

Bird Migration Patterns: Conditions for Stable Geographical Population Segregation

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Migration costs, increasing with increasing distance, and asymmetric competition between stationary and migratory individuals, and between individuals arriving early and late at the same destination, lead to latitudinal as well as longitudinal segregation between migratory bird populations. The evolution of leapfrog migration (winter quarters of different populations situated in reverse latitudinal sequence to the breeding sites) is promoted by asymmetric competition, particularly if such competition occurs for both breeding and wintering resources, and if migration costs are important as well. Asymmetric competition may also lead to a chain migration pattern (winter and breeding ranges in the same latitudinal sequence), if breeding and/or wintering suitability increases markedly towards the latitudinal extremes. Furthermore, chain migration also develops if there are migration costs but no asymmetric competition. Transition patterns between leapfrog and chain migration are stable under a narrow range of intermediary conditions. Strong asymmetric competition is expected to be associated with adaptive strategies used by the migrating birds to minimize the total time for the migratory journey, whereas high migration costs are expected to be associated with adaptations for minimizing risks and energy expenditure during migration.

1. Introduction

The breeding and wintering ranges of many migratory bird species have a wide latitudinal extension. Nilsson (1858) proposed that the winter quarters of different populations are situated in the same latitudinal sequence as their breeding areas, a pattern we will call "chain migration". Palmén (1874) compiled information about the nonbreeding occurrence of several species breeding in the North Palaearctic. On this basis, he concluded that, besides chain migration, a "leapfrog migration" pattern is often manifest, both within species and between closely related and ecologically similar species. According to this pattern the latitudinal sequence of different populations' wintering areas is the reverse of their breeding areas, i.e. the most northerly breeding populations winter farthest to the south, overflying southerly breeding populations.

Ringing results have since confirmed Palmén's conclusion, and Salomonsen (1955) reviewed many examples of chain and leapfrog migration, as well as cases with no wintering segregation between different breeding populations. In some species the situation is complex, with elements of both chain and leapfrog migration. Salomonsen noted that a leapfrog tendency is widespread, whereas chain migration "is not so commonly established as should be expected".

Salomonsen (1955) stressed the importance of intraspecific competition as an ultimate selection force for the development of wintering segregation between populations, but he made no attempt to determine which conditions lead to the different migration patterns observed.

Alerstam & Högstedt (1980) suggested that leapfrog migration primarily arises because of a differential advantage of wintering close to the breeding sites, between southerly (temperate)-breeding and northerly (arctic)-breeding populations. In the former populations, birds remaining during winter in the temperate climatic zone can migrate to their adjacent breeding areas as soon as suitable spring conditions develop. Such an early spring arrival, adapted to yearly variations in spring climate, may constitute an important advantage in the competition for breeding resources. This is not feasible for birds breeding in the arctic zone, which they must leave during winter, thereby losing the possibility of adjusting spring migration to the yearly variation in spring development within their breeding range. Hence, arctic birds may migrate far to the south, avoiding competition with temperate populations, relying on their circannual clock to return to their breeding range at the optimal average time.

This idea was criticized by Pienkowski *et al.* (1985), suggesting an alternative hypothesis: They assumed that, because of migration costs, it is advantageous for birds to winter as close to their breeding grounds as possible. Dominant individuals, from populations with a relatively large average body size, will outcompete individuals from populations with a smaller body size, forcing the latter birds to continue their autumn migration to more southerly latitudes. Hence, leapfrog migration will occur when southerly-breeding populations, for reasons unknown, have the largest average body size, while the reverse will lead to chain migration.

Alerstam & Högstedt (1985) pointed out that there exists evidence contrary to both of these hypotheses. They also noted that a more general understanding of the conditions promoting geographical wintering segregation between different breeding populations, and breeding segregation between different wintering populations, is still lacking.

Asymmetric competition between stationary and migratory individuals, and between individuals arriving early and late, probably is of crucial importance in the evolution of bird migration (von Haartman, 1968; Alerstam & Enckell, 1979). Northerly residents (throughout this paper we adopt a northern hemisphere-perspective) have temporal priority to the most favourable nest-sites and breeding territories. Migration to southerly wintering areas will evolve when the associated benefit in survival more than compensates for the disadvantage in the competition for breeding resources (von Haartman, 1968).

