Review

Migration mortality in birds

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Bird migration is one of the greatest wildlife spectacles, producing massive global changes in the distributions of birds twice each year. To understand the evolution of this phenomenon, it is important to know the costs of these journeys in terms of the mortality they impose. The use of mark/re-sighting and tracking studies has now made it possible, for some bird species, to separate mortality during migration from mortality during stationary periods. This paper aims to assess this information, based mainly on 31 published studies, most of which concern long-distance migrations of passerines, large waterfowl and raptors. Most of these studies revealed that mortality rates were greater during migration than at other times – in some species more than 20 times greater. Overall, on the basis of median values, mortality per unit time during autumn journeys was about 3.0 times greater than mortality during stationary periods, during spring journeys about 6.3 times greater, and during autumn and spring journeys combined 4.4 times greater. The greater overall mortality on spring journeys was largely associated with more adverse wind conditions in spring than in autumn. High mortality rates were especially evident in birds crossing large ecological barriers, such as the Sahara Desert or the Gulf of Mexico, and were higher in that part of their journey than when crossing more benign terrain. There was no increase in mortality during migration in the adults of some long-lived species with high annual survival and predominantly overland journeys; for these birds, much larger samples of year-round tracked individuals will be needed to reveal any seasonal variations in mortality. Within certain species, birds that travelled long distances experienced greater mortality over the journey than those that travelled short distances, but in other species no such relationship was found. In species in which adults and juveniles were followed over the same journey, juveniles showed greater mortality. To judge from other studies, this difference could be attributed to the inexperience of juveniles, their lower feeding rates and flight efficiency, greater vulnerability to hazards such as weather and predation, or more frequent navigational errors. Broadly speaking, the risks of migration vary with features of the birds themselves, with the terrain to be crossed and with weather at the time. It may be assumed that migration persists in the long term because the costs (in terms of associated mortality) are more than offset by the benefits of breeding and wintering in different areas (in terms of improved overall survival and breeding success). To provide further understanding of migration mortality, suggestions are made on the types of studies required and on how they could best be conducted.

Keywords: bird mortality, ecological barriers, migration hazards, mortality during migration, seasonal survival.

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Bird migration is one of the most impressive events of the natural world, producing massive changes in the distributions of birds over the earth's surface every spring and autumn (Newton 2008). The hazards of travel have long been considered a major cost of these journeys, but the mortality involved has proved difficult to measure as a distinct component of overall annual mortality. Early studies used ringing or other means of marking, relying on resighting attempts several times each year to gain the necessary information. As migrants occupy two or more areas each year, this involved expensive labour-intensive programmes (Owen & Black 1989, Sillett & Holmes 2002, Menu *et al*. 2005). In recent years, however, the development of tracking methods has allowed individual birds to be followed on their journeys, potentially providing another way to assess on-route mortality (Sergio *et al*. 2018). In this paper, I examine estimates of migration mortality that have been obtained through ringing or tracking studies, and compare them with similar estimates made during stationary periods. The 31 studies eligible for inclusion involved long-distance migrants, mainly of passerines, waterfowl and raptors. Using a wider range of studies, I also explore several other aspects of migration mortality, including age differences, and for future work, make recommendations on the types of studies needed and how they could best be conducted.

METHODS USED TO ESTIMATE MIGRATION MORTALITY

Ringing and other marking studies

General ring recoveries are usually of little value for assessing migration mortality because: (1) in most species of interest, recovery rates are low; (2) recovery chances vary along migration routes, and birds migrating to the tropics typically provide few or no recoveries from their wintering areas; and (3) birds that die on route in the sea or desert are virtually impossible to recover (Wernham & Siriwardena 2002). These circumstances combine to provide a paucity of information, which is in any case likely to be temporally and geographically biased.

