Delayed autumn migration as an adaptive strategy of birds in northern Europe: evidence from Finland

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We define delayed autumn migration as an attempt by migratory birds to stay in the north throughout the winter, but to retain the ability to migrate if conditions become unbearable.

Theoretically, the strategy can be expected to evolve in conditions where each winter consists of both mild and cold periods of unpredictable order and strength, and the food supply varies from year to year. The strategy is thus an individual-level one, and the proportion of delay strategists in the population may vary. Support for the existence of delayed autumn migration as an adaptive strategy of birds is found in more southern areas as well, e.g. southern Sweden. The concept is discussed in relation to the strategy of partial migration — dimorphism at the population level — and the phenomenon of "Winterflucht" or "hard weather movements".

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Introduction

The migration patterns of birds are adaptive solutions to the pronounced seasonality of the weather and food supply in northern areas (e.g. v. Haartman 1968, Lack 1968; for a recent review, see Gauthreaux 1982). Food is the crucial factor; the effect of a severe cold spell and snow storms can be alleviated by a good supply of food (e.g. Mikkola 1968, Hildén & Koskimies 1969). Of course, cold weather and a snow cover greatly reduce the food resources available to wintering birds, while the higher metabolic rates in cold weather increase their food requirements (e.g. Kendeigh et al. 1977). Consequently, the climate is a good indicator of wintering conditions in northern areas.

In areas where the winter conditions are critical every year, a bird population is selected for either residents or migrants. But what happens in areas where the conditions vary from year to year with respect to the harshness of the winter, the date of the onset of winter, and the food available to the birds ? The concept of partial migration has been used by Lack (1943–44) and others (see Gauthreaux 1982:130–131) to describe a situation where part of the population leaves the breeding range but another part stays in or near the breeding areas. This kind of partial migration implies that the wintering conditions near the breeding areas are good for part of the population, but not for all of it in all years; usually socially dominant individuals stay, and subordinates migrate (Gauthreaux 1978).

However, the annual variation in wintering opportunities in the north may be determined by climatic changes in the middle of the winter. Might it be possible in such conditions for individuals of some populations to adopt a strategy of *delayed autumn migration*, defined as an attempt to stay in the north through the winter combined with the ability to start migration as late as mid-winter if conditions become unbearable?

Two general considerations support the feasibility of this strategy. First, Lack (1968) and Morse (1971), among others, have maintained that the amount of resources on wintering grounds may often be a decisive limiting factor for northern populations. Second, from the standpoint of resource utilization and territory (including nest site) establishment, it is evidently an advantage to be among the first to arrive at the breeding grounds in spring (Snow 1956, v. Haartman 1968, Fretwell & Lucas 1969, Krebs 1971, Gauthreaux 1982). Both of these factors make it advantageous to stay close to the breeding grounds over the winter whenever this is possible. The same factors are also preconditions for partial migration.

The concept of delayed autumn migration

First, we put the concept of delayed autumn migration into a wider conceptual framework by starting from Levins' (1968) theory of adaptive strategies. Let us assume that winter is always either cold or mild. Then, in Levins' terms, the fitness set defining and measuring the relative fitness of migratory and sedentary populations is concave, i.e. any member of the population breeding in the area is expected either to migrate or to stay. These alternatives can now be compared with each other in different climate conditions; in Levins' scheme, the adaptive function defines a field realizing the fitness set in a certain environment. If mild winters predominate for a longer period (Fig. 1a), the isoclines of the adaptive function are bent towards the sedentary part of the population, which accordingly is selected for. If cold winters predominate (Fig. 1b), the opposite takes place: the isoclines are bent towards the migratory part of the populations, which is favoured.

If cold and mild winters are about equally frequent (Fig. 1c), the adaptive function is symmetrical relative to the two strategies and the population is divided into migratory and sedentary parts. The dichotomy of cold and mild winters is reproduced at the population level, and dimorphism (the strategy of partial migration, e.g. Lack 1943-44) is the result.

In reality, the situation is not symmetrical, however, because harsh winters reduce or even eliminate the sedentary part of the dimorphic populations, while the migratory part is unaffected by winter weather conditions in areas north of its wintering grounds. Great fluctuations of northern wintering populations should follow; indeed, fluctuations in wintering subpopulations are known for several species in Finland (Hildén 1968, 1982, Hildén & Koskimies 1969).

The assumption of a strict dichotomy between cold and mild winters is, however, obviously unrealistic. A more realistic assumption is that each winter consists of both mild and cold periods in a relatively unpredictable order and strength. We examine this situation in Fig. 2. The adaptive function is symmetrical relative to the two strategies as in Fig. 1c, but now the dichotomy between favourable and unfavourable periods is realized within each winter.