Analogously, southerly residents have priority to the most favourable wintering sites. Migration to northerly breeding areas will evolve when the benefit in reproduction more than compensates for the competitive disadvantage in the southerly survival areas. Consequently, the evolution of bird migration will be facilitated in situations with a not too strong influence of asymmetric competition associated with temporal priority, like in highly seasonal and unpredictable habitats, or with resources that are difficult to monopolize and defend (Alerstam & Enckell, 1979). But this

does not preclude that there may be many instances where asymmetric competition associated with temporal priority to breeding or wintering sites, or both, is in operation between individuals from different migratory (and resident) populations. The evolution of migration systems may also be affected by interspecific competition, as discussed by Cox (1985).

We will investigate the importance of such asymmetric competition, under different regimes of migratory costs and resource availability, for the development of bird migration patterns. We will try to throw light, besides on latitudinal patterns, also on longitudinal segregation between migratory populations, i.e. "parallel migration" in Salomonsen's (1955) classification, including the development of migratory divides.

2. Latitudinal Segregation

(A) A POPULATION SIMULATION MODEL

Let a matrix $x = (x_{ij})$ describe the migration pattern of a species. Each entry x_{ij} of this matrix denotes the number of individuals breeding at site i and wintering at site j . Sites are numbered latitudinally from north to south, and $i \leq j$. For our calculations we have adopted a system with five latitudinal sites, where breeding is possible only at sites 1, 2 and 3, and over-wintering only at sites 3, 4 and 5. Basic types of migration patterns are exemplified in Fig. 1.

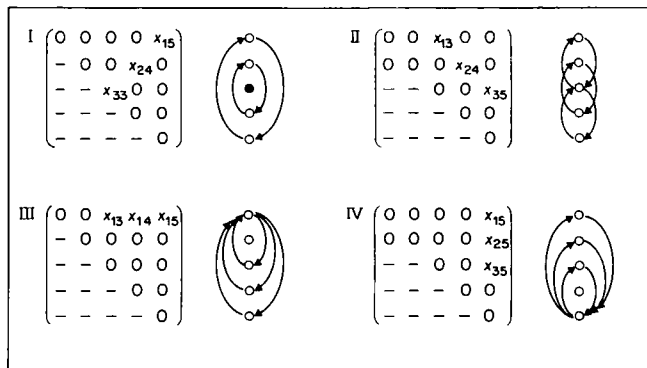


FIG. 1. Matrices showing some basic types of latitudinal bird migration patterns. Rows correspond to different breeding latitudes and columns to wintering latitudes. Migrations between the five latitudinal sites are illustrated for each matrix to the right. Filled symbols denote sites with a resident population. Breeding is assumed to be possible only at sites 1, 2 and 3, and wintering only at sites 3, 4 and 5.

The change in population x_{ij} from one year (breeding population size) to the next is given by

$$(x_{ij})_{t+1} = (x_{ij})_t R_{ij} p_{ij} S_{ij} q_{ij} \quad (1)$$

where R_{ij} is the reproductive rate, S_{ij} the winter survival, and p_{ij} and q_{ij} the autumn and spring migration survival, for individuals breeding at site i and wintering at site j .

The reproductive rate is given by

$$R_{ij} = B_i \left[1 - K_{b,i}^{-1} \sum_k (\alpha_{i,jk} x_{ik}) \right] \quad (2)$$

where B_i is the breeding suitability at site i (i.e. the reproductive output without competition), $K_{b,i}$ is a measure of the total availability of breeding resources at this site, and $\alpha_{i,jk} = \exp[a(j-k)]$ is the competition effect at breeding site i of individuals from population x_{ik} on x_{ij} . Hence, with $a > 0$ asymmetric competition takes place, favouring individuals from northerly wintering sites because they presumably can arrive first to the breeding site. With $a = 0$, individuals from all different wintering sites compete on equal terms.

Migration costs are assumed to be proportional to migration distance, such that $p_{ij} = S_1 - d_1(j-i)$, and $q_{ij} = S_2 - d_2(j-i)$ for $0 < p, q, S_1, S_2 \leq 1$.

