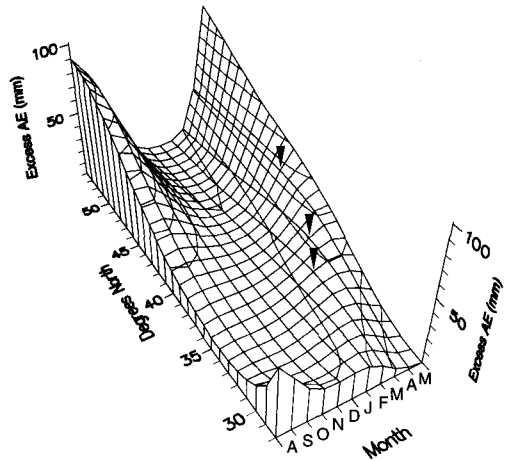


FIGURE 2. Model of excess AE (actual evapotranspiration) between August and May, for the coastal region of western North America. Estimates of actual evapotranspiration for eight locations along the west coast of North America (data from Bryson and Hare 1974) were derived using the method of Thornthwaite and Mather (1957). Monthly excess AE was then calculated subtracting from each estimate the lowest monthly value for the location (data available from author). The polynomial is of the form  $a + 1 + l^2 + l^3 + l^4 + m + m^2 + m^3 + m^4 + m^5 + lm + lm^2 + lm^3 + lm^4 + lm^5 + l^2m + l^3m + l^4m$ , and explains 83.5% of the variance in excess AE among estimates calculated for eight locations. Arrows denote latitude corresponding to peak excess AE at the end of February, March and April, respectively.

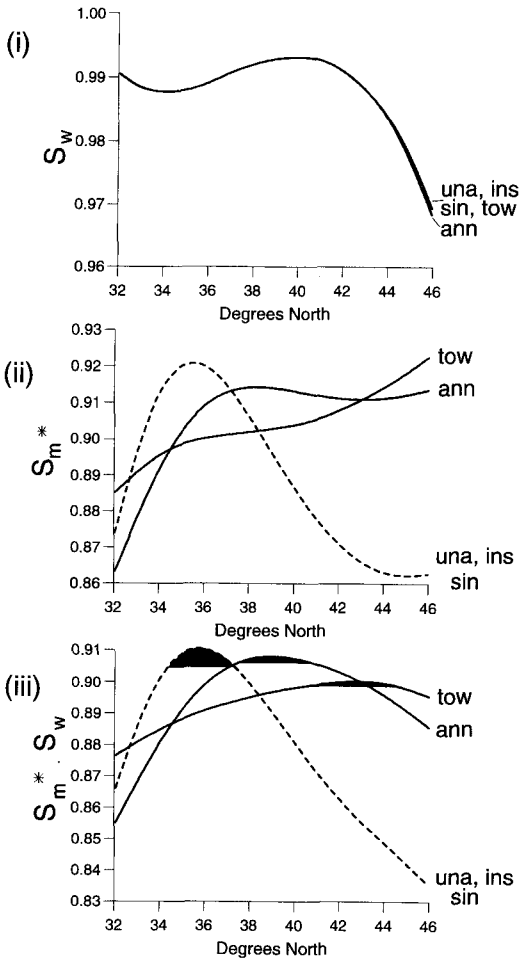


FIGURE 3. Consequences for fitness of (i) winter residence period, (ii) spring and fall migration combined, and (iii) migration and winter residence, according to the model of optimal wintering latitude, for the populations with breeding ranges and migratory habits corresponding with those of the western races of the Fox Sparrow (see text for definition of  $S_w$  and  $S_m^*$ ). All populations are assumed resident in the wintering area from the beginning of October, and  $V_i$  values for a given latitude are derived from the model of excess AE shown in Figure 2. *P. i. townsendi* is assumed to breed at 56°N and to depart the wintering area in mid-March, *P. i. annectens* is assumed to breed at 60°N and to depart in mid-April. The populations of western Alaska are represented by a population assumed to breed at 58°N and to depart at the end of March. Dates are derived from information given in Swarth (1920) and Bent (1968). Parameters of the model are given the following values:  $a = 0.5$ ,  $b = 1.0$ . For *P. i. townsendi* and *P. i. annectens*,  $C = 0.01$  and  $d = 0.0004$ , whereas for the western Alaskan subspecies,  $C = 0.02$  and  $d = 0.0012$ , reflecting the greater rate of migration mortality resulting from a trans-oceanic migration, and the greater benefit derived from

north, increasing in magnitude as it does so, with a low peak at about 35°N at the end of February, a higher peak at about 37°N at the end of March, and a still higher peak at about 42°N at the end of April.

Similar wave patterns are detectable crossing the wintering ranges of other leap-frog migrants during the period of spring migration (Bell 1996), so that frequently only late-departing populations wintering in the southern part of the wintering range experience any improvement in food availability before departure for the breeding grounds. As a seed eater, the Fox Sparrow might be expected to experience a peak in food availability somewhat later than the peak of primary productivity. However, this species shows a marked preference for weed seeds outside the breeding season (Bent 1968), and in California the growth cycles of annual herbs take place in advance of other forms of vegetation, starting in the fall after the breaking of the summer drought and ending in spring when the surface layers of the soil begin to dry out (Mooney 1983). Consequently, production of seeds of the kind favored by Fox Sparrows should coincide with the spring peak in productivity, at a time when deeper rooted plants are undergoing maximum growth and still preparing for fruiting. Northern breeding Fox Sparrow populations which remain longer on the wintering grounds, may be able to take advantage of this surge in food availability for premigratory fattening, thereby reducing the cost of a longer migration. This is not an option for southern breeding populations which leave the wintering area before food availability improves anywhere in the viable wintering range and therefore winter as far north as possible.