In this situation, especially when it is accompanied by unpredictable availability and duration of food supplies, a mixed strategy may evolve at the individual level. Two alternatives are depicted in Fig. 2. Point F describes the situation in areas that are far from favourable wintering areas. The fitness of the mixed strategy is lower than the fitness of the migratory strategy, because birds trying to migrate in the winter only infrequently reach more favourable southern areas. The fitness of the mixed strategy may also be lower than the fitness of the sedentary strategy because a flexibly moving part of the population may be more vulnerable to harsh climatic conditions than a sedentary part.

The opposite alternative, favouring evolution of the mixed strategy, is shown in Fig. 2 by the point W. It describes the situation in an area where successful migratory movements are possible even in midwinter, i.e. individuals staying in the north in early winter can react flexibly to changing weather and food conditions and reach more benign areas in midwinter. In this case, the fitness of the mixed strategy is higher than that of the migratory strategy, because birds arriving later in crowded southern areas avoid resource competition with their conspecifics and ecologically similar species during part of the winter (assuming that the resources in the southern winter grounds are limiting, see, e.g., Keast & Morton 1980). After mild winters, individuals adopting the mixed strategy enjoy the advantage of early acquisition of the breeding territory. Obviously, the mixed strategy is more advantageous than the sedentary strategy if conditions in late winter are so harsh that

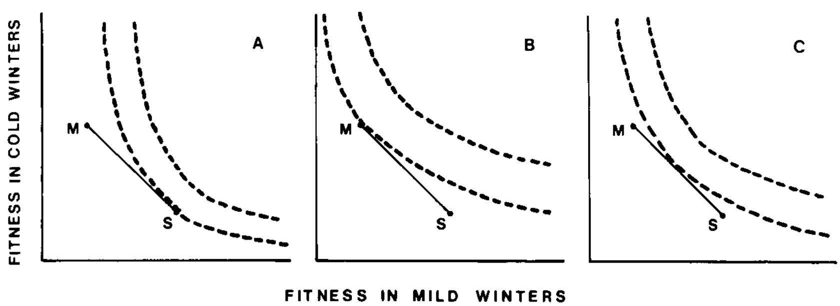

Fig. 1. The fitness set of populations living in regions with uniformly cold or mild winters; M = migratory subpopulation, S = sedentary subpopulation, the isoclines of the adaptive function are drawn with broken lines. Note that the concave fitness set has been drawn as an extended one by connecting the two alternative specialist strategies of migratory behaviour; this facilitates the search for optimal combinations of the migratory types. 1a: mild winters predominate, 1b: cold winters predominate, 1c: cold and mild winters are equally frequent.

sedentary birds staying in the north through the winter will perish.

The important difference between our concept of a mixed strategy and the strategy of partial migration is that the former strategy combines the advantages at the individual instead of the population level.

To conclude, depending on the ecological conditions in the north - climatic conditions, food resources in winter, possibility of winter movements - individuals adopting the mixed strategy may encounter the disadvantages of both the migratory and sedentary strategies (mixed strategy at point F in Fig. 2), or they may reap many of the benefits of both strategies (point W in Fig.2). The mixed strategy in Fig. 2 corresponds exactly to our concept of delayed autumn migration as an adaptive strategy.

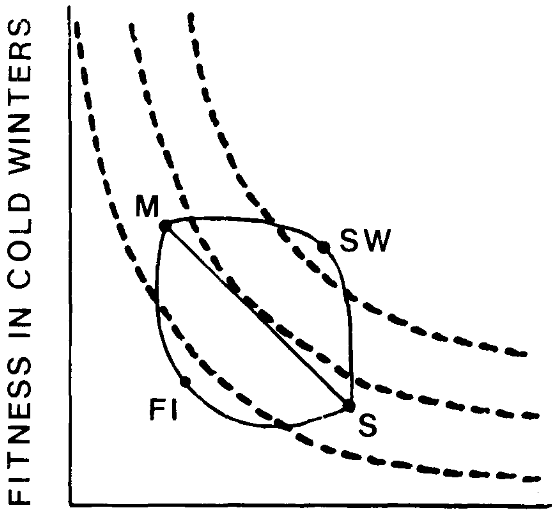

Fig. 2. The fitness set of populations living in conditions with unpredictable climatic fluctuations during each winter. The convex and concave sets refer to the mixed strategy in, respectively, W conditions, which offer an easy retreat to the south in winter, and in F conditions, with virtual geographic isolation in winter. The adaptive function as in Fig. 1.