The winter survival is given by

$$S_{ij} = W_j \left[1 - K_{s,j}^{-1} \sum_v (\alpha_{iv,j} x_{vj} R_{vj} p_{vj}) \right] \quad (3)$$

where W_j is the wintering suitability at site j (i.e. the winter survival without competition, $0 \leq W_j \leq 1$), $K_{s,j}$ is a measure of the total availability of winter survival resources at site j , and $\alpha_{iv,j} = \exp[c(v-i)]$ is the competition effect at wintering site j of individuals from population x_{vj} on x_{ij} . With $c > 0$ asymmetric competition is assumed, favouring individuals from southerly breeding areas because they presumably can arrive first to the wintering site. With $c = 0$, winter competition takes place on equal terms between all individuals.

Computations for a particular set of conditions (defined by the variables in equations (1)–(3)), were initiated with all entries x_{ij} in the migration pattern matrix equal, and lasted 150 iterations (breeding and wintering cycles). After that number of iterations the resulting migratory pattern generally was stable or almost stable (differing to an insignificant extent from the stable pattern emerging after additional iterations). Supplementary computations indicated that the emergent stable migration patterns were not dependent on the set of initial x_{ij} values.

The influence of asymmetric competition and migration costs on the development of different migration patterns is illustrated in Fig. 2. When assuming latitudinal gradients in breeding and wintering suitability, we have restricted our attention to what is probably the most general conditions, i.e. that breeding suitability increases towards the north and that wintering suitability increases towards the south. However, one might note that in cases without suitability gradients, the effects caused by migration costs are similar to what would result by assuming reverse suitability gradients, where breeding in the far north and wintering in the far south is less favourable than breeding and wintering at intermediate latitudes.

Segregation will not occur if there are neither asymmetric competition ($a, c = 0$) nor migration costs ($d_1 = 0, d_2 = 0$; Fig. 2(a), bottom row). Hence we examine the conditions promoting leapfrog or chain migration with one or both of these factors in operation.