However, two methods using rings or other identification marks have been used in mark/resighting studies to provide more reliable estimates of migration mortality in certain species. An assumption was that the rings or other markers used to identify individuals did not themselves affect the survival or behaviour of the birds concerned. One method has been applied to species in which individuals normally remained on territories throughout their periods in breeding and wintering areas, and also returned to the same territories in successive years. Individuals were marked on their arrival in winter quarters and followed through the winter to assess what proportion survived (calculated directly or with the aid of mark/re-sighting models). The same procedure (usually with different birds) was adopted in the breeding area to estimate survival through the breeding season. Overall annual survival was estimated from the return rates to either breeding or wintering areas in successive years. With knowledge of winter mortality, summer mortality and annual mortality, losses during the rest of the year (on autumn and spring migrations) could be calculated. This method was used by Sillett and Holmes (2002) on Black-throated Blue Warblers *Setophaga caerulescens* in eastern North America, and subsequently on other species (Paxton *et al*. 2017, Rockwell *et al*. 2017).

The second method has been used on geese and swans in which pairs normally remain together year-round and from year to year, and retain their young into winter, while also remaining faithful to the same breeding and limited wintering places from year to year. Adults and juveniles were marked or recorded on breeding areas before they left on autumn migration, and deliberately re-checked after their arrival in a limited wintering area to find what proportion of each age group had survived the journey. Birds not found were generally counted as dead, and emigration to other populations was either not detected or assumed to be negligible (for Barnacle Goose *Branta leucopsis* see Owen & Black 1989). A similar procedure involved visually recording the brood sizes of neck-banded females before and after migration to estimate the loss of young during the journey (for Greater Snow Goose *Anser caerulescens* see Menu *et al*. 2005).

Tracking of individuals on migration

Tracking via satellites enables individual birds to be followed year-round, wherever they travel. To obtain reliable estimates of migration mortality by this means requires that: (1) the tags themselves impose no significant additional mortality, and (2) deaths should be clearly separable from tracking-device failures. As devices and their methods of

attachment have improved over the years, these problems are now less than in the past, and various criteria have been used to separate deaths from equipment problems.

Methods of death detection through radio-tags, together with quantitative separation of deaths from transmitter failures, have been intensively examined and reviewed by Sergio *et al.* (2018). Commonly used indicators of death include: (1) signals coming from a constant location over an appropriately long period, indicating lack of movement or slow drifting at sea before loss of signal (e.g. Klaassen *et al.* 2014, Oppel *et al.* 2015); (2) the finding and reporting of the carcass, in some instances by a deliberate ground search (e.g. McIntyre *et al.* 2006); (3) an appropriate change in body temperature where a temperature sensor was fitted along with the transmitter (e.g. Hupp *et al.* 2008, Ely & Meixell 2016, Ibáñez-Álamo *et al.* 2019); and (4) constancy of readings from an activity sensor fitted along with the transmitter (e.g. Cheng *et al.* 2019). Commonly used indicators of impending transmitter failure include a drop in battery charge or in the frequency, regularity or quality of signals, before their termination (Sergio *et al.* 2018). Some researchers also applied other information to identify deaths. For example, among European Honey Buzzards *Pernis apivorus*, the monitoring of adults proved particularly helpful in clarifying reasons for signal termination, because these birds were faithful to their breeding locations in successive years. This often made it possible to determine whether the birds were still alive after signals had ceased. Some individuals were still wearing their transmitters but sending no signals, indicating transmitter failure (Meyburg & Ziesemer 2023). Some other raptor species (notably eagles and falcons) sometimes bite through the harness so the tag becomes detached, and this knowledge can also help in separating death from equipment failure. In the early days of platform transmitter terminals, batteries lasted only a few months and equipment failures were frequent, making it impossible to get reliable data on migration mortality. However, owing to subsequent improvements in tag technology and use of solar panels to re-charge batteries, and collect and transmit data, our ability to separate deaths from equipment failure or detachment has improved greatly in recent years, from which most of the tracking-based studies discussed here derive. Devices have also become smaller over the years, increasing the range of species eligible for study. Note that only transmitting tags can be used in mortality studies, because information from archival tags (geolocators) can normally be recovered only from surviving birds that return to places where they can be re-caught or otherwise interrogated.