Evidence of winter migrations from Finland

Next we can look for evidence of winter migrations and of the existence of the mixed strategy at the individual level in the Finnish avifauna. Two kinds of data are relevant: records of winter fluctuations in local bird populations explainable only by migratory (regional) movements, and direct observations of migration in winter.

We had at our disposal published reports on the local wintering faunas in different parts of the country. The most complete data proved to be those from the Helsinki district (since 1965/66), Turku district (since 1965/66), Lahti district (since 1971/72) and Suomenselkä and the adjacent part of southern Pohjanmaa (since 1970). Supplementary data were collected from bird stations. Data from Finnish bird stations could be most useful, as the stations are usually situated on the coast or the archipelagoes, but unfortunately observation has been irregular in winter. On the basis of the data, the following four groups of species were formed (summarized in Table 1):

(1) Species regularly performing large-scale regional movements during the winter.

Calidris maritima occurs in small numbers in Finland during migration periods, and small flocks are encountered at the Jurmo bird station until the shores freeze (Joutsamo & Kivivuori 1965, and others).

Buteo lagopus. The autumn migration continues on a small scale until the second half of January, delayed migration being most frequently observed in autumns with high numbers of small rodents (Mikkola 1968).

Bombycilla garrulus is a well-known "irruptive" species of good rowan-berry (*Sorbus aucuparia*) years (Siivonen 1941, Kolunen & Vikberg 1978, among others). The migration to southern areas is irregular, delayed as late as February in good rowan-berry years (v. Haartman et al. 1963–72).

Cinclus cinclus is tied to waters which do not freeze in winter, its southward migration continuing through the winter according to the freezing of northern streams and creeks (v. Haartman et al. 1963-72). In the Turku region the highest numbers are generally observed in February (Gustafsson & Peltola 1977), and migrating individuals have occasionally been observed in mid-winter in the Åland archipelago (Kökar 25 January 1969 1 + 1 ind., Y. Haila; L. Laine, pers. comm.).

Turdus pilaris is another well-known "irruptive" species, staying in great numbers in Finland until January/February in years with a good crop of rowan-berries (v. Haartman et al. 1963–72, Tyrväinen 1970, 1975). Observations of small flocks of *T. pilaris* e.g. in Lahti in December/January 1971/72, 1975/76 and 1976/77 (Kolunen 1972, Reinikainen 1976, 1977) show, however, that its occurrence in Finland in early winter is not limited to good rowan-berry years.

Carduelis spinus depends mostly on the crop of alder *Alnus* spp. seeds and accordingly occurs irregularly in Finland in winter. It is generally known that the species may change its wintering region during the winter within the country, and it probably also leaves the country, but exact data are scanty (v. Haartman et al. 1963–72, Hildén & Mikkola 1968). In Lahti, an "irruption" was observed in the early winter of 1971/72 (Kolunen 1972). In winter bird census data the numbers of *C. spinus* often decrease from the December census to the February/March census, which cannot be attributed solely to mortality (increase also observed, e.g. in 1969/70; Sammalisto 1974).

C. carduelis is observed in greater numbers in early than in late winters (v. Haartman et al. 1963–72, Reinikainen 1976, Gustafsson & Peltola 1977, 1978). According to Sammalisto (1979), the winter census data suggest regular winter movements (see also Sammalisto 1974).

C. cannabina is normally scarce in Finland in winter, but in some years may even be seen in large flocks in December/January; later the birds disappear (v. Haartman et al. 1963–72, Hildén 1968, Huhta-Koivisto 1976).

C. flavirostris is scarce and irregular, with a general pattern of occurrence similar to that of *C. cannabina* (v. Haartman et al. 1963–72). In the exceptional winter of 1951/52 large flocks (up to 70 ind.) were observed in Helsinki in the beginning of January, but later the numbers decreased (Hildén 1968). In the Turku district small flocks of *C. flavirostris* are often seen in January–February, but the species is very seldom seen throughout the winter (Gustafsson & Peltola 1977).

C. flammea depends mostly on birch *Betula* spp. seeds. Sometimes the species stays in Finland in early winter, even in large numbers, but later disappears (v. Haartman et al. 1963–72). Great changes in the numbers of *C. flammea* are observed almost every year in the winter bird censuses (Sammalisto 1974).

Pyrrhula pyrrhula performs regional movements within the country almost regularly in winter, but very few individuals have been observed at the bird stations in winter (v. Haartman et al. 1963–72). Migration has been observed in the interior of Finland in winter, e.g. in Lahti (Hyytiä 1972). In the Helsinki district, migratory movements of *P. pyrrhula* are often observed along the coast, sometimes even in a seaward direction in December–January (e.g. in 1974/75 and 1975/76; Lukkarinen et al. 1974, Huhta-Koivisto & Uusivuori 1975, Huhta-Koivisto 1976, 1977, Karvonen 1978).