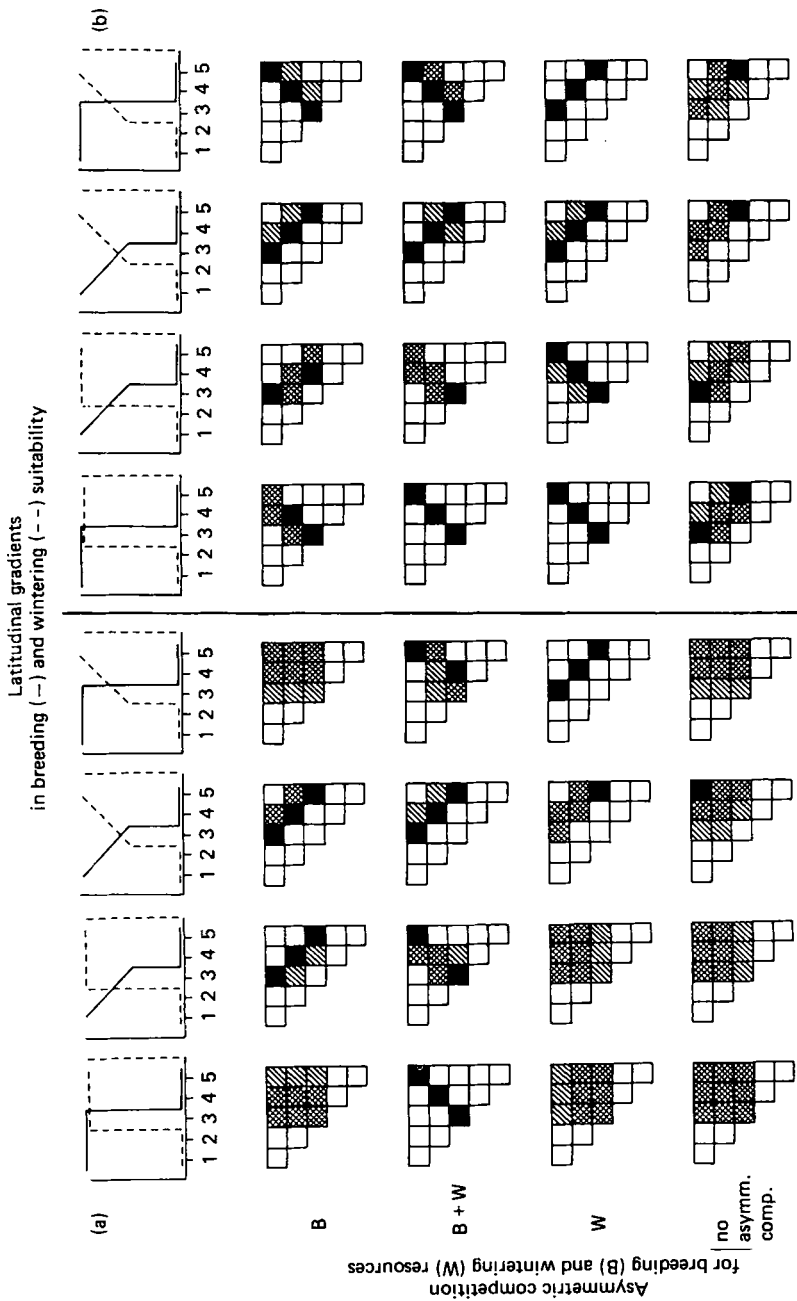


FIG. 2. Stable migration patterns under different latitudinal gradients in breeding and wintering suitability (four conditions, one for each column in (a) and (b), as illustrated), with asymmetric competition for breeding ($a > 0$) or wintering resources ($c > 0$), or both ($a, c > 0$), or without asymmetry in the competition between individuals from different migratory populations ($a, c = 0$). (a) and (b) illustrate cases without ($d_1, d_2 = 0$) and with migration costs ($d_1, d_2 > 0$), respectively. Matrices, show sizes of the different populations x_{ij} in relation to the total species population size (breeding population). $\square < 4\%$, $\square 4-10\%$, $\square 10-20\%$, $\blacksquare > 20\%$.

(B) MIGRATION PATTERNS WITH ASYMMETRIC COMPETITION BUT
WITHOUT MIGRATION COSTS

Asymmetric competition is a sufficient agent to bring about either leapfrog or chain migration; the outcome depends on the latitudinal gradients in breeding and wintering suitability (Fig. 2(a)).

Chain migration is the typical outcome when asymmetric competition takes place during one season only and when there is a suitability gradient present that season. Asymmetric competition for breeding resources conveys an advantage to individuals in the northern part of the winter range, because they can arrive first at the breeding sites. If the breeding suitability increases towards the north, it will be favourable for those individuals with a competitive edge to migrate to the northernmost breeding latitudes. In such a case, populations of birds wintering northerly and migrating to less distant breeding sites will become reduced or eliminated by the combined pressure of winter competition from northerly breeders and breeding competition from birds arriving from more southerly winter latitudes (although the latter competition pressure will be alleviated by the asymmetry in breeding competition). As a consequence, chain migration will develop.

However, if breeding suitability does not increase towards the north, as assumed above, but rather decreases, leapfrog migration will develop (not shown in Fig. 2). Without latitudinal differences in breeding suitability, there will be no geographical segregation.

Asymmetric winter competition conveys an advantage to individuals in the southern part of the breeding range. By an argument analogous to that given above for asymmetric breeding competition, one can see why chain migration develops when wintering suitability increases towards the south (Fig. 2(a)), leapfrog migration if there is a reverse latitudinal gradient in wintering suitability (not shown in Fig. 2), whereas there will be no segregation in absence of gradients.

Leapfrog migration tends to develop more readily if there is asymmetric competition for both breeding and winter resources. Individuals using their competitive advantage in the breeding season to migrate from northerly wintering latitudes to northerly breeding latitudes, will incur the costs of ranking lowest in the competitive hierarchy during the winter. By the same token, individuals using their competitive edge in the non-breeding season to migrate from southerly breeding latitudes to southerly wintering latitudes will be competitively inferior during summer. Only birds using northerly wintering grounds in combination with southerly breeding areas benefit from a competitive advantage in both seasons. As a consequence, leapfrog migration will be promoted, even if there is a moderate increase in breeding suitability towards the north or a moderate increase in wintering suitability towards the south.

