

# The interaction between migration strategy and population dynamics: is there higher winter mortality in short-distance migrants and lower juvenile survival in long-distance migrants?

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Short-distance migrants may trade-off the costs of wintering in cold latitudes with the benefits of a less dangerous and less energy demanding flight while long-distance migrants adopting the converse trade-off may be following a strategy that is equally successful. I discuss ways in which these strategies might be evaluated through studies of the European and Afro-Siberian Bar-tailed Godwit populations.

## INTRODUCTION

All living organisms have to compromise on how much energy is allocated to survival and how much to reproduction. Thus, by increasing current reproductive effort an individual decreases its survival and therefore its future reproductive chances (Begon & Mortimer 1986). If lifetime energy expenditure is limited to a certain level (Prinzinger 1996), organisms have to decide when and how much energy should be devoted to which activities so that, within the constraints affecting them, their fitness, as measured by lifetime reproductive success, is maximised. Migratory movements are often a trade-off between wintering in colder, more energy-expensive environments close to the breeding area with low energy expenditure on migration and wintering in more benign and remote places that are reached at greater cost. Birds can optimise their migration strategy by spending as little time or energy as possible on migration and/or by reducing the risk of being depredated (Alerstam & Lindström 1990, Alerstam & Hedenström 1998, Butler *et al.*, this volume).

Although migration is a risky activity for most birds (Owen & Black 1991), it appears that waders suffer their highest mortalities during winter (Evans 1991). Birds wintering close to their breeding grounds have higher thermostatic costs and a higher energy turnover than birds migrating to warmer areas (Piersma *et al.* 1991, 1996, Wiersma & Piersma 1994). Waders may also suffer mortality through infection with parasites or predation, but there is no reason to suppose that these risks change systematically with latitude. At least in intertidal habitats, where most arctic waders spend the winter, the chances of becoming infected with parasites is rather low, even in the tropics (Piersma 1997). Therefore it is likely that parasites are not a major cause of winter mortality for them. In contrast, predation can be a major cause of wader mortality and it can vary considerably from place to place and with season (Butler *et al.*, this volume), but, so far as I am aware, no systematic latitudinal trend in the risk of predation has yet been identified.

If we combine all these factors and assumptions, it follows

that birds wintering in north-temperate latitudes should have a higher mean annual mortality than birds wintering in the tropics. This was shown to be the case for two populations of Red Knot *Calidris canutus* where a temperate wintering population had higher mortality than one that migrated to the tropics (Piersma 1994). If population sizes do not show long-term changes, according to equilibrium theory (e.g. Goss-Custard 1993) temperate wintering birds must adapt their recruitment to the elevated mortality.

## HOW MIGHT BOTH SHORT- AND LONG-DISTANCE MIGRANTS MAINTAIN STABLE POPULATIONS?

Ideal species for testing these ideas should be those that perform a leap-frog migration, where populations breeding at high latitudes pass over both the breeding and wintering ranges of populations breeding further south (Salmonsén 1955). The Bar-tailed Godwit *Limosa lapponica* populations that migrate through the European Wadden Sea show such a system. There is an Afro-Siberian population that migrates between West Africa and Siberia and a European population that migrates between wintering areas around the North Sea and breeding areas ranging from northern Scandinavia to the Kanin peninsula (Drent & Piersma 1990). Although to some extent European Bar-tailed Godwits are able to balance high thermostatic costs during winter by following an energy minimising migration strategy (Scheiffarth 2003), they have a higher annual energy turnover than Afro-Siberian Bar-tailed Godwits (Drent & Piersma 1990). In contrast, Afro-Siberian birds have their highest energy turnover during migration as they follow a time minimising migration strategy with high body mass increase rates during stopover (Scheiffarth *et al.* 2002). If the assumptions raised above are valid, European Bar-tailed Godwits should have a higher annual mortality than Afro-Siberian birds. Consequently, in order to maintain a more or less stable and, in the long term, viable population, they must have either a higher reproductive output or better immature survival than Afro-Siberian birds to balance the elevated mortality (see Boyd & Piersma



2001 for the importance of recruitment in a Red Knot population). Several different mechanisms, which are not mutually exclusive, may influence the number of recruits to a population:

- 1) European birds have higher breeding success, and/or
- 2) Juveniles of the European population have higher winter survival than juveniles of the Afro-Siberian population and/or
- 3) Juveniles of the European population have lower mortality during their first migration to the wintering grounds than juveniles of the Afro-Siberian population.

It is likely that these three possible mechanisms are of different potential relevance to Bar-tailed Godwits. Whether breeding conditions are better or parental investment, e.g. in producing larger eggs or guarding chicks, is higher for European than for Afro-Siberian birds remains to be investigated. Higher winter survival of European juveniles compared with juveniles of the Afro-Siberian population is unlikely, since the same environmental conditions, which result in a higher mortality in European adults, should also act on juveniles. Therefore, the opposite case is expected, namely that European juveniles have higher winter mortality than Afro-Siberian juveniles.

### THE DIFFERENTIAL JUVENILE SURVIVAL HYPOTHESIS

It would seem likely that the third possible mechanism – differential survival of juveniles during migration – is the one that explains how both Bar-tailed Godwit populations remain broadly stable. If migration is hazardous (Evans 1991, Owen & Black 1991), the chances of failing to reach the wintering area could increase with migration distance, particularly where juveniles do not migrate in the company of adults on their first migration (as is the case in Bar-tailed Godwits). It would appear probable that the migration from Scandinavia to the North Sea is much less demanding than that from the Taymyr peninsula to Mauritania, involving a major change in compass direction that juveniles have to manage without any previous experience.

For many arctic-breeding waders, population parameters are still unknown. Moreover, they have been subject to change during recent decades, as shown for the Red Knot by Boyd & Piersma (2001). Measuring adult mortality in Bar-tailed Godwits would be a first step in evaluating the consequences of different migration strategies on population dynamics. Since European Bar-tailed Godwits seem to be site-faithful to spring stopover sites (Scheiffarth 2001), this could be achieved through a colour marking study.

Comparison of the breeding conditions and performance of the two Bar-tailed Godwit populations should be an excellent test of ideas on how migration strategies are connected to life history parameters. However, if we want to understand the processes behind population parameters, we have to investigate the consequences of individual decisions on reproduction and survival. This should become feasible if we can manage to follow individual birds throughout major portions of their annual cycle.

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