Plectrophenax nivalis. Hietakangas & Tenovuo (1965) analysed the occurrence of the species in the Turku district and proposed a pattern which fits our model of delayed autumn migration. Large flocks (up to 100–200 ind.) are often observed along the west coast of Finland in early winter (see also Saarinen 1979); they move southwards and arrive in the Turku district in January-February, presumably continuing to the southwest. Considerable movements were also observed in Helsinki in the winter of 1951/52 (Hildén 1968), and scattered observations are made regularly (Lukkarinen et al. 1974, Huhta-Koivisto & Uusivuori 1975, Huhta-Koivisto 1976). In the southwestern archipelago single individuals and small flocks are often observed in December–January (L. Laine, pers. comm.).

(2) Species wintering occasionally in Finland with migratory individuals observed infrequently in December–January.

Buteo buteo and *Falco tinnunculus* sometimes try to overwinter in southern Finland (v. Haartman et al. 1963–72). In peak years of small mammal populations they may delay the autumn migration. The retreat takes place before midwinter (Mikkola 1968, Sammalisto 1974, Munne & Sammalisto 1975).

Alauda arvensis. Single individuals of the species are observed almost every winter in southern Finland, but very few cases of successful wintering have been recorded (v. Haartman et al. 1963–72). Some observations of migratory individuals in early winter are known to us (e.g. Jurmo bird station in December–January 1975/76).

Lanius excubitor winters regularly in southern Finland (v. Haartman et al. 1963–72). Movements may take place during the winter; e.g. in the Åland archipelago the species has been observed in early winter on islands too small for successful wintering (L. Laine, pers. comm.).

Sturnus vulgaris. The number of individuals staying until winter in Finland fluctuates from year to year; as many as some hundreds of birds are sometimes observed in towns and around garbage dumps in southern parts of the country (v. Haartman et al. 1963–72). Single migrating individuals are seen in many years in December–January along the southern coast (e.g. Helsinki district; Tennilä and Uusivuori 1970, Huhta-Koivisto & Uusivuori 1975, Huhta-Koivisto 1977, Karvonen 1978; also observed at Jurmo bird station in several years in December–January). In Helsinki, the number of wintering individuals typically decreases steadily through the winter, presumably because of mortality (L. Laine, pers. comm.). The pattern seems similar to that of *Alauda arvensis*, but the species is somewhat more abundant in winter.

Fringilla coelebs. Small flocks of up to some tens of individuals are commonly seen near human habitation in southern Finland in early winter (v. Haartman et al. 1963–72); the numbers usually decrease through the winter e.g. in the Turku (Gustafsson & Peltola 1977, 1979) and Helsinki district (in the winter of 1976/77 from 1000 to 200 individuals, Huhta-Koivisto 1977). The decrease is probably mostly due to mortality, as surprisingly few individuals have been observed in migratory flight in early winter (e.g. Helsinki district 8 January 1977 1 ind. and 17 January 1977 1 ind., Huhta-Koivisto 1977).

F. montifringilla is more irregular in its winter occurrence than *F. coelebs*, the numbers of observed individuals varying greatly from year to year (v. Haartman et al. 1963–72). Mass occurrences are even known, e.g. about 3500 ind. in Helsinki in the winter of 1951/52 (Hildén 1968). The food supply is certainly a crucial factor; on Åland, flocks of some hundreds of individuals have been observed a few times in December–January on fields with unharvested cereals (L. Laine, pers. comm.). The numbers generally decrease during the winter, e.g. in the Turku district (Gustafsson & Peltola 1977, 1979). Some evidence exists of inland movements during the winter; thus in the winter of 1977/78 "another peak of occurrence" was recorded in Turku in February–March (Gustafsson & Peltola 1979); similar observations have been made in Helsinki. Observations of migrating individuals are, however, very scarce (only one known to us: Rönnskär bird station 2 January 1976, 1 ind., Huhta-Koivisto 1977).

(3) Species changing their habitat during the winter, but not known to perform regional movements.

Parus major moves to human habitations in autumn, and is utterly dependent on food provided by man (v. Haartman et al. 1963–72, Reinikainen 1979, Järvinen 1980, Haila 1981). During spells of warm weather in winter Hietakangas (1976) observed regular migration back to the forests near Turku.

Corvus monedula concentrates around human habitations, especially towns and large villages (v. Haartman et al. 1963–72, Tast & Rassi 1973, Haila 1981). We have found only one observation of a migratory individual of *C. monedula* in winter; Helsinki 22 January 1974 (Lukkarinen et al. 1974).

