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Can conditions experienced during migration limit the population levels of birds?

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Abstract Populations of migratory birds are usually considered to be limited by conditions in breeding or wintering areas, but some might be limited by conditions encountered on migration. This could occur at stopover sites where competition for restricted food supplies can reduce subsequent survival or breeding success, or during the flights themselves, when adverse weather can occasionally kill large numbers of individuals. Competition for food could act in a density-dependent manner and help to regulate populations, whereas weather effects are more likely to act in a density-independent manner. The evidence for these views is explored in this paper. When preparing for migration, birds must normally obtain more food per day than usual, in order to accumulate the body reserves that fuel their flights. Birds often concentrate in large numbers at particular stopover sites, where food can become scarce, thus affecting migratory performance. Rates of weight gain, departure weights, and stopover durations often correlate with food supplies at stopover sites, sometimes influencing the subsequent survival and reproductive success of individuals, which can in turn affect subsequent breeding numbers. Many studies have provided evidence for interference and depletion competition at stopover sites, relatively few for migration conditions influencing the subsequent breeding or survival of individuals, and even fewer for effects on subsequent breeding numbers. Migrants in flight occasionally suffer substantial mortality in storms, especially over water, sometimes involving many thousands of birds at a time. Other mass mortalities have resulted from atypical 'winter-like' weather, occurring soon after the arrival of summer migrants in

their breeding areas or just before their departure in autumn. Again, many thousands of birds at a time have been killed in such incidents, causing reductions of 30–90% in local breeding densities. In some bird species, migration-related events can at times have substantial effects on the year-to-year changes in breeding population levels. Nonetheless, the difficulties involved in investigating migrating birds at different points on their migration routes have so far limited the number of studies on the influence of events during migration periods on population levels.

Keywords Migration · Population regulation · Stopover ecology

Introduction

While the numbers of some migratory bird species are apparently influenced primarily by conditions in breeding or wintering areas (Newton 2004), the numbers of others could be influenced by conditions experienced on migration, mainly at stopover sites, but also during the flights themselves. Conditions on migration can be considered limiting if they slow a population's increase, or cause its decline. Such conditions can seldom account entirely for a given population level, however, because both mortality and reproduction are also influenced by conditions at other times of year. In this paper, therefore, when migration events are described as limiting, they may be essential to explain a given population level, but only in conjunction with other factors, operating at other times of year. Moreover, migration events may limit numbers in a density-dependent or largely density-independent manner. Density-dependent regulation implies competition (perhaps for food or predator avoidance), as a result of which the percentage of birds affected is greater when numbers are high than when they are low. In density-independent limitation, competition is unimportant, and the proportion of birds affected bears no consistent relationship to population

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size. Probably few situations occur in which there is no competitive (density-dependent) element in migration effects, although this may often be slight or hard to discern.

It would be surprising if bird breeding numbers were unaffected by conditions on migration. First, the process can in some species occupy several weeks or months each year (including stopovers), outward and return journeys together taking up to 6 months in extreme cases. Substantial mortality is therefore likely to occur during this period, and annual variations in such mortality could be reflected in annual variations in subsequent breeding densities. Second, in order to accumulate the body fat and other reserves necessary to fuel migration, and sustain themselves over the flight periods involved, birds need to obtain more food per day than usual. Although they have various ways to increase their energy consumption, such as change of diet, gut structure or daily foraging routine, their fattening rates are still constrained by intake rates or digestive capacities. Third, because the same stopping sites can be used by large numbers of birds at a time, densities are often high, and competition intense, resulting in severe depletion of food supplies (see later). The problems are magnified at those staging sites where birds must accumulate the extra large reserves necessary to cross an 'ecological barrier', such as a stretch of water or desert. Hence, obtaining sufficient food in the limited time available could be a major constraint on the timing and success of migration.

The potential for limitation on staging areas is perhaps especially acute in shorebirds and waterfowl, which in many regions have only a limited number of possible refueling sites, often at widely spaced intervals along the migration route. This situation contrasts with many landbird species, which migrate through mainly favourable habitat, and would seem to have feeding opportunities at many places along their route. However, the quality of any stopover site depends not just on the available food supplies, and levels of competition, but also on the security the site offers against predation, disturbance and other threats (for trade-offs between feeding rate and predation danger, see Lindström 1990; Cresswell 1994; Ydenberg et al. 2002).

Events at stopover sites may thus affect not only the migratory performance of birds, but also their subsequent reproduction or survival, with potential consequences on population levels. This paper therefore examines evidence that conditions at stopover sites can influence: (1) refueling rates and migration speeds; (2) subsequent reproduction or survival; and (3) eventual population level or trend. Previous reviews of particular aspects of this subject area have been provided by Moore and Simmons (1992), Moore et al. (1995), Drent et al. (2003), Jenni and Schaub (2003), and Newton (2004). A secondary aim is to consider the potential effects of storms and other extreme weather events that are sometimes experienced by migrants just before, during, or just after their journeys.

Conceptual models

Imagine a population in which both per capita reproduction and per capita mortality are density dependent, as shown in Fig. 1a. The place where the lines depicting these relationships intersect marks the equilibrium population level (E), to which numbers tend to return after any perturbation. If mortality during migration is also density dependent, and additive to other mortality, the equilibrium population level (E^1) is reduced as shown. The same holds if either reproduction or mortality is density independent. In Fig. 1b, for example, breeding is shown as density dependent and mortality as density independent. Again the point where the lines depicting these relationships cross marks the equilibrium population level. If migration mortality is also density independent, and additive to other mortality, the equilibrium population level would decline as shown. Whether migration mortality is density dependent or density independent, for it to reduce subsequent breeding density it must be additive to other mortality, and not be compensated by reduction in some other form of mortality before the breeding season. Where mortality in the non-breeding season is density dependent (as found in some migratory species; Newton 1998), mortality on autumn migration could be offset by reduced winter losses, and have no effect on subsequent breeding numbers, but mortality on spring migration leaves little or no time for any such compensation to occur before breeding begins.

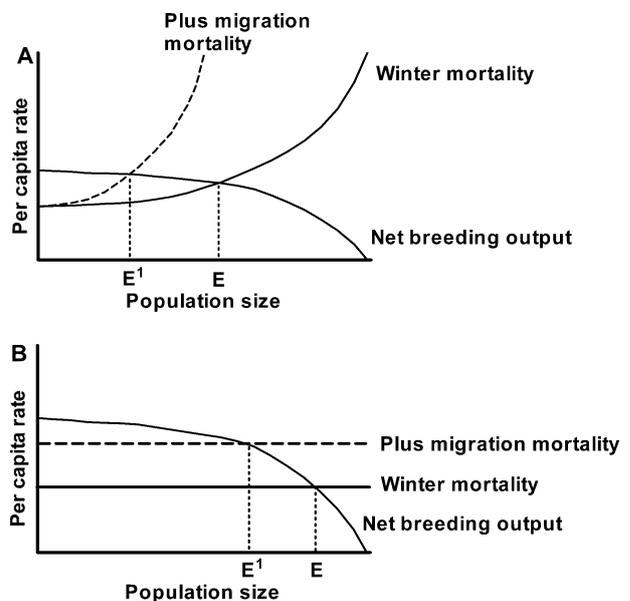


Fig. 1 Model depicting the relationship between per capita reproduction and per capita mortality in a population. Where the lines cross marks the equilibrium population size (E). In diagram **a**, both reproduction and mortality are density dependent, as is additional migration mortality, which reduces the equilibrium population size (E^1). In diagram **b**, reproduction is density dependent while mortality is density independent, including additional migration mortality, which again reduces the equilibrium population size

The above models concern events at the population level, but events on migration can also influence the subsequent performance of individuals. An important element of competition among migrants concerns the timing and speed of the journey, especially in spring. Within populations, those individuals that arrive in breeding areas in the early part of the arrival period usually take territories in the best habitat (identified as such from previous work in the area), begin breeding first, and show the highest nest success. Later arrivals are relegated to poorer habitat, and the latest birds to arrive may fail to acquire a mate, or a territory and a mate, so cannot reproduce that year. Examples of species showing relationships between arrival date, territory quality and reproductive success include pied flycatcher *Ficedula hypoleuca* (Lundberg et al. 1981), painted bunting *Passerina ciris* (Lanyon and Thompson 1986), great reed warbler *Acrocephalus arundinaceus* (Bensch and Hasselquist 1991), Savi's warbler *Locustella luscinioides* (Aebischer et al. 1996) and northern wheatear *Oenanthe oenanthe* (Currie et al. 2000) among passerines, and willow ptarmigan *Lagopus lagopus* (Moss 1972), greylag goose *Anser anser* (Nilsson and Persson 1994), barnacle goose *Branta leucopsis* (Dalhaug et al. 1998) and white stork *Ciconia ciconia* (Tryjanowski et al. 2004) among non-passerines. All these aspects of performance could be influenced by the quality of the individual birds and, without experiments, it is hard to tell to what extent reproductive success follows directly from arrival date, and to what extent from individual quality (though one experimental study confirmed the importance of date as such; Cristol 1995). Similar pressures may be assumed to affect arrival in wintering areas, if the first arrivals take the best habitats and thereby have greater chance of surviving the non-breeding season (for American kestrel *Falco sparverius*, see Smallwood 1988; for ruddy turnstone *Arenaria interpres*, see Whitfield 2002). These considerations give rise to the proposed model of migration ecology depicted in Fig. 2, which links individual migratory performance to subsequent survival or reproductive success. In due course, changes in the mean performance of individuals may lead to change in population size, perhaps the most difficult aspect to study in migratory birds.