Satellite tags should ideally record all deaths through the year, regardless of where they occur. The data can then be analysed in two main ways. The first involves noting the proportion of all recorded deaths that occur in different seasons, such as (1) during autumn migration, (2) during the period in the wintering area, (3) during spring migration and (4) during the period in the breeding area. These figures give the percentage of all deaths that occur in each of the four periods, and can be corrected to a per unit time basis by allowing for the differing durations of the four periods. Data from additional years can be added for birds followed for longer periods. Birds whose tags are judged to have failed or become detached can be included up to the end of the last complete period, and eliminated from the start of the next period in which failure occurred. Some species have such low annual mortality that large samples or long periods of years are required to gain meaningful results (see Meyburg 2021 for Lesser Spotted Eagle *Clanga pomarina*, in which individuals were tracked for up to 12 years). Examples of studies that have presented results in this manner (or modifications thereof) include those of Klaassen *et al.* (2014), Sergio *et al.* (2019), Watts *et al.* (2019) and others (Table 1).

A second procedure is to calculate the mortality rate through different periods of the year. Allowance then has to be made for the number of birds entering each period, and surviving through it. Hence, if 100 tagged birds started autumn migration and 20 died on the journey, 80 would begin the wintering period, and so on through the year. Again, individuals can be incorporated more than once if they are tracked over more than 1 year. Birds whose tags are judged to have failed or become detached can be censored as described above. Examples of studies that have used this procedure (or modifications thereof) include McIntyre *et al.* (2006), Casazza *et al.* (2015) and others in Table 1.

Selection of relevant papers

For this review, relevant papers fell into two categories: (1) those that provided estimates of

Table 1. Findings from studies that have examined mortality rates during migration compared with other parts of the year. Most of the figures were taken directly from the source references, but some were calculated for this table from the source data given. Among tracking studies, only those based on more than 10 individuals are included.

Black-throated Blue Warbler *Setophaga caerulescens*, New Hampshire to Jamaica, 1986–2000 (Sillett & Holmes 2002). Based on colour-ringing and re-sighting of 336 birds in breeding areas and 151 in wintering areas, survival rates were assessed during the summer breeding period, during the winter period in Jamaica, and over the year as a whole. During these periods, no difference was found between survival of first-year and older birds, so data from both age groups were pooled. Monthly survival probabilities during the summer (May–August) and winter (October–March) stationary periods were high: 1.0 for males in New Hampshire, and 0.99 ± 0.01 se for males in Jamaica and for females in both locations. Monthly survival probability during migration ranged from 0.77 to 0.81 ± 0.02 se, depending on method of calculation. More than 85% of apparent annual mortality occurred during migration, giving a mean monthly rate that was at least 15 times greater than in stationary periods.

Kirtland's Warbler *Setophaga kirtlandii*, Michigan (2006–11, *n* = 331) to Bahamas (2003–10, *n* = 215; Rockwell *et al.* 2017). Based on colour-ringing and re-sighting of adult males, monthly survival probabilities during the summer and winter stationary periods were relatively high (0.963 ± 0.005 se and 0.977 ± 0.002 se, respectively). Monthly survival probability during migratory periods was lower (0.879 ± 0.05 se), accounting for about 44% of all annual mortality. Mortality rates per unit time during migration periods were about four times higher than in stationary periods.

Willow Flycatcher *Empidonax traillii extimus*, Arizona to Costa Rica, 1999–2002 (Paxton *et al.* 2017). Based on ringing of mainly adults with some juveniles (sample sizes not given). Monthly survivorship during the migratory periods (approximately 3 months of the year, spring and autumn combined) was estimated at 91%, substantially lower than the monthly estimates for the breeding (99%) and wintering (98%) seasons. Allowing for the different durations of these periods, 62% of the total annual mortality occurred during the two migration periods, even though they together comprised only about one-quarter of the annual cycle. Monthly mortality rates were nine times greater during migration than in the breeding season, and 4.5 times greater than in winter (about seven times greater than for breeding and wintering combined).

