the cost of migration

TEXT **PETER RYAN**

It has long been assumed that migration is a risky undertaking for birds, but it is challenging to assess to what extent the risks are fatal. A recent review summarises findings from studies of 30 migrant species, with some fascinating results.

To demonstrate the direct cost of migration, it is necessary to make independent estimates of how many birds survive both the long-distance flights and the time they are more or less resident in their breeding and wintering areas. Traditionally, such estimates have been made from resightings of ringed birds, but this is extremely challenging. One approach that has been used for a few passerine species is to estimate survival during periods of residence and then infer migration survival from annual survival.

However, annual survival estimates may be confounded by emigration, which leads to overestimating the costs of migration. Alternatively, for some waterbirds such as geese and swans, which have well-known breeding and wintering areas, the proportion of birds surviving each migration can be estimated from resightings made immediately before and after each event.

In the past few decades, tracking studies not only have revolutionised our understanding of how birds structure their migration, but have also provided insights into the risks associated with migrating. Initially, when the devices used to track birds were relatively large, there were concerns that they might affect the birds' performance and thus inflate mortality. However, with tracking devices getting ever smaller, we can be reasonably confident that this is no longer a major consideration, at least for large birds. The main challenge now is that the much smaller sample sizes available for most tracking studies limit our ability to obtain robust survival estimates, especially for long-lived species.

Ian Newton's recent review in *Ibis* (doi: 10.1111/ibi.13316) combines evidence from ringing studies of 10 bird species (five passerines and five waterbirds) with tracking data from another 20 species (raptors, waterfowl, cranes, storks, waders, cuckoos and pigeons). All the species involved breed in the northern hemisphere in summer – 15 in North America, 14 in Europe and one in Asia – and then migrate south for winter. For a few populations, such as adult Greater Snow Geese and Whooping and Sandhill cranes, there is little evidence of any greater mortality risk during migration. However, for most species, the rate of mortality increases during migration.

The risk of migrating varies depending upon the bird's experience and when and where the migration occurs. For juveniles, the first southbound migration in autumn typically is much more challenging than subsequent journeys. This reflects the young birds' relative inexperience, resulting in poor feeding and flight efficiency, greater vulnerability to predators and adverse weather conditions, and more frequent navigational errors. >

OPPOSITE Hudsonian Godwits pay the price for having one of the most extreme migrations, from Alaska to Chile. Their mortality during migration is at least 10–20 times higher than when they are resident.

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The mortality rate among migrating juvenile White Storks is nearly double that before they leave on migration and almost four times that after arrival at their wintering areas. The distance they travel and the nature of the terrain they cross also play a role; the small proportion of tracked juvenile White Storks that wintered in southern Europe all survived, whereas 62 per cent of those that migrated to sub-Saharan Africa died. Crossing the Sahara is a particular challenge for many birds that winter in Africa.

The choice of migration route can make a huge difference. Egyptian Vultures migrating from the Balkans to Africa either fly over the Mediterranean Sea or take the longer route through Turkey and the Middle East. Among tracked juveniles, only one of 10 survived the direct sea crossing, whereas all eight that took the overland route survived. Interestingly, all those that reached Africa crossed the Sahara safely, whereas the desert is a more formidable barrier to Black Kites, accounting for most of the 5–8 times greater mortality rate for kites migrating from Spain to West Africa. The risk of dying is so great that juveniles do not return north to their breeding grounds for at least a year after their first southbound migration.

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The greater mortality of juveniles than adults on migration is not just a case of ignorance. Even among geese, where juveniles are guided on migration by their parents, the survival difference is stark. On average, about one-third of Greater Snow Geese juveniles perish on their first southbound migration, compared to only one per cent of adults. The proportion of juveniles dying varies greatly from one year to another, largely reflecting conditions on the breeding grounds. Few juveniles survive in cold years when breeding is delayed and chicks fledge with low body mass. Similar effects have been shown for Barnacle Geese migrating from Svalbard to Scotland. Juvenile survival was particularly low in 1986, when bad weather forced the geese to migrate south earlier than usual.

For adults of most species, the northbound spring migration is more risky than the southbound autumn migration. This probably reflects more challenging weather conditions in spring, and the greater speed of the northbound migration, when adult birds are pushed to return to their breeding grounds by the advantages of breeding early in the season. Evidence for this seasonal difference in migration cost comes from several raptors that winter in Africa, including Ospreys, European Honey Buzzards and Montagu's Harriers, as well as Eurasian Spoonbills and Black-tailed Godwits. The influence of the distance of migration is clearly demonstrated by spoonbills that breed in the Netherlands: the annual survival rate of those wintering in Mauritania, West Africa, is appreciably lower (80 per cent) than that of those wintering in south-western Europe (92 per cent).

The species demonstrating the most extreme cost of migration recorded to date is the Hudsonian Godwit, which undertakes one of the longest landbird migrations. The godwits, which breed in Alaska and winter at coastal wetlands in Chile, make a non-stop flight of some 10 000 kilometres, much of it over the ocean. Their mortality rate during the southbound migration is at least 10 times higher than when they are resident, and during the northbound spring migration this doubles to more than 20 times higher! The benefit they obtain from this very long and costly migration is an extremely low mortality rate on their wintering grounds; virtually all birds that reach Chile survive to attempt the arduous trek back to Alaska.

Across all 30 studies, the rate of mortality averages 3–6 times greater during migration than during stationary periods. However, Newton's review included only one seabird, the Northern Gannet, and was restricted to the initial southward migration of satellite-tagged juveniles from Bass Rock in Scotland to their wintering area off West Africa. More than half of the expected first-year mortality occurred while the gannets were moving south within two months of leaving Bass Rock, but this also is when they have to learn to forage for themselves. The high mortality rate at this time could simply reflect the weeding out of poor-quality individuals. It would be interesting to compare mortality rates among adult seabirds during migration and residence periods to see if they conform to the pattern seen in terrestrial birds and most waterbirds. ◆

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ABOVE Adult Ospreys that breed in Sweden and winter in West Africa are twice as likely to die on migration than in their breeding or wintering areas. They are three times more likely to die on the northbound spring migration than during the more leisurely southbound migration in autumn.

ABOVE Among juvenile Egyptian Vultures from eastern Europe, 70 per cent of first-year mortality occurred on their first migration to Africa. Only one in 10 survived a direct crossing of the Mediterranean, but all eight that detoured through the Middle East survived.

TOP Whimbrels, such as this Eurasian Whimbrel, are five times more likely to die on migration than while they are on their breeding or wintering grounds.