Food limitation at stopover sites

The following arguments have been used to support the view that food supplies at stopover sites could limit the migratory performance and numbers of birds (see also Appendix 1).

Migrant numbers in relation to food supplies

As at breeding and wintering areas, bird densities at stopover sites are often found to correlate with local food supplies, either from place to place, or from time to

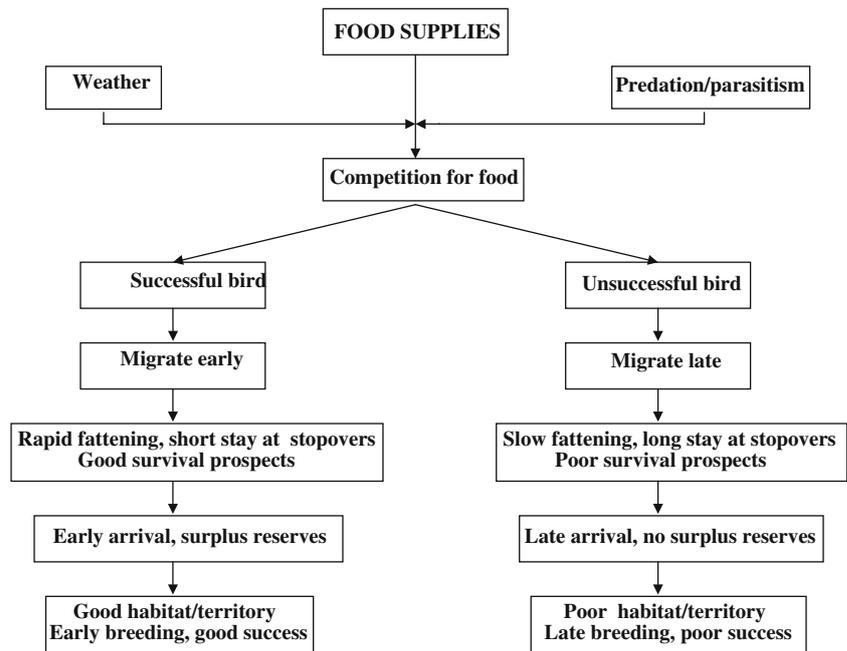
time. At some sites, the numbers of migrants vary between migration seasons, or even during the course of a single season, in relation to changing food availability. For example, rufous hummingbirds *Selasphorus rufus*, which breed in the northwest of North America, migrate southward in autumn, stopping to feed on nectar from flowers (especially *Castilleja linariaefolia*) that grow in mountain meadows (Russell et al. 1992). At each stopover, the birds establish individual territories around flower patches. Competition is usually intense and not all birds manage to acquire territories. Once a bird has obtained a territory, several days to 3 weeks are needed for it to reach an appropriate departure mass and move on. During 7 years of study, the density of nectar-providing flowers varied widely due to natural variation in flowering. Territory sizes and population densities of hummingbirds at the study site varied accordingly, both between and within years. During dry years of regionally poor flowering, the body masses of incoming birds were low and stopover durations were long. The peak migration date of hummingbirds roughly coincided with the peak date of local flowering, and both events varied by about a month among years, poor nectar supply delaying migration. These findings thus revealed effects of food supplies at stopover sites on the densities, behaviour, fattening patterns, staging periods and migrating dates of hummingbirds. Instances of hummingbirds starving while on migration were said to be 'not uncommon'.

Relationships between food supplies and migrant numbers have been shown in other species, too, and in widely different situations (e.g. Martin and Karr 1986; Kelly et al. 2002; van Gils et al. 2005). In one study in the Arizona Mountains, the relative numbers of insectivorous passage migrants in different habitats varied between seasons, in accordance with a seasonal changes in insect densities (Hutto 1985). In this area, 54% of bird species showed shifts in habitat use between seasons, which matched the changes in insect availability. Such relationships confirm that migrants can respond to food supplies en route, concentrating in greatest densities at times and places where food is plentiful.

Depletion of food supplies

Marked declines in food supplies, mainly through depletion, have been measured at stopover sites during the migration season. In some studies, this was done by excluding birds from some places, and comparing the trends in prey populations inside and outside the enclosures. For example, during the shorebird passage (July–September) in Massachusetts, USA, 7–90% declines in different prey species were recorded, mainly due to shorebird predation (Schneider and Harrington 1981). Similarly, following spring migration over the Gulf of Mexico, some passerine migrants were found to depress woodland insect supplies rapidly by up to 67% at coastal stopover sites (Moore and Yong 1991).

Fig. 2 Flow diagram showing the hypothetical links between spring food-supply, migratory performance, arrival in breeding area, and subsequent breeding success. The two columns show the extremes in a spectrum of variation between individuals



Depletion by migrants of some other types of foods, such as berry crops, can be observed each year by even the most casual of observers (for case studies, see Parrish 2000; Ottich and Dierschke 2003). There can be no doubt, therefore, that some birds can seriously deplete their food supplies at stopover sites, both in autumn and in spring. Some food supplies, such as the plant leaves eaten by geese, undergo repeated cycles of depletion and re-growth, a system which still limits the numbers of individuals that can feed effectively at a site at one time (Prop 1991).

This type of information is not necessarily useful without corresponding measures of bird performance, such as feeding or fattening rates. This is because, although food-stocks might be estimated accurately, we usually have no means of telling what proportion is available to the birds, or how much they could remove before losing weight. Nevertheless, depletion measures are sometimes useful in showing how close birds are to a food limit. If it is found that birds remove almost all their favoured foods from a site and that no apparent alternatives are available locally, then a big increase in the numbers of migrants able to fatten at that site is clearly not possible. At the other extreme, if food is replenished as it is removed (say by immigration, growth or reproduction of food organisms), then depletion is probably unimportant.

Some authors have taken a different approach and measured feeding rates, rather than food itself. For example, depletion of food supplies by pied flycatchers in autumn was evidenced by declining insect capture rates the longer a bird spent in a tree, and by increasing feeding rates with time since the last visit to a given tree (Bibby and Green 1980). Competition can come not only from conspecifics, but also from other species

taking the same foods, which can lower the feeding rates of several species at once (Moore and Yong 1991).

Where a food supply is depleted by passage migrants, late comers, arriving after most of the food has been eaten, could be penalised by reduced rates of feeding and fat accumulation. Bewick's swans *Cygnus columbianus bewickii* were studied at a staging site in the White Sea, the last stop on spring migration before the Siberian breeding grounds (Nolet and Drent 1998). In this locality, the swans could obtain their main food, tubers of fennel pondweed *Potamogeton pectinatus*, only during low tide. In the course of the staging period, the swans tended to forage at progressively lower water levels, indicating that they gradually depleted this food-supply and exploited increasingly deeper parts of the tuber bank as the days went by. This depletion reduced the swans' main foraging period from 6.0 h per tide on 20 May to 3.3 h per tide on 28 May. The authors calculated that this must have greatly reduced the refuelling rate during the staging period. Accordingly, swans arriving late stayed longer than those arriving early. It seemed important for the swans to arrive at the stopover site as soon after ice break-up as possible, for a month later the tubers were greatly depleted and any remaining began to sprout. The first swans to arrive could also leave the site first, and (in theory) reach the breeding grounds earliest, get the best territories and achieve the highest reproductive success. The latest swans to leave would have arrived in the nesting areas too late to breed that year.

This study hinted at how competition for limited food supplies at a stopover site, used for no more than a few weeks each year, could have helped to regulate the swan population. The White Sea provides the only sizeable stopover site for swans on this part of the spring migration route, so with severe food depletion there, the

birds would be limited in how much they could respond to any improvements in conditions that might occur in breeding or wintering areas.

Food supplies and fattening rates

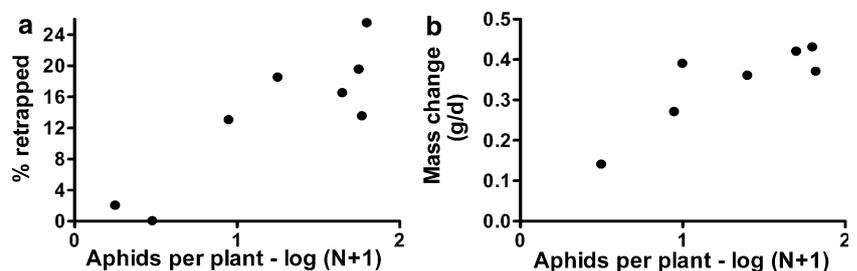
The importance of food availability at stopover sites is further shown by the findings that: (1) birds were more likely to stay at sites where food was plentiful, and move on rapidly from sites where food was scarce (Bibby and Green 1981; Spina and Bezzi 1990; Ottick and Dierschke 2003); but (2) when they stayed, fuel deposition rates were often correlated with spatial and temporal variation in food supplies (Fig. 3; Cherry 1982; Bibby et al. 1976; Bibby and Green 1981; Piersma 1987; Prop and Deerenberg 1991); (3) mean stopover durations were inversely correlated with food supplies, as birds put on weight more slowly where food was scarce than where food was abundant (Piersma 1987; Russell et al. 1992); (4) birds that arrived at particular sites with low body reserves stayed longer than those that arrived at the same sites with higher reserves (Dolnik and Blyumental 1967; Cherry 1982; Bairlein 1985; Petterson and Hasselquist 1985; Biebach 1985; Biebach et al. 1986; Moore and Kerlinger 1987; Dunn et al. 1988; Serie and Sharp 1989; Loria and Moore 1990; Ellegren 1991; van Eerden et al. 1991; Kuenzi et al. 1991; Morris et al. 1996; Yong and Moore 1997); (5) some populations could not accumulate fuel for spring migration until food availability increased in some way (for whimbrel *Numenius phaeopus*, see Zwarts 1990); (6) fuel deposition rates declined in weather conditions expected to reduce feeding rates (Schaub and Jenni 2001b); (7) the provision of supplementary food to migrants in the field led to increased rates of fuel deposition compared to rates in unfed birds (for bluethroat *Luscinia svecica*, see Lindström and Alerstam 1992; for greater whitethroat *Sylvia communis*, see Fransson 1998; for robin *Erithacus rubecula*, see Danhardt and Lindström 2001; for garden warbler *Sylvia borin* see Bauchinger 2002); and (8) rates of fuel deposition most commonly reported (1–3% of lean mass per day) were much lower than the maximum rates (>7% of lean mass per day) recorded from individuals in the same population. This finding implied that most individuals fed at rates too low to fuel at the maximum possible rate (Lindström 2003). Whether this matters depends of how fuelling rates affect migration

timing and subsequent performance. Some birds are apparently unable to accumulate sufficient body reserves in time to migrate at an appropriate date. They may then remain in wintering areas (e.g. van Dijk et al. 1990), at stopover sites (e.g. Spendelow 1985), or in breeding areas where they may die as winter approaches (e.g. Kolonen and Peiponen 1991). Such findings indicate the potential importance of food supply to successful migration.