C. corone also concentrates around human habitations (v. Haartman et al. 1963–72, Reinikainen 1979, Haila 1981) after snow has covered suitable feeding areas in the countryside. The autumn migration of *C. corone* is connected with cold northern fronts, and single individuals may migrate until early January (e.g. in 1954, 140 migrating individuals were observed at Signildskär bird station on 4–7 January, v. Haartman et al. 1963–72). Reinikainen (1975) reports a decrease in the numbers of wintering Hooded Crows in Lahti "in February", presumably caused by movements.

Carduelis chloris concentrates around human habitations in winter; winter censuses often show higher numbers in February/March than in December, e.g. in Helsinki (Hildén & Mikkola 1966). Migrating individuals have been observed in December–January at the bird stations, and ringing recoveries give evidence of regional movements in the interior during the winter (v. Haartman et al. 1963–72); on the other hand, the numbers of wintering *C. chloris* have been reported to have been quite constant, e.g. in Turku (Gustafsson & Peltola 1977). Thus the status of the species is unclear. It is obvious, however, that winter movements are less pronounced in *C. chloris* than in the other *Carduelis* finches.

Emberiza citrinella concentrates around human habitations in winter (Sammalisto 1974, Reinikainen 1979, Haila 1981). Occasional migrating individuals have been observed at bird stations in December–January (v. Haartman et al. 1963–72), but the species is evidently fairly sedentary in winter.

(4) Scarce winter species with no winter movements.

Turdus merula winters regularly, although the numbers are normally low (v. Haartman et al. 1963–72). In autumns with a good crop of rowan-berries the species stays in Finland in higher numbers than usual and the birds are believed to remain throughout the winter. E.g., at Lammi Biological Station (ca. 100 km N of the south coast of Finland), individual Blackbirds often try to overwinter, living on berries of *Crataegus*. They may disappear even before all the berries are eaten. Most probably they do not migrate, but die (once the wintering bird was found dead having lost more than a third of its body weight, T. Solonen & J. Tiainen, unpubl.). In winter 1964/65 some individuals were observed in Helsinki moving southwards in a flock of *T. pilaris* in January in Helsinki (v. Haartman et al. 1963–72).

Emberiza schoeniclus is an occasional winter bird in Finland (v. Haartman et al. 1963–72). No observations of individuals migrating in winter are known to us.

Single individuals of several other migratory species (e.g. *Prunella modularis, Erithacus rubecula, Sylvia atricapilla*) occasionally stay in Finland and sometimes even survive the winter, but they are not capable of retreating in winter.

Which species of birds adopt the delayed autumn migration strategy?

We have developed the idea of delayed autumn migration as a unifying conceptual framework, with the aim of analysing migratory movements of birds performed during the winter. We want to emphasize two general points:

(1) We do not wish merely to present a new typology. We regard our concept as a tool to be used in studying the adaptive significance of bird migration, and its value will depend on its applicability to certain bird species in specific conditions. The grouping presented in the preceding section is not intended as a rigid classification; some of the species might be placed under more than one heading.

(2) Migratory movements performed by birds in winter have been known for a long time, and discussed by several authors (e.g. Lack 1963, Mikkola 1968, Schüz 1971, Alerstam & Ulfstrand 1974, Pulliam & Parker 1979). However, we consider that winter migration is in need of a conceptual clarification from an evolutionary point of view. The crucial question is: Are winter movements the ordinary migration pattern of some species?

In the following, we try to define general, theoretical criteria for species adopting the strategy (keeping in mind that the concept involves behavioural flexibility with respect to the onset of autumn migration, see Fig. 3):

(1) The strategy is clearly unavailable to species quite unable to tolerate the winter conditions in the study area. Thus it does not make sense to discuss the possibility of delayed autumn migration of *Sylvia* warblers in northern Europe, while the strategy might be an important alternative for Mediterranean *Sylvia* warblers.

(2) The species must retain the physiological ability to start an exodus as late as mid-winter; this does not, however, exclude the possibility of a decline in physiological readiness resulting from environmental stress.

(3) The species may use fluctuating food resources (e.g. seeds, berries, small mammals) found with high probability in some areas every winter, possibly near the breeding grounds in the north, but only seldom occurring in the same area in successive years.

(4) The selection pressure for the delayed autumn migration strategy is presumably greater if the food resources in wintering areas that are climatically favourable to the species are (at least sometimes) a limiting factor. In this case individuals staying in the north as long as possible, sometimes even through the winter, are avoiding competition elsewhere with conspecifics and ecologically similar species.