Only if the suitability gradients are very steep, and particularly if they are present during breeding as well as during winter, will they override the benefit gained by birds both breeding and wintering at intermediate latitudes. In these cases, chain migration or transition patterns (see below) will be the result, rather than leapfrog migration. The stronger the effect of asymmetric competition, the more extreme

latitudinal suitability gradients are needed to counteract the development of leapfrog migration.

(C) MIGRATION PATTERNS WITHOUT ASYMMETRIC COMPETITION
BUT WITH MIGRATION COSTS

Somewhat paradoxically, the inclusion of migration costs in the absence of asymmetric competition leads to the elimination of resident populations, and to the development of chain migration (Fig. 2(b), bottom row). Long-distance migrants, travelling between the far north and the far south, suffer most from this cost. As a result there will be free space at the latitudinal extremes for birds from intermediate latitudes to occupy with moderate migration costs. At the same time, competition will be fierce at these latitudes during both winter and summer. Since there is no asymmetry giving the residents an upper hand in this competition, they will be eliminated.

(D) MIGRATION PATTERNS WITH ASYMMETRIC COMPETITION
AND MIGRATION COSTS

Comparing cases with asymmetric competition in Figs 2(a) and 2(b), one finds that the introduction of migration costs leads to an increased tendency to leapfrog migration. Why this should be so is not obvious, considering the fact that migration costs in isolation promotes chain migration.

From a competitive point of view, there is relatively little to be gained by birds from middle latitudes in exploiting the competitive release at northerly breeding latitudes or southerly winter latitudes, which is associated with the high migration losses suffered by populations of long-distance migrants. This is so because birds from intermediate latitudes already have a competitive advantage, due to asymmetric competition. Hence, for these birds the direct cost of migration to the northerly breeding latitudes or southerly winter latitudes overshadows the possible indirect competition benefits, and the development of leapfrog migration is promoted.

With gradients in breeding or wintering or both steep enough to counteract this benefit of residency to birds of middle latitudes, chain migration will develop, as seen for several cases in Fig. 2(b).

(E) TRANSITION PATTERNS BETWEEN LEAPFROG MIGRATION
AND CHAIN MIGRATION

A leapfrog migration system transforms to chain migration via intermediary patterns with geographical population segregation, with an accentuated increase in breeding suitability towards the north, or in wintering suitability towards the south, or a combination of both. Examples of such transition patterns are given in Fig. 3. The transition patterns show elements of both leapfrog and chain migration. They are stable only under a relatively narrow range of conditions in the total parameter space of different asymmetric competition coefficients, migration costs and suitability