In general, migrants seem to stay at a site if they have a good chance of replenishing their depleted body reserves there, but move on if conditions are unfavourable for replenishment, presumably in search of more suitable habitat elsewhere (Rappole and Warner 1976; Biebach 1985; Kuenzi et al. 1991). This inference is supported by feeding experiments in wild birds (for northern wheatear, see Dierschke et al. 2003) and by laboratory experiments with spotted flycatchers *Muscicapa striata* and garden warblers, in which migratory restlessness was greatly reduced during periods of weight gain (Biebach 1985; Gwinner et al. 1985). More specifically, birds with high fuel stores, or with low fuel stores and insufficient food, showed migratory restlessness, whereas birds with low food stores and abundant food did not. Overall, the fattening patterns of birds do not invariably conform to the simple model: arrive lean, fatten to a threshold, and then depart as soon as possible. In natural conditions stopover duration depends also on weather (as birds wait for conditions favourable for migration), on levels of competition, predation and disturbance (all of which influence feeding rates and fattening patterns), and the location of the stopover site with respect to a sea or other barrier. These other factors often influence the relationships between arrival mass and stopover duration, or rate of weight gain and stopover duration (Butler et al. 1997), and from many stopover sites departing birds can show a wide range of fuel loads. In landscapes with many potential stopping places, birds might stop and feed for a fairly constant period each day, and then fly whatever distance their reserves allow before they stop again, the durations of flights rather than the stopovers being the main variable in the journey (Schaub and Jenni 2001a).

Rates of feeding and weight gain are often greatest in lean birds, and then slow as body mass increases towards the departure value, a trend found in captive birds as well as wild ones (Rappole and Warner 1976; Yong

Fig. 3 Relationship between food-supply (aphid density) at a stopover site and **a** tendency to stay, and **b** rate of migratory weight gain in sedge warblers *Acrocephalus schoenobaenus*. From Bibby and Green 1981



and Moore 1993; Moore 1994). This is partly because lean birds take greater risks than fatter ones: they may spend less time scanning for predators, feed for longer each day, more actively, and in more dangerous places (Metcalfe and Furness 1984; Loria and Moore 1990; Moore and Aborn 2000; Ydenberg et al. 2002). But the maximum rate at which food can be obtained and processed is still limited by the available feeding time (set by day length, tidal rhythms or prey activity) and the type of food, and by bird features, such as crop capacity and digestive throughput. The bird must also do things other than forage, all of which limit the rate of weight gain.

The assumption, that long stopovers and associated low rates of weight gain slow the overall progress of migration, is supported by empirical data. For example, autumn migratory movement by six passerines between traps 12–50 km apart was 1.5–3.0 times faster in fat birds than in lean ones (Blyumental, in King 1972). When weight gain is slow at early staging sites, leading to late departure, it could affect the rates of fattening at later sites if food supplies have already been depleted there (the domino effect of Piersma 1987). On this basis, and in the absence of weather-induced delays, differences between individuals and age groups could be magnified during the course of a journey. In some species, individuals exposed to poor feeding conditions in late winter have been found to leave their wintering areas later and arrive later in their breeding areas than other individuals (Marra et al. 1998; Gill et al. 2001). Some studies at particular stopover sites have indicated a progressive lowering of body mass and fat levels among successive samples of birds caught during the course of the spring migration. Individuals that passed through earlier in the season were heaviest, and those that passed through latest were lightest: as for example, in three out of four of thrush species caught in spring at a stopover site in coastal Louisiana (Yong and Moore 1997), among steppe buzzards and levant sparrowhawks *Accipiter brevipes* caught in spring at a stopover site in Israel (Yosef et al. 2002, 2003). The same has been found for birds arriving on their breeding areas, with the earliest arrivals being the heaviest, as in barn swallows *Hirundo rustica* (Møller 1994), garden warblers *Sylvia communis* (Widmer and Biebach 2001), American redstarts (Smith and Moore 2005), and common terns *Sterna hirundo* (Dittman and Becker 2003). Such trends could result from the effects of competition relegating lighter birds to the later part of the spring migration season. However, not all species would be expected to show decline in the mean weights of samples taken through the spring migration season: at some stopover sites food supplies increase through spring (through growth or reproduction of prey items), and bird densities decline, as passage comes to an end. Both these changes could provide enhanced feeding conditions for the later migrants (for greater fattening rates in the latest of two godwit populations to pass through the Netherlands in spring; see Drent and Piersma 1990).

Social interactions

One consequence of variable arrival times and stopover periods is continual turnover in the birds present at particular sites, as new ones arrive and others leave. This turnover results in continual change in the social environment of individuals, with effects on the proportions of different sex and age groups present, and differences in their respective migration speeds. Nevertheless, dominance relationships influence the outcome of competitive interactions at stopover areas, just as in breeding or wintering areas, even though the individuals concerned may be together for only short periods (Pienkowski and Evans 1985). In some species, dominant individuals hold short-term territories at stopover sites, and subordinate individuals unable to obtain territories must feed in less good areas or leave (Rappole and Warner 1976; Kodric-Brown and Brown 1978; Bibby and Green 1980; Sutherland et al. 1982; Hixon et al. 1983; Veiga 1986; Carpenter et al. 1993; Sealy 1989).

Territorial northern waterthrushes *Seiurus noveboracensis* were found to accumulate body reserves at a rapid rate, whereas non-territorial ones gained no weight until after they had acquired a feeding territory (Rappole and Warner 1976). The same was found among robins (Mehlum 1983). Similarly, in non-territorial species, subordinates had lower feeding and fuel deposition rates than dominant conspecifics (e.g. for bluethroat, see Lindström et al. 1990; Ellegren 1991; for brent goose *Branta bernicla*, see Prop and Deerenberg 1991). At similar environmental food levels, average fattening rates were lower at high than low densities of individuals (Moore and Yong 1991; Kelly et al. 2002). Competition may thus not only help to regulate local densities in relation to resource levels, but result in some birds making longer stopovers, or leaving with low fat reserves, reducing the distance they could travel before the next stop.

Age and sex effects

In many species, adults trapped at stopover sites put on weight more rapidly, achieved greater body reserves, and stayed for shorter periods than first-year birds; and within age-groups, males put on weight more rapidly, achieved greater body reserves, and stayed for shorter periods than females (for age differences see Veiga 1986; Serie and Sharp 1989; Ellegren 1991; Carpenter et al. 1993; Holmgren et al. 1993; Gorney and Yom-tov 1994; Morris et al. 1996; Woodrey and Moore 1997; Lindström et al. 1990; Yong et al. 1998; Woodrey 2000; Heise and Moore 2003; for sex differences, see Morris et al. 1994; Otahal 1995). These differences may have arisen because young birds were at a competitive disadvantage in the presence of older ones, and females in the presence of males. Juveniles may also have foraged less efficiently than adults, resulting in generally slower fuel accumulation and migratory progress, with longer or more

frequent stopovers (for dunlin *Calidris alpina*, see Rösner 1990; for cranes and raptors, see Ueta and Higushi 2002).

Age-related effects, that are obvious in autumn, may be less apparent by the following spring, when the juveniles are older. Nevertheless, in three species studied in Japan by satellite tracking, namely Steller's sea eagle *Haliaeetus pelagicus*, black-faced spoonbill *Platalea minor* and white-naped crane *Grus vipio*, immatures on spring migration stayed about twice as long at stopover sites as adults, and took about twice as long over the whole journey (Ueta and Higushi 2002). The two age groups showed no differences in the mean distances between stopover sites or in the overall distance of migration.

Such differences could influence the travel speeds, departure and arrival dates, and survival chances of individuals during migration. However, age and sex differences were not apparent in all species studied, or at all stopover sites (Morris et al. 1996; Maitov and Izhaki 1994), and in some species, juveniles were heavier than adults (Alerstam and Lindström 1990; Woodrey 2000).

In conclusion, increasing bird densities have been shown to intensify competition, reducing food availability through depletion (Moore and Yong 1991) or interference (Carpenter et al. 1993), lowering food-intake and fat deposition rates, and thereby slowing migration. Some individuals are affected more than others. Interference competition may also redistribute birds among habitats, with younger less experienced migrants forced into sites where feeding rates are lower. While competition for food may limit the number of birds that can fatten simultaneously at particular sites, it may have little or no bearing at the population level if displaced birds find alternative places to fatten, or migrate more slowly with no adverse consequences.