Eurasian Reed Warbler *Acrocephalus scirpaceus*, Western Europe, based on 51 612 re-encounters of 47 938 ringed adults and juveniles reported during 1933–2014, available in the EURING databank (Procházka *et al.* 2017). Estimated annual survival was higher for adults (0.530 ± 0.019 sd) than for juveniles (0.232 ± 0.012 sd). Monthly survival during migration periods was higher for adults (0.922 ± 0.004 sd) than for juveniles (0.698 ± 0.011 sd), whereas monthly survival during stationary periods was similar for both age categories (adults: 0.976 ± 0.004 sd, juveniles: 0.977 ± 0.005 sd). Mortality rates were about three times higher during migration than stationary periods for adults, and about 13 times higher for juveniles.

Wood Thrush *Hylocichla mustelina*, southern Indiana to Belize, 2011–14 (Rushing *et al.* 2017). Based on ringing and re-trapping of 1807 territorial adults and 227 hatch-year birds, populations experienced the lowest apparent survival rates during migration and lower apparent survival during spring than during autumn migration. Among adults, autumn and spring migration accounted for 29% and 21% of apparent annual mortality, even though these stages occupied only 17% and 8% of the year, whereas in juveniles, autumn and spring migration amounted to 14% and 46% of annual mortality. Scaled to monthly rates, in adults, the estimated monthly mean summer (breeding season) survival was 0.96, mean winter survival 0.98, mean autumn (migration) survival 0.92 and mean spring (migration) survival 0.89, whereas in juveniles, autumn survival was 0.92 and spring survival 0.48. On these figures, monthly mortality of adults was about 2.7 times higher during autumn migration than during stationary periods, and about 3.7 times higher during spring migration. The equivalent figures for juveniles were 2.7 times and 17 times respectively. Based on the methods used, both mortality and dispersal may have contributed to low apparent survival during spring migration.

Great Spotted Cuckoo *Clamator glandarius*, Spain to West Africa, 16 adults tracked by satellite, 2013–15 (Ibáñez-Álamo *et al.* 2019). Nine died in breeding areas, five on autumn migration, one in the wintering area and one on spring migration. Allowing for the duration of these different activities, mortality emerged as nine times greater during autumn migration than in the breeding area, and seven times higher on spring migration than in the wintering area, although only two birds survived the winter and only one survived the spring migration.

Band-tailed Pigeon *Patagioenas fasciata*, tracked by satellite within western North America, 2006–08, *n* = 26 (Casazza *et al.* 2015). Adult survival probabilities for different periods were: winter 0.879 (16 November to 29 March); spring migration 0.889 (30 March to 14 June); breeding 0.926 (15 June to 13 September); and autumn migration 0.913 (14 September to 15 November). This gave weekly survival rates as being greatest during the nesting season (0.994) and winter (0.993) and lowest during spring and autumn migrations (0.989 and 0.990, respectively); although confidence intervals overlapped among all these estimates, the weekly mortality rates emerged as 1.8 and 1.7 times higher during spring and autumn migration than during the nesting season.

Table 1. (continued)

Black-tailed Godwit *Limosa limosa*, West Africa to Iberia, 2012–15, *n* = 57 adults (Senner *et al.* 2019). From satellite-tracking, daily survival rates were lowest on flights from sub-Saharan West Africa to staging areas in Spain and Portugal at 0.9445 per day, whereas the daily average over the year as a whole was 0.998 per day, leading to an annual survival rate of 0.52. In other parts of the migration over more benign areas, survival rates were similar to those during stationary periods. Daily mortality during the first part of the spring journey, mainly over the Sahara, was therefore nearly 28 times greater than daily mortality during the rest of the year. Of all deaths recorded, 13% occurred during autumn migration, 21% in winter, 36% during spring migration and 30% during the breeding season.