The passerines adopting the strategy in northern Europe (Table 1) are mostly seed-eaters, several being traditional "irruptives", with extreme fluctuations in winter occurrence in the north. This accords with the assumptions made above. Indeed, no strict limit can be drawn between "irruptive" and "normally migrating" species, when irruptions are recognized as migratory movements in response to great yearly fluctuations in the food supply (Svärdson 1957, Ulfstrand 1963, Schüz 1971, Bock & Lepthien 1976). Pulliam & Parker (1979) adopted the term "facultative migrators", which resembles our concept.

Table 1. Delayed autumn migration strategy in the Finnish avifauna; the species list is divided into four loose groups according to the winter movements of the birds; see text.

1) Species regularly performing large-scale movements during the winter	*Calidris maritima* *Buteo lagopus* *Bombycilla garrulus* *Cinclus cinclus* *Turdus pilaris* *Carduelis spinus* *C. carduelis* *C. cannabina* *C. flavirostris* *C. flammea* *Pyrrhula pyrrhula* *Plectrophenax nivalis*
2) Species occasionally wintering in Finland with migratory individuals observed infrequently in December–January	*Buteo buteo* *Falco tinnunculus* *Alauda arvensis* *Lanius excubitor* *Sturnus vulgaris* *Fringilla coelebs* *F. montifringilla*
3) Species changing their habitat during the winter, but not known to perform regular movements	*Parus major* *Corvus monedula* *C. corone* *Carduelis chloris* *Emberiza citrinella*
4) Scarce winter species with no winter movements	*Turdus merula* *Emberiza schoeniclus*

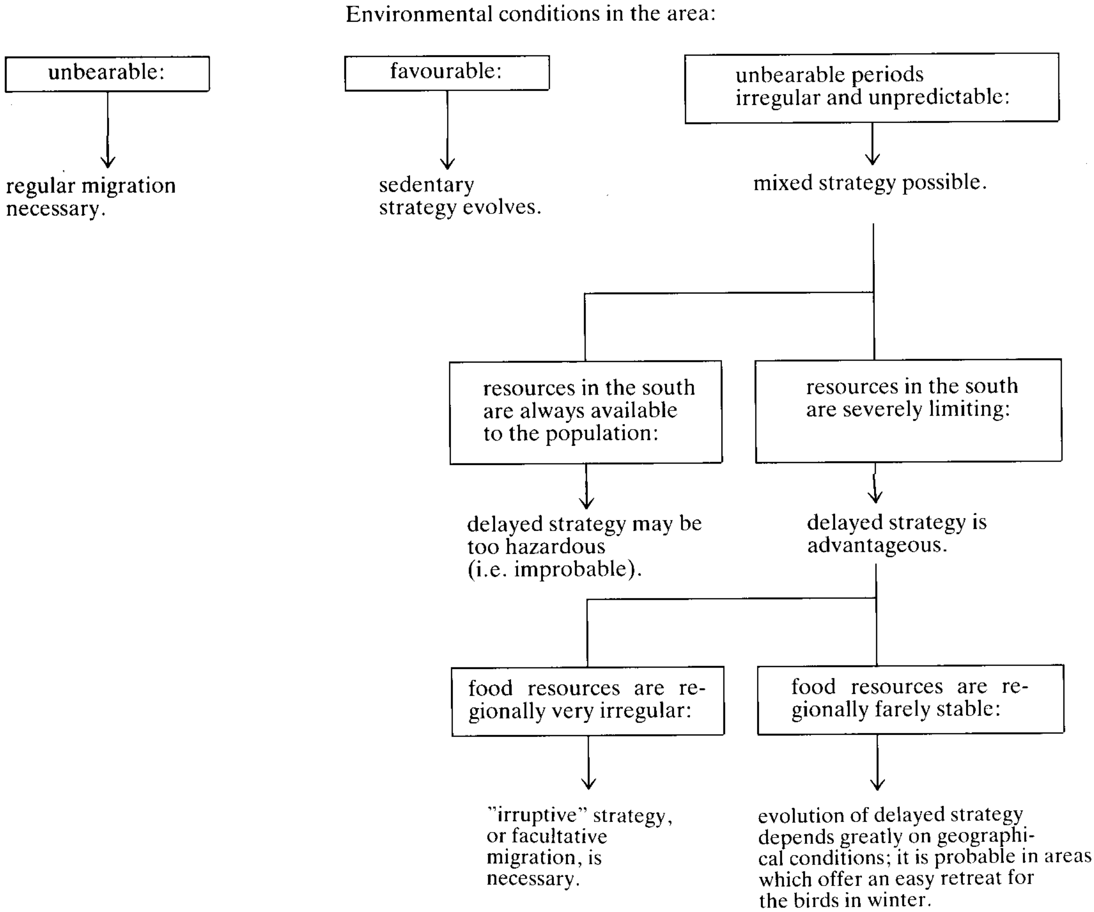

Fig. 3. A schematic illustration of factors affecting the evolution of the delayed autumn migration strategy. Note that partial migration is a population-level strategy, but the other strategies are both population and individual-level ones.