Poor condition and mortality at stopover sites

Birds caught soon after their arrival at stopover sites often show great variation in body condition. Some seem on the point of starvation, devoid of body reserves, while others have enough residual reserves for several hundred kilometers of further flight. Over three different years, some 39% of 1,903 thrushes (*Catharus*, *Hyllocichla*), caught on arrival in a Louisianan coastal woodland after crossing the Gulf of Mexico, carried no obvious body fat. The body weights of 23% of these thrushes were at or below the estimated fat-free body mass; while only 5% had estimated fat stores that exceeded 20% of lean body mass (Yong and Moore 1997). Between 21 March and 9 May 1987, 13 individuals of 5 migrating species were found dead in the wooded interior of a coastal island off Louisiana, apparently having starved, and another 66 corpses of 18 species were found on daily walks on a 2-km stretch of beach (Moore et al. 1990). Other instances of birds arriving in Panama in autumn in very poor condition (below fat-free mass)

were given by Rogers and Odum (1966), and other severely emaciated birds were collected from oil drilling platforms in the Gulf of Mexico (Gauthreaux 1971).

Birds weakened by starvation are more easily caught by predators, and may account for some of the raptor kills found at stopover sites, in which young birds often predominate (Bijlsma 1990). Many other records of exhausted and starving migrants are mentioned incidentally in the ornithological literature, often in association with sea or desert crossings (for hirundines and others, see Paynter 1953; Spendelov 1985; for shorebirds, see Dick and Pienkowski 1979; Bijlsma 1990; for raptors see Smith et al. 1986). They indicate that some birds die of starvation during the course of their journeys.

It is common for newly arrived birds, especially of long distance migrants, to lose mass for another day or two before they begin to regain it (Rappole and Warner 1976; Moore and Kerlinger 1987). Explanations for this initial mass loss include: (1) effects of capture and handling (Nisbet and Medway 1972), (2) inefficient foraging because of unfamiliarity with the stopping site (Yong and Moore 1997), (3) rebuilding of the digestive system in birds that have undergone long non-stop flights (Piersma and Gill 1998), and (4) competition among conspecifics (Rappole and Warner 1976; Moore and Yong 1991).

Body condition and subsequent performance

Several studies have shown an association between the body condition of individual birds at migration sites and their subsequent survival or, more strictly, re-sighting rates, whether in autumn or spring (for great reed warbler *A. arundinaceous* in spring, see Nisbet and Medway 1972; for semi-palmated sandpiper *Calidris pusilla* in autumn, see Pfister et al. 1998; for pink-footed goose *Anser brachyrhynchus* in spring, see Drent et al. 2003; for barnacle goose in spring, see Prop and Deerenberg 1991; for bar-tailed godwit *Limosa lapponica* in spring, see Drent et al. 2003; for red knot *Calidris canutus* in spring, see Baker et al. 2004; Table 1). In some of these studies (Nisbet and Medway 1972; Pfister et al. 1998; Drent et al. 2003), re-sighting was restricted to the capture site, so it was uncertain whether the lower re-sighting rate of low-weight birds reflected poor survival or a reduced tendency to return to the same stopover site. However, in the other studies, re-sighting occurred at several different points along the migration route, allowing the whole population to be surveyed more thoroughly, and on repeated occasions in subsequent years. In these studies, therefore, lower re-sighting rates almost certainly reflected poorer survival (as concluded by the authors).

The body weight of ducks on autumn migration was also related to their subsequent survival. After allowing for age and sex differences, individuals that were light in weight when banded at stopover sites or soon after arrival in wintering areas, survived less well than

Table 1 Examples of associations between body weights at migration time and subsequent re-sighting probability (reflecting survival)

	Evidence	Reference
Autumn		
Semi-palmated sandpiper <i>Calidris pusilla</i>	Departure weight from a stopover site estimated from a previously established relationship between stopover duration and departure weight. Estimated heaviest birds were more likely to be seen at the same site in a later year	Pfister et al. 1998
Mallard <i>Anas platyrhynchos</i>	Birds trapped, weighed, ringed and released soon after arrival at a wintering site. Lightest birds were more likely to be shot in the ensuing months	Dufour et al. 1993
Lesser scaup <i>Aythya affinis</i>	Birds trapped, weighed, ringed and released soon after arrival at a wintering site. Lightest birds were more likely to be shot in the ensuing months	Pace and Afton 1999
American redhead <i>A. americana</i>	Birds trapped, weighed, ringed and released soon after arrival at a wintering site. Lightest birds were more likely to be shot in the ensuing months	Bain 1980
Canvasback <i>A. valisineria</i>	Birds trapped, weighed, ringed and released soon after arrival at wintering site. Lightest birds were more likely to be found dead in the ensuing months	Haramis et al. 1986
Spring		
Great reed warbler <i>Acrocephalus arundinaceus</i>	Birds trapped, weighed, ringed and released at a migration/wintering site. Heaviest birds were more likely to be re-caught at the site in a later year	Nisbet and Medway 1972
Red knot <i>Calidris canutus</i>	Birds that were above average weight at a spring stopover site in Iceland were most likely to survive poor spring weather in Greenland breeding areas	Wilson 1988
Red knot <i>C. canutus</i>	Birds trapped, weighed, ringed and released at a migration site. Heavy individuals were more likely to be seen again in subsequent years than lighter ones. In years when many birds failed to achieve normal departure weight, mean survival of ringed birds declined (by 37%)	Baker et al. 2004
Pink-footed goose <i>Anser brachyrhynchus</i>	Annual survival declined over a period of years in parallel with a decline in a body condition at a spring stopover site	Drent et al. 2003
Barnacle goose <i>Branta leucopsis</i>	Birds at a spring stopover site judged to be in good condition (from the abdominal profile) were more likely than poor condition birds to be later re-sighted in a wintering or migration areas	Prop and Deerenburg 1991
Bar-tailed godwit <i>Limosa lapponica</i>	Birds trapped, weighed, ringed and released at a stopover site. The heaviest individuals (with the most advanced plumage development) were most likely to be recaptured at the site in subsequent seasons	Drent et al. 2003

Table 2 Examples of associations between body weight at migration time and subsequent breeding success

	Evidence	Reference
American redstart <i>Setophaga ruticilla</i>	Birds trapped and weighed soon after arrival in breeding areas. Heavier individuals laid earlier, and had higher clutch-sizes, egg volumes and chick weights	Smith and Moore 2003
Mallard <i>Anas platyrhynchos</i>	Birds caught soon after arrival in breeding areas. Females in best spring body condition laid earlier, larger clutches	Krapu 1981, Pattenden and Boag 1989
Snow goose <i>Anser caerulescens</i>	Birds shot after arrival in breeding areas. Heavier females, with greatest body reserves, had more developing egg follicles (taken to indicate larger clutches)	Ankney and MacInnes 1978
Greater snow goose <i>A. c. atlantica</i>	Birds at a spring stopover site judged to be in good condition (from abdominal profile) laid earlier and larger clutches	Bêty et al. 2003
Pink-footed goose <i>A. brachyrhynchus</i>	Birds assessed at spring stopover site. Individuals in good condition (from abdominal profile) were most likely to produce young	Madsen 1995, 2005, Drent et al. 2003
Barnacle goose <i>Branta leucopsis</i>	Birds assessed at spring stopover site. Individuals in good condition (from abdominal profile) were most likely to produce young	Prop and Black 1998
Brent goose <i>B. bernicla</i>	Birds assessed at spring stopover site. Individuals in good condition (from abdominal profile) were most likely to produce young	Ebbinge and Spaans 1995

individuals in good condition. Such variation was documented in mallards *Anas platyrhynchos* (Hepp et al. 1986; Dufour et al. 1993), redheads *Aythya americana* (Bain 1980), canvasbacks *Aythya valisineria* (Bain 1980; Haramis et al. 1986), and lesser scaups *Aythya affinis* (Pace and Afton 1999). In adult male canvasbacks, these

survival differences were due to natural factors (because the birds were not hunted at the time; Haramis et al. 1986), but in the other species they resulted from greater proportions of poor-condition birds being shot within the next few months. In addition, the body condition of shot birds varied between habitats and between hunting

methods (poor-condition birds being more readily attracted to decoys; Greenwood et al. 1986; Heitmeyer et al. 1993). These studies showed that the body condition of ducks at autumn stopovers influenced not only their subsequent survival, but also their use of habitats, behavioural responses to decoys and vulnerability to hunting.

Among geese and other waterfowl, food availability at wintering and spring migration sites has long been known to affect body condition and subsequent reproductive success (Table 2; for lesser snow goose *Anser caerulescens caerulescens*, see Ankney and MacInnes 1978; Bêty et al. 2003; for pink-footed geese, see Madsen 1995; for Canada goose *Branta canadensis*, see Hanson 1962; Raveling 1979; for barnacle geese, for brent goose, see Ebbinge and Spaans 1995; for mallard, see Krapu 1981; Pattenden and Boag 1989; for lesser scaup, see Afton and Ankney 1991; Anteau and Afton 2004). In a few species, the mechanisms have been studied. For example, among brent geese in the Netherlands, females that had accumulated the greatest body reserves at a spring stopover site were more likely to return with young in the following autumn than were females that had accumulated smaller reserves, whereas males, which accumulated smaller reserves than females, showed no such relationship (Ebbing and Spaans 1995). The favoured spring staging habitat is saltmarsh where nutrient-rich plants allow the geese to fatten rapidly. However, the number of geese that can feed in saltmarsh is limited, so as the population grew over a period of years, increasing proportions of birds were relegated to less nutritious agricultural grassland. The geese used body reserves accumulated in spring for migration and reproduction, and individuals that had fed on saltmarsh showed better breeding success than those that had fed on grassland (Ebbing 1992).