The data needed for estimation of the values of constants used in equations 1–4 are unavailable. Nevertheless all values of  $a$  and  $b$  which give reasonable over-winter survival rates result in very similar latitudinal survival profiles for populations which vary in departure date, and predict a steady decline in survival north of about 40°N, even when (food-related) survival

←  
good conditions during the period of pre-migratory fattening. The resulting curves predict the wintering latitudes of the populations in question, with shaded areas in (iii) showing latitudinal ranges for an arbitrary population size for each subspecies under ideal free conditions.

is assumed to be close to unity in southern parts of the wintering area (Fig. 3i). Low over-winter survival may therefore explain the absence of Fox Sparrows from northern latitudes in winter, but cannot account for differences in wintering latitude between various populations.

In contrast, when migration costs per unit distance are significant, migration cost curves vary markedly with breeding latitude (Fig. 3ii). The cost of reaching viable wintering latitudes are obviously greater for northern breeding populations which have further to travel. Moreover, if food availability prior to spring migration significantly affects migration costs, then the outcome also varies according to timing of spring departure. Greater food availability further south reduces the cost of extending migration, but this effect is much more pronounced in *P. i. annectens* than in *P. i. townsendi*, as the former departs later in the year when the productivity wave is larger and farther north (Fig. 3ii). The optimal wintering latitude for *P. i. annectens* predicted by the model therefore will be always south of that predicted for *P. i. townsendi*, regardless of the values ascribed to  $C$  and  $d$  in equation 4; the observed wintering latitudes can be easily reproduced given an appropriate ratio between these two constants (Figure 3iii).

The extreme southern winter distribution of *P. i. sinuosa*, *P. i. insularis* and *P. i. unalaschensis* would appear to defy explanations based on the relationship between migration cost and timing of spring migration however, as their breeding ranges cover much the same latitudinal range as those of the more northern wintering *P. i. annectens* and *P. i. townsendi*, so they should quit the wintering grounds over a similar time period (Fig. 1). However, a number of observations reported by Swarth (1920) suggest a fundamental difference between the migration strategies of the three western subspecies and the two eastern ones. Swarth reported a dearth of specimens from the three western subspecies from the western coast of Canada, suggesting that their migration follows a great circle route involving a trans-oceanic journey, and a landfall on the western coast of the United States (Fig. 1). If this is so, while the migrations of the two eastern subspecies merely follow the coast, the costs involved in migration almost certainly differ profoundly between the two groups, so that different values of the migration cost parameters in the model ( $C$  and  $d$ ) are appropriate. In partic-

ular, a trans-oceanic journey is likely to increase the criticality of acquiring a sufficient fat load, so that the effect of  $V_n$  on  $S_m^*$  (equation 4) is likely to be greater than in populations which follow the coastline. This difference can be accommodated in the model by increasing the value of  $d$  in relation to  $C$  in equation 4, the effect of which is to shift the predicted optimum wintering latitude to the south (Fig. 3iii). A similar principle may apply in other cases where some populations of a species have a trans-oceanic journey, whereas others do not. For instance, some populations which winter in the Old World and breed in Iceland or Greenland have more southerly winter distributions than populations which breed on the European continent (Davis 1966, Taylor 1980), resulting in a leap-frog pattern of sorts.

## DISCUSSION

Individual optimization of wintering latitude by populations with different breeding latitudes, timing of spring migration, and migration routes, seems therefore to offer a sufficient explanation of leap-frog migration among west coast Fox Sparrow populations without recourse to assumptions concerning asymmetric competition. Moreover, the two main competition scenarios seem unlikely in this case. Linear measurements of samples of each sub-species taken by Swarth (1920) give no indication of a decreasing size gradient from north to south among wintering populations, and bill size at least is larger in southern winterers. No particular pattern is apparent in dates of arrival on the wintering grounds of different populations, which all arrive in northern California in mid to late September, with *P. i. annectens* and *P. i. townsendi* on the coast and the western Alaskan populations in the northern Sierra Nevada (Swarth 1920). The presence of Fox Sparrows in the Sierra foothills is mainly confined to the fall, with very few records from mid-winter (cf. appendices in Swarth 1920). Birds following a great circle route from Alaska to southern California would overfly the western flank of the Sierra Nevada, and their presence there during the fall parallels the habits of migrants elsewhere, which seem attracted to highland areas during post-nuptial migration, perhaps because of high food availability (Dolnik 1990).

If the model presented here is an accurate account of the processes which give rise to the

migration pattern of Pacific coast populations of the Fox Sparrow, it should be possible to confirm a number of critical predictions concerning the feeding and fattening behavior of the various populations in the period before spring migration. Under a time minimization strategy, the population of *P. i. townsendi* would be expected *a priori* to take on lesser fat loads than *P. i. annectens*, as they have a shorter journey. However, they also should fatten more slowly because of lower food availability, which should be reflected by a lower peck rate during the pre-migratory period, or a greater proportion of the time budget devoted to feeding. The western Alaskan subspecies should experience the highest food availability and achieve the highest rate of fattening, despite doing so earlier than *P. i. annectens*, and also may accumulate substantially greater fat loads than the two more northerly wintering populations in order to complete successfully their trans-oceanic migration.

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