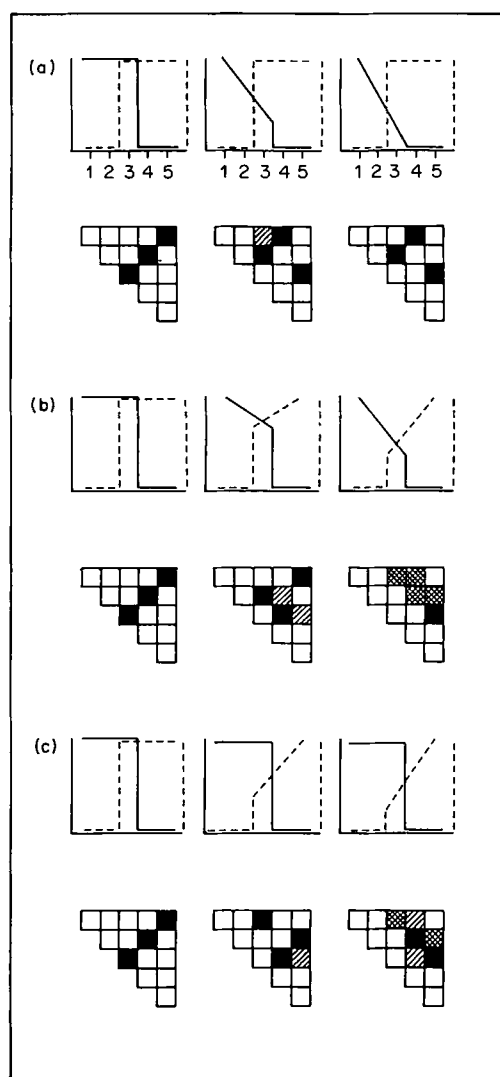


FIG. 3. Stable transition patterns between leapfrog and chain migration occur under intermediary conditions of latitudinal gradients in breeding suitability (a), in both breeding and wintering suitability (b) or in wintering suitability (c). Below the graphs illustrating latitudinal gradients in breeding and wintering suitability are shown the associated migration pattern matrices (cf. Fig. 2). Cases exemplified in this figure were calculated assuming asymmetric competition for both breeding and winter resources, with no migration costs (same conditions as for cases shown in Fig. 2(a), second row). \square <4%, \square 4–10%, \square 10–20%, \blacksquare >20%.

gradients. Hence, these complex patterns are expected to occur only rarely or exceptionally in nature.

3. Longitudinal Segregation

We analysed longitudinal breeding segregation between two major wintering populations by a simulation model incorporating the effects of migration costs (proportional to the straight-line distance between breeding and wintering sites), asymmetric winter competition (disfavouring individuals from successively more distant breeding populations) and asymmetric breeding competition (disfavouring individuals from the most distant of the two wintering areas). Hence, birds with a short migration distance are assumed to have a competitive advantage, because presumably they can arrive relatively early to the breeding and wintering quarters.

Distinct longitudinal breeding segregation with a sharp migratory divide occurs when there are significant migration costs and/or asymmetric winter competition (Fig. 4). With asymmetric breeding competition, such segregation emerges only when winter carrying capacity (K_s) is similar for the two wintering areas. In other cases of asymmetric breeding competition (without migration costs and asymmetric

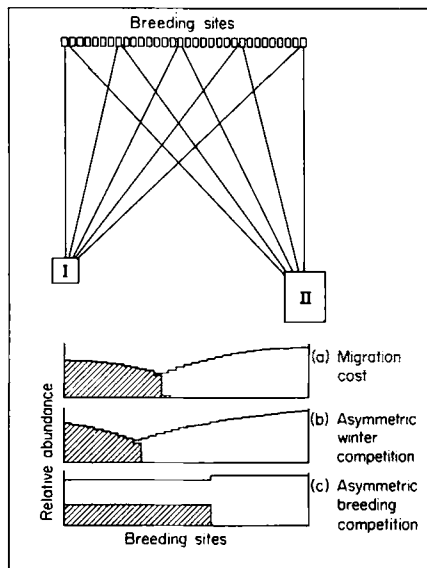


FIG. 4. Relative abundance at different longitudinal breeding sites of individuals from two major wintering populations, I (hatched) and II. Stable patterns with migration costs (a), and with asymmetric competition for wintering (b) and breeding (c) resources, respectively, are shown in the lower three diagrams. The basic model is illustrated in the uppermost part of the figure: Two major wintering sites, one with three times as much resources for winter survival as the other, are situated at slightly different distances from the breeding latitude. We used a system with 32 longitudinal breeding sites. Computations were initiated with all possible migratory populations equal, and lasted 250 iterations. Migration distances were calculated along the straight lines between the different breeding and wintering sites.

winter competition), longitudinal overlap like that illustrated in Fig. 4 will be the result.

Increasing migration costs and/or asymmetric winter competition may lead to a gap between the breeding distributions of the two populations (cf. the reductions in breeding abundance towards the migratory divides, Fig. 4), to an increasing extent with a decreasing ratio of total resources for winter survival to total breeding resources.

Analogous results apply to the reverse case of longitudinal winter segregation between birds from two major breeding populations.

4. Discussion

Migration costs as well as asymmetric competition between early- and late-arriving individuals are selective agents in the evolution of population segregation among migratory birds. The development of leapfrog migration is promoted by such asymmetric competition, particularly if it applies to both breeding and wintering resources and operates in combination with migration costs.