In some other species of geese, smaller proportions of females laid, and clutches were smaller, in years when feeding conditions in staging areas were poor than in years when they were good (for barnacle geese, see Cabot and West 1973; for lesser snow geese, see Davies and Cooke 1983). From these various studies, breeding success of some migratory waterfowl depends partly on body reserves accumulated in wintering and spring staging areas, and the effects of such reserves are evident at the level of the individual and at the level of the population. Breeding success in some ducks is also influenced by body reserves, accumulated partly before and partly after arrival in breeding areas. However, most studies of ducks were based on carcass analyses, concentrating on changes in average body condition during the season; few studies examined variation in the body condition of individuals at stopover or arrival in relation to their subsequent breeding performance (Table 2).

Among shorebirds nesting in the high arctic, the extent to which body reserves are available for egg production may depend on climatic and other conditions in particular years, and may differ between protein and lipid. In one study, isotope analysis revealed that in

several species egg protein was formed from terrestrial rather than marine foods, and hence was influenced by food eaten after arrival in breeding areas (Klaassen et al. 2001). On the other hand, in another study, eggs in the earlier clutches of red knots and turnstones in the northeastern Canadian high arctic were rich in ^{13}C and ^{15}N , which suggested that some residual marine nutrients were used in their production (Morrison and Hobson 2004).

Some studies of passerines have also suggested that conditions in wintering areas can influence both the timing of spring migration, and also the timing and success of reproduction (e.g. Marra et al. 1998; Bearhop et al. 2004). In such small species, the weight of a clutch is so large, relative to body weight, that body reserves could provide at most a tiny proportion of the material necessary for egg production. Presumably they serve some other function, such as maintenance, and the nutrients required for eggs must come mainly from food eaten at the time (Sandberg and Moore 1996). However, both sexes of American redstarts *Setophaga ruticilla* arrived to breed in northern Michigan with surplus fat, but females arrived with more than males in two out of three years (Smith and Moore 2003). Individuals of both sexes, but especially females, that had more body fat on arrival also showed higher reproductive success than birds arriving with little or no fat, with higher clutch sizes, egg volumes and nestling weights. In cases like this, where the reserve is small, it is hard to tell whether the association with subsequent breeding success reflects a cause-effect relationship, or merely a correlation, with birds that achieve good body condition on migration also achieving good body condition at other times, and hence showing high survival and reproductive rates.

Studies based on ringing or isotope analyses have provided evidence of apparent carry-over effects in individuals from one time of year to another. Those individuals that occupied the most productive habitats in winter started their spring migration at an earlier date, arrived earlier on breeding areas where they obtained a place in good habitat, and bred with higher success (for black-throated blue warbler *Dendroica caerulescens*, see Marra et al. 1998; Bearhop et al. 2004; for black-tailed godwit, see Gill et al. 2001; Norris et al. 2004). The role of dominance was shown in an experiment in which 28 American redstarts (largely adult males) removed from their territories in optimal mangrove habitat were rapidly replaced by 23 other individuals (females and juvenile males) from poor scrub habitat (Studds and Marra 2005). Initially, the replacement birds had blood isotope signatures typical of scrub, but 2 months later they had isotope signatures typical of mangrove. Compared to control birds in scrub, the upgraded birds maintained weight over winter, departed earlier in spring, and returned in greater proportion the next autumn. Insect biomass was greater in mangrove than scrub, suggesting the food availability caused the differences. This experiment indicated that prime winter habitat was limited, and that winter conditions

influenced the subsequent performance of individuals. Birds that are able to get a place in good habitat in their first winter may be well-positioned to breed productively the next spring, and possibly throughout their lives. Other carry-over effects from winter to summer, affecting morphology and breeding, were described in barn swallows *Hirundo rustica* (Møller and Hobson 2004; Saino et al. 2004).

Influence of predation, disturbance and parasitism

Sometimes large numbers of predators accumulate at stopover sites, relative to the numbers of potential prey. This can make individual prey more vulnerable than usual. In addition, when accumulating body reserves, avian prey species often feed intensively, reducing vigilance and spending more time in places where the danger is greater. Accipiters and falcons are often seen catching birds at stopover sites (Rudebeck 1950; Kerlinger 1989; Lindström 1989; Moore et al. 1990). On the basis of studies at Falsterbo in south Sweden, Lindström (1989) estimated that raptors (mainly sparrowhawks *Accipiter nisus*) removed 10% of all chaffinches *Fringilla coelebs* and bramblings *F. montifringilla* during the 1.5-month period of autumn migration. This rate of predation was much greater than expected from the annual mortality rate in these species, if losses had been evenly spread through the year.

Although prey-birds can respond to the presence of predators through greater vigilance and selection of safer habitats, both these measures may reduce feeding rates (Metcalf and Furness 1984; Lindström 1990). Moreover, the weight increase associated with fuel deposition reduces lift-off speed and agility, supposedly making prey easier for a predator to catch (Witter et al. 1994; Metcalfe and Ure 1995; Lee et al. 1996; Lind et al. 1999). Fat blackcaps *Sylvia atricapilla* exposed to simulated predator attacks suffer reductions of up to 32% in angle of ascent and 17% in velocity, compared to lean blackcaps (Kullberg et al. 1996). Little wonder that some birds increase their vigilance and feed in safer places as they increase in weight (Burns and Ydenburg 2002).

Disturbance of birds at stopover sites, caused by natural predators or people, can have marked effects on the rates and extent of weight gain by migrants, and hence on subsequent survival or breeding success. Pink-footed geese that migrate from the Netherlands to breed in Svalbard make a major feeding stop at Vesterälen in north Norway. For many years, this population had been increasing. From about 1993 on, however, the local farmers began systematically to disturb geese from their grasslands. This continual harassment prevented most of the geese from accumulating adequate body reserves, as was apparent from their 'abdominal profiles'. In contrast, geese using small areas of undisturbed habitat still achieved high levels of reserves. Progressively, the geese began to abandon this site in favour of a less-good site further south, their spring–summer mortality increased,

and the mean production of young per pair declined. The population stopped increasing, but so far has not begun to decline (Madsen 1995; Drent et al. 2003).

A second example comes from an experiment in North America, designed to curb the population growth of the greater snow goose *Anser caerulescens atlantica*. On the main spring staging areas beside the St. Lawrence River, the geese had been protected since 1917, and their numbers had increased greatly, but in the 1990s a spring hunt was re-instated. The main effects of this hunting came not from the numbers killed, but from the effects of disturbance on the accumulation of body reserves and subsequent nest success. The migration and breeding behaviour of large samples of radio-tagged geese were compared between two non-hunting years and the first two years with spring hunting (Mainguy et al. 2002). In the non-hunting years, 85% of the 80 radio-tagged females identified on the spring staging areas in the St. Lawrence River valley were subsequently found in breeding areas on Bylot Island, where 56% were known to have nested that year. By contrast, in hunting years, only 28% of 80 radio-tagged females identified in the St. Lawrence valley reached the nesting areas on Bylot Island, and a mere 9% nested. The differences between years in these proportions were statistically significant (proportion present, $\chi^2 = 57.6$, $P < 0.001$; proportion nesting, $\chi^2 = 16.9$, $P < 0.001$). They were not due mainly to losses of birds to spring hunting, because most of the missing radio-tagged birds turned up again in the autumn. Many radio-marked geese had shortened their migration and stopped on Baffin Island, where they moulted but did not breed. Moreover, females shot near the nest in hunting years were lighter in weight ($F = 12.7$, $df = 37$, $P < 0.001$) and contained less breast muscle ($F = 12.3$, $df = 36$, $P < 0.001$), and less abdominal fat ($F = 6.1$, $df = 34$, $P < 0.02$) than some shot in earlier years with no spring hunt. Egg laying in the colony was delayed about a week in both hunting years, and clutches were significantly smaller, compared with four previous years (Bêty et al. 2003). The implication was that disturbance at the St. Lawrence staging sites reduced the feeding rates and body condition of geese which survived the hunt, adversely affecting their subsequent migration and reproduction.

It is not just waterfowl that are susceptible to human disturbance. The mean body mass of sandhill cranes *Grus canadensis* dropped by more than 7% at a staging area in North Dakota after the hunting season was brought forward from November (when most of the cranes left) to September (Krapu and Johnson 1990). In another study, the disturbance effects of autumn shooting of waterfowl were tested by setting up experimental reserves in two Danish coastal wetlands (Madsen 1995). Over a 5-year period, these undisturbed reserves became important staging areas for waterfowl, increasing the national totals of several species. Hunted species increased the most in these reserves, some 4–20 times, while non-hunted species increased 2–5 times. Furthermore, most quarry species stayed in the area for up to

several months longer each winter than in earlier years. No declines in bird use were noted at other sites still open to hunting, so the accumulation of birds in the reserves was attributed to the short stopping of birds that would otherwise have migrated further south. In this and other studies, hunting disturbance emerged as a major factor influencing the migration and winter distribution of waterfowl, on both local and regional scales.