Concluding remarks

The timing of autumn migration. Dorka (1966) and Berthold & Dorka (1969) presented a model for determining the onset of autumn migration in birds. They noted that the autumn migration of "typical migrants (ausgeprägte Zieher)" occurred every year in a regular fashion compared with that of "less typical migrants (weniger ausgeprägte Zieher)", and that, furthermore, the temporal distribution of migrants at several observation stations was skewed to the right for the former but to the left for the latter. This was interpreted as evidence that hereditary factors are crucial for the timing of autumn migration in typical migrants, but that environmental cues are important for the others. In recent years, evidence has accumulated that the genetic determination of migration patterns can vary (Berthold & Querner 1981, Berthold 1983, Biebach 1983).

We want to point out the essential agreement between the conclusions of Dorka and Berthold and our approach: In the species (individuals) adopting the delayed autumn migration strategy, the time chosen to migrate can be considered to depend entirely on environmental factors. Thus we think it probable that these species retain the physiological potential for migration (see Schüz 1971:294), but this question certainly requires experimental study.

Effect of geographic differences. In the theoretical discussion of our concept we suggested that geographic conditions may influence the feasibility of delayed autumn migration: the strategy should be more common in regions that offer an easy retreat in winter and are not too far from favourable wintering areas. Finland definitely does not belong among such regions (except, possibly, for the waterfowl in the Baltic; several species stay by the Finnish coasts in substantial numbers until the archipelagoes are covered with ice, see Haila 1983). Birds in southern Finland have to cross the Baltic, which is certainly a formidable task, especially for small passerines during a cold winter storm (see Lack 1959).

A natural area for comparison is central and northern Scandinavia, where the climatic conditions in winter are similar to those in Finland, but the distances to the Atlantic or North Sea coasts are shorter. According to a valuable survey by Roos (1962, see also 1970) on the winter occurrence of birds at Falsterbo, on the southernmost tip of the Swedish mainland, the list of species showing mid-winter migratory movements in southern Sweden is impressive. It includes all the species that are migratory in winter in Finland and, in addition, several species of birds of prey (see also Lönnberg 1929, Weibull & Weibull 1979), and several species belonging to other categories in our Finnish list (e.g., *Alauda arvensis, Sturnus vulgaris* and *Carduelis chloris*) together with more southern species (e.g. several waders, *Columba palumbus* and *Anthus pratensis*, see also Lennerstedt 1963). Migratory movements were also reported by Gyllin (1966, 1967), Gyllin & Larsson (1969), Tyler (1963, 1968) and Wahlstedt (1955) in local reports on the numbers of birds wintering in southern and central Sweden. It is possible that some species, e.g., *Alauda arvensis, Turdus pilaris, Corvus corone* and *Sturnus vulgaris*, show more pronounced winter movements in Sweden than in climatically comparable areas in southern Finland, but the data are too small for definite conclusions.

In areas south and southwest of Sweden the milder winter climate may allow many more species to adopt the strategy. Indeed, in Western and Central Europe winter movements are a regular and well-known, though poorly documented and partly misinterpreted (see below), phenomenon, and many species may even migrate back and forth during the winter, depending on the weather and snow cover ("Randzug" or "Pendelzug" Schüz 1971), or "incipient migratory movements" (Gauthreaux 1978)). There is also a gradient in the harshness of the winter within Finland. Consequently, delayed autumn migration might be expected to occur within this country as well. This was indicated above for *Cinclus cinclus, Carduelis* finches and *Pyrrhula pyrrhula*.

"Winterflucht". In Western and Central Europe attention has been paid to the phenomenon called "hard weather movements" or "escape from winter", "Winterflucht" (e.g. Schüz 1971). Drost (1929) noted that "Winterflucht" was a regular event resulting from "the inclination of many birds to stay in the northern home areas, if the weather conditions are favourable, in spite of the threat of winter". The word "Flucht" emphasizes the risks run by these birds; mass mortality can occur when they are surprised by sudden winter storms (as observed on Helgoland, see Drost 1937, Schüz 1971). A distinction should be made, however, between delayed migration and "Winterflucht". We regard winter migration as adaptive behaviour for many bird species, and only in extreme conditions can it be considered "Flucht", although regular winter migrations and "escapes" certainly grade into each other.