In contrast, without any asymmetry in the competition between individuals from different populations, the effect of migration costs is to promote the development of chain migration. Chain migration will evolve also when asymmetric competition prevails, if there are strong enough latitudinal gradients in breeding and/or wintering suitability to make it beneficial for individuals from middle latitude populations to use their competitive precedence to migrate to highly suitable sites at the most northerly breeding latitudes or the most southerly winter latitudes.

Transition patterns between leapfrog and chain migration are stable under a narrow range of intermediary conditions with respect to the strength of asymmetric competition and the steepness of latitudinal gradients in breeding and wintering suitability.

Our results demonstrate that leapfrog migration may evolve under a wide range of conditions with asymmetric competition operating in a very generalized way. The hypothesis proposed by Alerstam & Högstedt (1980) to account for leapfrog migration, represents a special case, where asymmetric competition for breeding resources between birds from different winter latitudes is assumed to be important in the temperate zone but not in the Arctic zone.

Our results also show that the conditions stipulated for leapfrog migration according to the alternative explanation suggested by Pienkowski *et al.* (1985) are not sufficient to account for leapfrog migration. Migration costs in combination with asymmetric competition for winter resources through body-size dominance can lead to chain or leapfrog migration, or transition patterns, depending on latitudinal differences in wintering suitability.

Greenberg (1980) advanced a model of optimal allocation of time by migratory birds between the breeding and winter range. Reproductive output was assumed to increase with increasing time in the former range, while survivorship was assumed to increase with time spent in the latter. Given certain gradients in survival and migration costs, leapfrog migration was predicted although no effects of competition

were incorporated in this model. Greenberg claimed that northerly breeding populations should be characterized by a relatively low annual survival rate in a competition-mediated leapfrog migration system, whereas the opposite was predicted from the time-allocation model. However, according to calculations from our simulation model, different cases of leapfrog migration associated with asymmetric competition may show an increase as well as a decrease in survival rate towards the north.

Knowledge about the importance of asymmetric competition and migration costs in migratory birds is critical to judge if our model may provide at least part of the explanation for the development and maintenance of observed migration systems, or if a "non-competition" model like Greenberg's may be relevant (cf. Pienkowski & Evans, 1985). Direct investigations of differences in fitness between individuals arriving early and late, at breeding as well as winter sites, and of mortality associated with migration over different distances, are much needed.

The relative importance of asymmetric competition and migration costs may also be assessed indirectly by analysing behavioural strategies during migration in relation to three main optimization criteria: (1) minimal risk (for predation, disorientation, drift, etc.); (2) minimal energy expenditure; (3) minimal duration of the migratory journey. The first and second criteria are expected to be most important when migration costs are relatively high, whereas the third criterion should be associated with keen asymmetric competition at the destination.

The optimal foraging behaviour of migrants at stop-over sites and the amount of fat reserves deposited before departure are expected to differ with respect to these criteria. Furthermore, the flight speed minimizing transportation costs differs from that minimizing the total duration of the migratory journey. More specifically, the maximum flight range velocity on a given energy reserve, V_{mr} , is found by solving $dP(V)/dV = P(V)/V$, where $P(V)$ is the power curve for bird flight (cf. Pennycuik 1975). In comparison, the flight speed associated with a minimal total migration time to the breeding or wintering destination can be calculated by solving $dP(V)/dV = [P(V) + E]/V$, where E is the average rate of energy accumulation during the refuelling periods in between the successive migratory flights (cf. Alerstam, 1985).

Hence, differences in foraging behaviour, fat reserves and flight speeds between the spring and autumn migratory seasons, and between sex and age classes, populations and species, may provide valuable indications about associated differences in the importance of safety, fuel economy and early arrival, and ultimately about the balance between asymmetric competition and migration costs. These two ultimate factors will act as selective agents not only in the evolutionary process leading to geographical population segregation, but also to differential migration between sex and age classes (cf. Myers, 1981; Gauthreaux, 1982; Ketterson & Nolan, 1983).

We suspect that the advantage of arriving early, in relation to competitors, at their seasonal living stations, is of widespread importance to migratory birds. Much of the migrants' ways of existence, characterized by swiftness and impatience, as well as of the development and maintenance of large-scale migration systems with migratory divides and latitudinal segregation, may derive from this selection force: to be, relative to others, an early bird.

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