Other changes in the behaviour of migrant birds towards shorter stopovers at certain sites have been attributed to increased vulnerability to predation associated with the recovery of peregrine falcons *Falco peregrinus* and other raptors from the organo-chlorine pesticide impacts of earlier years. For example, the Strait of Georgia in British Columbia is a major autumn staging site for western sandpipers *Calidris mauri* on southward migration. Birds caught on the extensive mudflats of the Fraser estuary were significantly heavier (by 10%) than others caught on the small mudflat on Sidney Island (Ydenberg et al. 2002). The weight difference could not be attributed to seasonal timing, age or sex effects, but was linked with vulnerability to predation. The open expanse of the Fraser estuary offered safety from avian predators, but a lower fattening rate, while the small Sidney Island was more dangerous, but offered a higher fattening rate. The inference was that sandpipers arriving in the Strait with little fat (and hence more rapid escape responses) chose to take advantage of the high feeding rate at small dangerous sites like Sidney Island, whereas individuals encumbered by higher fat reserves elected to feed in larger but safer sites such as the Fraser estuary. Large open sites are safer because they make it difficult for raptors to approach undetected, giving the shorebird prey earlier warning and longer escape times. From 1985, as peregrine numbers increased, average migratory body mass and stopover durations of western sandpipers at Sidney Island fell steadily (Ydenberg et al. 2004). An accompanying steep decline in sandpiper numbers at Sidney Island was accounted for by shortening stopovers (mean 8.4 days, falling to 2.7 days), rather than by fewer individuals using the site. Under greater danger from predation, these birds seem to have switched from a long stay / high fuelling strategy at this site to a short stay / low fuelling strategy, using only safer sites for further weight gain. The authors believe that such behavioural adjustments could be widespread among shorebird species, and suggest that predation could be a major factor shaping the migratory routes, migratory timing and migratory behaviour of shorebirds (Lank et al. 2003).

Parasites are also likely to affect migratory performance in birds, not only because their effects can be debilitating, but also because, when abundant (especially gut parasites), they can absorb a substantial part of the host's food intake. Their effects are tantamount to lowering the feeding rates of their hosts. In addition, birds might pick up parasites at stopover sites that affect them later in the annual cycle. Migratory birds have often been found to contain a greater range of parasites,

such as haematozoa, than closely related resident species, a difference, which has been attributed to the exposure of migrants, as they pass through different regions, to a wider range of parasite species (Bennett and Fallis 1960; Figuerola and Green 2000). Migratory birds may also help to disperse disease organisms, transferring them from one region to another to infect different populations, avian flu being a topical example.

Effects of stopover events on populations

The above sections illustrate different types of evidence suggesting that events at stopover sites could influence migrant populations. They show that food supplies at staging sites can be heavily depleted, slowing rates of fattening, which in turn can delay spring migration so much that it reduces breeding success, or prevents breeding altogether. Moreover, the intra-specific crowding, or the disturbance caused by predators or human hunters, can affect the behaviour and fattening rates of migrants, causing them to leave stopover sites prematurely and with lower fuel reserves than otherwise, with affects on their subsequent survival and breeding success. The next question is whether these effects on individuals are sufficient to reduce population sizes below what they would otherwise achieve.

In the greater snow goose and pink-footed goose mentioned above, increased disturbance at a major spring stopover site led to reduced breeding success, and also, at least in pink-footed geese, to reduced survival. This would be expected to influence the subsequent population trend, and the pink-footed goose population has now ceased its long-term increase. In the red knot *Calidris canutus rufa* population that breeds in arctic Canada and winters in Tierra del Fuego, marked decline has also been tied to changed conditions at a major spring stopover site. At Delaware Bay, this population fell from 51,000 to 27,000 individuals between 2000 and 2002. Decline coincided with collapse (through human over-fishing) of the horseshoe crab *Limulus polyphemus* population, the eggs of which form the main food of knots at this site (Baker et al. 2004). This locality is the last refueling site of these birds en route to their arctic breeding areas. From 1997 to 2002, increasing proportions of knots studied in the Bay failed to reach the usual departure mass of 180–200 g. Survival of adults fell by 37%, and the proportions of immature birds in wintering flocks by 47%. Of birds caught in the Bay, known survivors were heavier at initial capture than were birds not seen again. By 2004, the numbers of knots had fallen even further, along with those of turnstone and sand-erling *Calidris alba*. However, a moratorium was introduced on crab fishing during May–June, and enough crab eggs were produced that year to feed the reduced numbers of shorebirds, enabling them to fatten at the normal rate. Because horseshoe crabs do not breed until they are about 10 years old, the situation could remain precarious for several further years.

Recent problems at stopover sites may have influenced the population levels of some other species too. Widespread decline in the numbers of lesser scaup in North America has been linked with females arriving on breeding areas in poorer condition than before (Anteau and Afton 2004). In breeding areas in Minnesota and Manitoba, mean body mass of females was about 8% lower in the 2000s than in the 1980s, and lipid reserves were 30% lower. Mineral reserves were also lower in the Manitoba females. Mean body mass of males was 41% lower in Minnesota. All these downward trends were statistically significant ($P < 0.05$). With lower body reserves, scaup are unable to breed or must wait until they have replenished reserves on breeding areas, a delay which reduces breeding success. The differences in body condition were evident at the end of the migration route (in Minnesota–Manitoba), but further down the route (in Louisiana and Illinois) birds were actually heavier in the 2000s than in the 1980s.

These various observations suggest that competition and predation/disturbance at stopover sites can influence the migration speeds, reproduction and survival chances of individual migrants, and in extreme cases can affect their numbers. Such processes can act in a density-dependent manner, at least among the individuals that are present at one time at particular sites. Where most individuals depend on the same small number of stopover sites (as in pink-footed goose and red knot), and birds are competing largely at the same time in the same area, such processes could have density-dependent effects at the level of the entire population. It remains to be seen whether the same holds in species in which

individuals are spread over a large number of stopping sites at all stages of the journey, each individual competing with whichever other individuals happen to be at the same sites at the same times, as in many passerines that migrate overland.

Other migration-related mortality

Other forms of mortality occur among migratory birds, and can occasionally inflict heavy losses. They can be divided into three categories: (1) in-flight losses, caused by storms or other adverse weather en route, usually involving land birds over water; (2) atypical cold weather soon after arrival on breeding areas; and (3) atypical cold weather before departure from breeding areas. These losses are density independent, in that the proportion of individuals affected bears no consistent relationship to population size. Cold and snow act to cut off the food supply of vulnerable species, and have been shown to have a major selective effect on the timing of migration (Brown and Brown 1998).

In-flight mortality

Table 3 gives some examples of in-flight mortality, involving hundreds or thousands of birds at a time. They have involved mainly small passerines, but also larger birds, including eagles and swans. Because such mass mortality incidents mostly occur over water, many must presumably pass unnoticed. Moreover, because they

Table 3 Examples of some in-flight mass mortality incidents in migratory birds, associated with adverse weather en route

Species	Date	Location	Conditions	Numbers	Source
Spring					
Lapland longspurs <i>Calcarius lapponicus</i>	March 1904	Minnesota-Iowa	Snowstorm	1.5 million	Roberts 1907, 1907a
Magnolia warblers <i>Dendroica magnolia</i> and others (39 species)	May 1951	Off Texas coast ^a	Rainstorm	> 10,000	James 1956
Various (43 species)	May 1962	Minnesota ^a	Mist and rain	5,500	Green 1962
Various (> 32) species	May 1974	Off Texas coast ^a	Rainstorm	5,000	Webster 1974, King 1976
Jays, thrushes, warblers	May 1976	Lake Huron, Michigan ^a	Rainstorm	200,000	Jansson 1976
Raptors and others (> 12 species)	April 1980	Off Israel coast ^a	Wind	> 1,300	Zu-Aretz and Leshem 1983
Mainly rooks <i>Corvus frugilegus</i> and many others (20 species)	April 1985	Off Swedish coast ^a	Dense fog	> 20,000	Alerstam 1988
Various (45) species	April 1993	Off Louisiana coast ^a	Tornado	40,000	Wiedenfield and Wiedenfield 1995
Autumn					
Various species (26 species)	October 1906	Lake Huron, Ontario ^a	Snowstorm	> 10,000	Saunders 1907
Various ducks (5 species)	October 1951	South Dakota	Fog, rain, snow	c.a. 500	Schorger 1952
Various, mainly warblers (37 species)	October 1964	Florida	Low cloud, heavy rain	> 4,707	White 1965
Mainly song thrush <i>Turdus philomelos</i> , blackbird <i>T. merula</i> and many others (12 species)	October 1988	Off Swedish coast ^a	Dense fog	> 20,000	Alerstam 1991
Eared (black-necked) grebe <i>Podiceps nigricollis</i>	January 1997	Utah	Snowstorm	35,000	Jehl et al. 1999

^aMuch or all of the mortality occurred over water

would be expected to involve birds from a large part of the breeding range, their effects on local populations may often be small and hard to assess, although, as explained earlier, events in spring may have greater effects than those in autumn.

Among Nearctic–Neotropical migrants, recent population declines were less frequent and less marked among western populations, which migrate entirely overland, than among eastern ones, which migrate partly over water, crossing the western Atlantic or Gulf of Mexico (Butler 2000). In autumn, storms are common in these sea areas. Moreover, among the eastern populations, declines were also more frequent among those species that made long water crossings (to winter in South America) than among those that made shorter crossings (to winter in Central America or the Caribbean Islands). So for 25 passerine species, which had declined over the period 1966–1996, Butler (2000) examined the annual population levels (as measured by the Breeding Bird Survey) in relation to the numbers of storms that had occurred over these water areas during the previous autumn migration period (15 August–15 October). Storms occurred on an average of 39 days during this period, varying between 18 and 59 days in different years. In 2 of the 25 species examined (red-breasted grosbeak *Pheucticus ludovicianus* and mourning warbler *Oporornis philadelphia*), breeding population levels were negatively correlated with the numbers of days with storms during the preceding autumn migration period.