Wintering. Our discussion implies that the phenomenon of bird "wintering" has often been classified too rigidly. Bird migration generally consists of two phases, i.e. autumn and spring movements, with a period of rest and physiological recovery between them. From the evolutionary viewpoint, however, the most important part of a bird's life is reproduction. The possibility should be considered that some species survive from one breeding season to the other by migrating all the time, in search of suitable food resources. These species may start "wintering" by utilizing resources close to the breeding area, and move southwards only when the resources are depleted, possibly in the middle of the winter.

A plea for systematic recording of winter movements of birds

In this paper we have demonstrated theoretically the evolutionary significance of migratory movements performed by birds very late in the autumn or even in mid-winter. The most serious problem we have met in developing our concept is shortage of data. Therefore, in conclusion, we wish to appeal for more systematic recording of bird movements during the winter. At least the data listed below are needed:

(1) Regular counts of winter birds in the same localities throughout the winter. These would show fluctuations in numbers resulting from mid-winter movements.

(2) Bird censuses and records of food availability made in the same areas in several winters. These would allow one to assess the flexibility in the choice of wintering localities and the influence of the climate and resources.

(3) Direct study of movements in winter, by either visual observation or ringing.

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Selostus: **Syysmuuton viivästyminen lintujen sopeutumana Pohjois-Euroopassa suomalaisen aineiston nojalla**

Määrittelemme syysmuuton viivästymisen muuttolintujen sopetumana: 'viivyttelymuuttajat' pysyttelevät pesimäalueidensa läheisyydessä mahdollisimman pitkälle syksyyn ja alkutalveen, suotuisina vuosina jopa läpi talven, mutta kykenevät olosuhteiden huonontuessa muuttamaan etelään vaikkapa keskitalvella. Pysyttely pohjoisessa läpi talven voi olla edullista, koska (1) on edullista saapua pesimäalueelle keväällä mahdollisimman aikaisin, ja (2) eteläisillä talvehtimisalueilla saattaa esiintyä kilpailua ravinnosta. Syysmuuton viivästyminen on lintuyksilön reaktio ympäristön ennustamattomaan vaihteluun, jota aiheuttavat ennen muuta (1) ravinnon määrän vaihtelu talvien välillä (esimerkiksi tärkeiden ravintokasvien siemensato), sekä (2) sääolojen vaihtelu talvien välillä ja kunkin talven kuluessa.

Kuvissa 1 ja 2 tarkastelemme teoreettisesti syysmuuton viivästymistä sopeuttamana käyttäen hyväksi Richard Levinsin kehittämää 'sopeutumisstrategia'-analyysiä. Mikäli talvien leutoudessa on vaihtelua, joka ei ole ennalta ennustettavissa, voi syysmuuton viivästymis -sopeutuman kehittymiselle olla ratkaisevaa, onko tarkastelun kohteena olevalta alueelta mahdollista saavuttaa suotuisammat talvehtimisalueet keskitalven ankarissa oloissa.

Kävimme läpi kirjallisuustiedot Suomessa talvisin esiintyvien muuttolintujen talvisista liikkeistä, ja jaoimme lajit niiden perusteella neljään ryhmään (taulukko 1): (1) Lajit, jotka säännöllisesti liikkuvat laajalti talven kuluessa; (2) satunnaistalvehtijat, joista on tiedossa talvisia muuttohavaintoja; (3) lajit, jotka vaihtavat esiintymisbiotooppiaan talvella, mutta ilmeisesti eivät liikehdi laajemmilla alueilla; sekä (4) satunnaistalvehtijat, joista ei ole tehty talvisia muuttohavaintoja.

Aineisto osoittaa, että talviset muuttoliikkeet ovat useilla lajeilla maassamme sääntö; niiden 'syysmuutto' voi siis itse asiassa jatkua läpi talven. Tämä osoittaa tarkastelemamme 'viivyttelymuuton' eron perinteisen 'osittaismuuttaja'-käsitteeseen, joka on sopeutumista talvien väliseen olosuhteiden vaihteluun populaatiotasolla: osa populaatiosta muuttaa syksyllä etelämmäksi, osa yrittää selviytyä pohjoisessa läpi talven. Monet vaelluslajit noudattavat selvästi viivyttelystrategiaa (esimerkiksi siemensyöjät kuten räkättirastas, vihervarpunen ja urpiainen). Kuvassa 3 esitämme kaavamaisesti, millaisissa olosuhteissa, ja millaisille lajeille, viivyttelystrategian voi odottaa kehittyvän.

On ilmeistä, että 'talvehtiminen' on lintujen elämänkaaressa dynaamisempi vaihe kuin usein on ajateltu, mutta lintujen talvisesta esiintymisestä, erityisesti talvisista muuttoliikkeistä, on valitettavan vähän aineistoa.

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