Although such statistically significant correlations need not necessarily indicate cause–effect relationships (in particular, weather in autumn may be related with weather elsewhere at other seasons), they do suggest that further investigation of potential over-water weather effects on land bird populations is warranted. To these various natural losses associated with migration must be added the many others inflicted by human artefacts, such as tall illuminated structures.

Post-arrival mortality on breeding areas

Records of post-arrival mortality, associated with cold and snow on breeding areas, have involved mainly small insectivores (especially hirundines), but also a wide range of other birds, including waders and waterfowl (Table 4). Such incidents, have killed large numbers of birds, and in some species for which effects could be estimated, local breeding densities were reduced by 30–90%, depending on species and area (Table 5). In the common sandpiper *Actitis hypoleuca*, year-to-year changes in breeding density in one area were strongly correlated with mean temperatures during April, the month of arrival (Hollands and Yalden 1991). In the two coldest years, breeding pairs fell by 33 and 40% (from 21 to 14, and from 20 to 12). After both years, recovery in population level was slow, with annual increments of only 1–2 pairs. In this species, weather around the time

Table 4 Examples of some mass mortality incidents in migratory birds, associated with adverse weather soon after arrival in breeding areas

Species	Date	Location	Conditions	Numbers	Source
Various (32) species	April–May 1975	Utah	Snowstorms	569	Whitmore et al. 1977
American coots <i>Fulica americana</i>	March 1964	Iowa	Re-freezing	‘Hundreds’	Fredrickson 1969
King eider <i>Somateria spectabilis</i>	May–June 1964	Beaufort Sea	Re-freezing	100,000	Barry 1968
Northern lapwings <i>Vanellus vanellus</i>	April 1966	Finland–Sweden	Cold and snow	‘Many thousands’	Vepsäläinen 1968, Marcström and Mascher 1979
Various (42 species)	May 1968	Finland	Cold and snow	> 3,000	Ojanen 1979
Cliff swallow <i>Petrochelidon pyrrhonota</i>	May 1996	Nebraska	Cold and rain	‘Thousands’	Brown and Brown 1998

Table 5 Some local population reductions recorded after snowstorms, which occurred soon after migrants had arrived in their breeding areas, or in autumn just before they could leave

Species	Area (Year)	Estimated reduction in breeding density (%)	Reference
Spring			
Cliff swallow <i>Hirundo pyrrhonota</i>	Nebraska (1996)	53	Brown and Brown 1998
Scarlet tanager <i>Piranga olivacea</i>	New Hampshire (1974)	35	Zumeta and Holmes 1978
Scarlet tanager <i>P. olivacea</i>	Maine (1974)	50	Robbins and Erskine 1975
Various hirundines	Nova Scotia, Maine, New Hampshire (1974)	30	Robbins and Erskine 1975
Various warblers	New Brunswick (1974)	25	Robbins and Erskine 1975
Northern lapwing <i>Vanellus vanellus</i>	Sweden–Finland (1966)	30–90	Marcström and Mascher 1979
Common sandpiper <i>Tringa hypoleucos</i>	England (1981, 1989)	33–40	Hollands and Yalden 1991
Autumn			
House martin <i>D. urbica</i>	Switzerland (1974)	25–30	Bruderer and Muff 1979

of spring arrival seemed to have a big influence on year-to-year survival, and consequently on year-to-year breeding densities.

Pre-departure mortality on breeding areas

Records of late-summer pre-departure mortality on breeding areas have mainly involved hirundines. Two major periods of freezing weather in central Europe in 1931 and 1974 killed hundreds of thousands or even millions of birds (Alexander 1933; Bruderer and Muff 1979; Reid 1981). After the 1974 incident, house martin *Delichon urbica* populations in Switzerland were reduced by an estimated 25–30% in the following year (Bruderer and Muff 1979). Other incidents refer to arctic-nesting waterfowl, unable to leave breeding areas before falling temperatures froze them into the ice for the winter (Barry 1968).

Relative importance of migration-related mortality

Migration mortality has proved difficult to measure as a distinct component of the overall annual mortality. This is because the chance of getting ring recoveries varies along a migration route so does not reflect the scale of mortality in different places and, with radio-marked birds, it is not usually possible to distinguish death from radio-failure. However, in a recent study of black-throated blue warblers, Sillett and Holmes (2002) assessed survival rates during the summer breeding period in New Hampshire, during the winter period in Jamaica, and over the year as a whole, respectively. They concluded that more than 85% of apparent annual mortality occurred during migration, giving a rate, which was at least 15 times higher than at other times.

Among barnacle geese, travelling 3,200 km between Svalbard via Bear Island to Scotland, it proved possible in 1986 to check for colour rings in the same group of birds just before and after this migration (Owen and Black 1989). About 35% of the juveniles were found to have disappeared (presumed dead) on this one journey, compared with about 5% of older birds (about half the annual total). The losses were greatest among young hatched latest in the season, which were lightest in weight at the date of departure. This amount of mortality was deemed exceptional, however, because severe weather in the breeding area forced the birds to leave earlier than usual and also stopped some from staging on Bear Island. Once juveniles reached their wintering areas, annual mortality dropped to a level equivalent to 10% per year, the same as adults. Evidence of similar mortality during the autumn journey of light-bellied brent geese *B. bernicla hrota* migrating from northern Canada to Ireland was provided by O'Briain (1987). Their migration covers at least 2,500 km, part of which crosses the Greenland ice cap. In each of two years, loss of young averaged 33%, compared with 5% for adults.

Similarly, greater snow geese, migrate from breeding areas on Bylot Island in the Canadian Arctic to staging areas on the St. Lawrence River in Quebec. Mortality on this autumn journey was calculated in five successive years, both from banding studies and from comparison of the brood sizes of neck-banded females before and after migration (Menu et al. 2005). The two approaches yielded similar survival estimates, and the same pattern of year-to-year variation. The average monthly survival of juveniles over this journey was 66% and that of adults 99%. However, after this migration, juveniles survived as well as adults (both 97%). The survival of juveniles over the migration period also varied greatly between years (range 12–71% over 5 years), and most mortality appeared to be natural (rather than due to shooting). Juvenile survival was lowest in years when: (1) temperatures at the time of fledging and migration were low (at or below freezing), (2) the mean body mass of goslings at fledging was low, and (3) the mean fledging date was late. These studies indicate how conditions on breeding areas can influence subsequent survival on migration.

In some other species, too, most of the difference in annual mortality between juveniles and adults was attributed to greater losses among juveniles before they reached their wintering areas (Cavé 1983; Gromadzka 1989; Pienkowski and Evans 1985). However, comparison of age-ratios among museum skins of pacific slope flycatchers *Empidonax d. difficilis* at the start and end of each migration indicated a higher mortality among first-year birds than among adults on both autumn and spring journeys (Johnson 1973).

Concluding remarks

Limitation of breeding populations through migration events has been viewed in this paper mainly as a three-step process, involving: (1) food availability at stopover sites, which influences the migratory performance of individuals, as reflected in rates of weight gain, departure weights, frequency and duration of stopovers, and overall migration speed; (2) carry-over effects of migration performance on subsequent survival or breeding success; and (3) which in turn influence population trend (Fig. 2). Many studies have been concerned with the first aspect, providing evidence from stopover sites on interference and depletion competition and for effects of disturbance and predation on the fattening rates of individuals (involving some age and sex effects). Relatively few studies have provided evidence of migration conditions influencing subsequent breeding and survival, and even fewer of effects on subsequent breeding numbers. It is not easy to obtain evidence for effects on breeding numbers, and the paucity of examples may reflect the difficulties of study rather than the rarity of the phenomenon. Moreover, on all aspects, the evidence is based primarily on correlations, giving no direct evidence for causal relationships, although the provision of extra food and contrived disturbance to migrants can be

classified as experimental. Nevertheless, the main challenge for future research is to test whether the main types of correlation discussed above reflect causal relationships.

All the various processes envisaged involve competition for food or feeding rates (coupled with predation and parasitism). They could all act in a density-dependent manner to regulate overall populations partly in relation to the availability and quality of stopover habitat. The second type of mortality affecting migratory bird populations, caused by storms or other adverse weather, is likely to act in a density-independent manner, in that the proportion of birds removed each year bears no consistent relationship to overall population size. However, the likelihood of any one individual succumbing in an extreme weather event may depend partly on its body condition at the time, and in turn on conditions (including competition) at previously attended stopover sites.

While we as yet have few examples of bird populations in which changes in breeding numbers have been unequivocally linked to events at a stopover site, in many species changes in breeding numbers are known to be influenced by conditions in wintering areas (Newton 2004). Many of these examples of apparent winter limitation could operate through effects on spring migration, which often occurs when food sources reach their lowest level of the year. For example, many Eurasian migrants have declined in numbers following years of drought in the Sahel zone of Africa (review: Newton 2004). Most mortality is likely to have occurred towards the end of their stay in the Sahel, at the time of migratory fat deposition, or in the Sahara as a result of inadequate body reserves. Some of the species that have shown declines winter mainly south of the Sahel in wetter habitat, but they still have to migrate through the Sahel in spring. More careful investigation of migration in this region may reveal that much of the apparent over-winter mortality is related to spring migration.

Competitive interactions and food shortage

Although few would question the importance of food supply to successful migration in birds, the precise effects of food shortage are not always easy to quantify, for they do not always result in direct starvation (loss of body condition to the point of death). At stopover sites, territorial and other interactions between individuals can operate to adjust densities to local food supplies at the time, causing hungry birds to move elsewhere, to places where they may survive or die of any one of various causes, including starvation. Second, food shortage at stopover sites may reduce population size through lowering breeding rates (as in some geese), not necessarily entailing the starvation of full-grown birds. This type of effect may be hard to detect because of the time lag between the food shortage and the resulting decline in breeding numbers. In some long-lived species,

individuals do not normally breed until they are several years old, so it may take several years before the effects of poor breeding are reflected in poor recruitment. As a further complication, the effects of food shortage on any population may be accentuated by the presence of people or natural predators, which limit feeding opportunities, and by parasites, which directly or indirectly take part of the host's nutrient intake for themselves.

Interactions between populations

Another much neglected aspect concerns the interactions that occur between different populations or different sectors of the same population. If individuals from two or more breeding populations occur together in the same staging or wintering areas (like many shorebirds), and feed on the same limited prey supply, the dynamics of the separate breeding populations can be interlinked, as the survival rate of individuals from one population is likely to depend on the overall size of both populations (Dolman and Sutherland 1995).

Despite so many travel lanes in bird migration, populations from different breeding or wintering areas may often use the same staging sites. This gives great potential for intra- and inter-specific competition: if one population passes first, it may deplete the food stocks for a later one, and if different populations are present at the same time, the individuals in both may suffer from depletion and interference. In other words, although living apart for most of their lives, the annual few weeks of contact on stopover sites could ultimately influence the size of one or both of any two competing populations. This is an aspect of stopover ecology that has so far received little attention, but it could have great repercussions for the numbers and behaviour of individuals in competing populations.

Residual body reserves

Residual body reserves could be advantageous at any stage of migration, cushioning the bird against adverse weather or other unexpected circumstances during a flight, and also after a flight, whether in a stopover site, a wintering or a breeding area. Such residual reserves give a margin of safety against bad weather immediately after arrival, and allow the bird time to establish itself in a new area. In many species, however, it is after arrival in breeding areas in spring that residual body reserves may be most useful. Links between body reserves and breeding success of arctic nesting geese are now well established. But it is still uncertain to what extent the residual reserves in smaller birds promote subsequent survival and breeding success. In small passerines, the weight of a clutch of eggs is so great, relative to body weight, that no species could produce a clutch from body reserves alone. Feeding experiments in small birds have shown the value of supplementary food in

influencing both laying date and clutch size (Newton 1998). Four benefits of residual spring body reserves have been suggested, which are not mutually exclusive, namely that they could: (1) increase survival chances if weather conditions deteriorate; (2) allow birds to spend more time on other activities important to reproduction, such as territorial defence, song and mate selection; (3) relieve food demands in the early stages of breeding, allowing an earlier start; and (4) allow females to forage selectively for nutrients important to reproduction, such as calcium, while living mainly on their fat (Sandberg and Moore 1996). Surplus weight on migration could also enable the migrants to fly economically at a faster speed, since the maximum range speed increases with total body mass (Pennycuik 1975). These benefits must presumably be set against the costs of longer stopovers needed to accumulate the extra reserves, the energy to transport them, and any associated predation risks incurred.

Conservation considerations

Migratory birds depend on encountering suitable conditions at various staging places on their routes. If conditions deteriorate at any one point, a bottleneck might develop that could begin to limit the population. When conditions are deteriorating everywhere at once, it becomes hard to pinpoint that bottleneck except in the most obvious cases. But the fact that migrants use two or more essential areas each year means that they are inevitably more susceptible to the effects of habitat destruction than are resident birds. Residents suffer only if their particular area is destroyed, but migrants could suffer if any one of several areas important to them is lost. In this sense they have, on the average, more chances than residents of being affected—adversely or otherwise—by human action. In fact, any factors that increase the cost of migration, especially in spring, could influence subsequent population size.

Constraints on migratory fuelling are likely to be most obvious in landscapes where patches of suitable habitat are few and widely scattered, because such patches usually attract large numbers of passing birds. Such conditions are encountered, for example, by forest species migrating through essentially open landscapes, or wetland species through essentially arid landscapes. These are the conditions that, through their effects on individual birds, are likely to lead to the 'high-fuel/ long-stopover / long-flight' strategy, rather than the 'low-fuel / short-stopover / short-flight' strategy appropriate in more continuous habitat. Because of human effects on landscapes, the situation encountered by migrants has altered greatly in recent centuries. The migrations of many forest birds, for example, evolved in landscapes very different from those found now, as once-continuous forest has been greatly reduced and fragmented. There must presumably come a point in the process of habitat fragmentation when such landscapes become 'ecological

barriers' that are best crossed by long non-stop flights requiring large fuel loads.

Loss of habitat presumably has its most severe effects on migrants where that habitat lies adjacent to an ocean or other barrier, and forms the last possible feeding place before the barrier, or the first encountered after it. Examples include the remaining woodland and scrub patches on the coastlines of the Mediterranean Sea in Europe or the Gulf of Mexico in North America.

Zusammenfassung

Können die Bedingungen während des Zugs die Populationsgröße von Vögeln begrenzen?

Es wird üblicherweise angenommen, dass Zugvogelpopulationen durch die Bedingungen in den Brut- oder Überwinterungsgebieten begrenzt sind, aber einige Populationen könnten durch die Bedingungen, die sie auf dem Zug erfahren, limitiert werden. Dies könnte in Rastgebieten stattfinden, wo die Konkurrenz um beschränkte Nahrungsressourcen die Zuggeschwindigkeit, die Überlebenswahrscheinlichkeit oder den Bruterfolg reduziert, oder während der Flüge selbst, bei denen gelegentlich viele Individuen ungünstigen Wetterbedingungen zum Opfer fallen. Konkurrenz um Nahrung könnte in einer dichteabhängigen Weise wirken und dazu beitragen, Populationen zu regulieren, während Wettereffekte wahrscheinlich eher in einer dichteunabhängigen Weise wirken. In dieser Arbeit werden Hinweise für diese Annahmen erörtert. Bei der Vorbereitung auf den Zug, müssen Vögel mehr Nahrung pro Tag als üblich aufnehmen, um Fettreserven für ihre Flüge zu akkumulieren. Vögel verdichten sich häufig in großer Zahl in bestimmten Rastgebieten, in denen die Nahrung verknappt und so die Zugleistung beeinflusst wird. Geschwindigkeit der Gewichtszunahme, Abfluggewichte und Rastdauer korrelieren häufig mit dem Nahrungsangebot auf Rastplätzen, was zuweilen die Überlebenswahrscheinlichkeit und den Reproduktionserfolg von Individuen beeinflusst und was wiederum Auswirkungen auf die Brutzahlen hat. Viele Studien haben Hinweise auf Interferenz und Konkurrenz durch Nahrungsverknappung in Rastgebieten geliefert, wogegen verhältnismäßig wenige Studien Zusammenhänge zwischen Zugbedingungen und Bruterfolg bzw. Überlebenswahrscheinlichkeit von Individuen untersuchen und in noch geringem Maße Studien über Effekte auf Populationsebene vorliegen. Im Flug erleiden Zugvögel gelegentlich erhebliche Verluste durch Stürme, vor allem über offenen Wasserflächen, was manchmal mehrere Tausend Vögel gleichzeitig betrifft. Ferner kommt Massensterblichkeit bei untypischen, winterlichen Wetterverhältnissen vor, die kurz nach der Ankunft in den Brutgebieten oder kurz vor dem Wegzug im Herbst einbrechen. Durch solche Ereignisse sind wiederholt viele Tausende Vögel gleichzeitig getötet worden, was zu einer 30 bis 90-prozentigen Reduktion lokaler

Brutdichten geführt hat. Bei manchen Vogelarten können Ereignisse, die mit dem Zug in Verbindung stehen, bisweilen erhebliche Effekte auf zwischenjährliche Veränderungen der Brutbestände haben. Doch haben die Schwierigkeiten, die mit der Erforschung von Zugvögeln an den unterschiedlichen Stationen ihrer Zugrouten einhergehen, bis jetzt die Zahl der Untersuchungen über diesen Aspekt der Populationslimitierung eingeschränkt.

Appendix 1

In the ornithological literature, two other types of findings have been cited as evidence that food supplies at stopover sites can be limiting for migrants. Because these types of evidence are open to other interpretations, and are not amenable to experimental testing, they are discussed separately below.

Ecological segregation

Nearly all bird species show some degree of ecological separation during migration stopovers, whether in habitat, foraging sites, foraging times or diet (Berthold 1988; Bairlein 1981; Streif 1991; Spina et al. 1985; Farola and Fraticelli 1990; Moore et al. 1990). It has been argued that such segregation helps to reduce competition between species at stopover sites, as well as on breeding or wintering areas.

While this may be true, the demonstration of ecological differences between species at a stopover site does not necessarily imply that food is limiting there. Such differences, which depend on the structure and behaviour of the species themselves, may result from food-based competition in the past, or in areas other than stopover sites, or they could result from causes other than food-based competition. Such ecological differences are thus consistent with the idea that inter-specific competition for food is limiting for individual migrant performance, but cannot prove it. Nor can the idea be tested satisfactorily.

Temporal segregation of migration seasons

Closely related species with similar ecology often pass through particular sites at somewhat different dates during the migration seasons (for shorebirds see Recher 1966, for warblers see Howlett et al. 2000). The same is also true for different populations of the same species. In general, different populations pass north in spring in the sequence in which their breeding areas become habitable, and south in autumn in the sequence in which their breeding areas become unsuitable (for yellow wagtail *Motacilla flava*, see Curry-Lindahl 1958). Although such temporal segregation may reduce the opportunity for

competition between the individuals in different populations, it might not have evolved for that reason, but have some quite different basis, related to the dates and periods that the nesting areas of different populations are suitable for occupation. Also, the early migratory populations might, in some situations, deplete the food for later ones, in which case competition would not be eliminated, but its effects would fall especially heavily on the later-migrating populations.

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