Hudsonian Godwit *Limosa haemastica*, Alaska (2014–17) to Chile (2007–12), based on re-sightings and re-captures of 118 adults colour-marked in Alaska and 774 colour-marked in Chile (Swift *et al.* 2020). Godwit survival rates were high throughout the annual cycle, but lowest during the breeding season (0.915), only slightly higher during southbound migration (0.855–0.978) and highest during the stationary non-breeding season (0.987), and slightly lower through the northbound migration (0.958–0.979). Allowing for the different durations of these four periods, weekly survival probability during autumn migration was estimated at 0.855–0.928, during the non-breeding period in Chile at 0.999, during spring migration at 0.958–0.979 and during the breeding period in Alaska at 0.992. The two values for survival during the migration periods depended on whether they were based on annual survival values calculated from data obtained in breeding or wintering areas. These figures imply that the mortality per week was 9–18 times greater during autumn migration than in breeding areas, and 21–42 times greater during spring migration than in non-breeding areas. This godwit undertakes one of the longest migrations of any landbird, including one non-stop flight of 10 000 km and some long over-sea stretches.

Eurasian Whimbrel *Numenius phaeopus*, northwestern Canada to northern South America, 2008–16, 33 adults satellite-tracked (Watts *et al.* 2019). With an average annual adult survival of 54% in a declining population, daily mortality was five times greater during migration than during stationary periods (0.0049 vs. 0.00092, respectively), a significant difference. Around one-half of annual mortality occurred during the autumn hunting season, and one-third during spring migration, but values may also have been elevated by the tags.

Eurasian Spoonbill *Platalea leucorodia leucorodia*, Netherlands to France, Iberia or Mauritania (c.1000, 2000 and 4500 km), 2005–12, based on re-sightings of 538 individually marked adults (Lok *et al.* 2015). Summer, autumn and winter survival were very high and independent of migration distance, but mortality during spring migration was 18% for birds that flew to Mauritania, 5.6% for birds that flew to Iberia and 5.1% for those migrating to France. Mortality therefore increased with migration distance, probably in this case because of the Sahara Desert and adverse weather and fuelling conditions on route. It reduced the annual survival of Mauritanian winterers to 80% compared with 93% and 92% for the French and Iberian winterers. Survival in Mauritanian winterers was about 16% higher during autumn migration than in spring migration. Uncorrected for duration, mortality during spring migration was about three times higher than during the rest of the year in Spoonbills that migrated within Europe and about eight times higher in those that migrated to Africa.

White Stork *Ciconia ciconia*, central Europe to southwest Europe, North Africa and sub-Saharan Africa, 2013–17 (Cheng *et al.* 2019). Of 169 juveniles GPS-tagged at fledging and tracked to the end of winter, 148 (87.5%) survived to the start of migration (mean 30 days), 103 (60.9%) to the end of migration (mean 49 days) and 77 (45.6%) to the end of winter (mean 151 days). The initial population was therefore reduced by 45 deaths in 49 days during migration and by 26 deaths in 151 days during winter, giving daily rates of 0.92 deaths on migration and 0.17 in winter. So daily losses were about 5.4 times higher during autumn migration than during winter.

Whooping Crane *Grus americana*, northwest Canada–Texas, 2009–14 (Pearse *et al.* 2019). Of 68 individuals of mixed ages that were satellite-tagged, 19 were deemed to have died: eight in breeding areas, eight in wintering areas, two in autumn migration areas and one in spring migration areas. Allowing for the different times spent on these areas, mortality per unit time was roughly the same in all four periods, providing no evidence that mortality was higher during this overland migration.

Greater Sandhill Crane *Grus canadensis tabida*, various sites in North America, 2009–15 (Fronczak *et al.* 2015). Of 42 satellite-tagged adults, five died during the study period, all after spring migration, in late spring and early summer. Annual mortality was estimated at 0.950 (95% CI 0.885–0.979), and statistical analysis gave no evidence that mortality was any greater during this overland migration than at other times.

Four raptor species combined (Osprey *Pandion haliaetus*, European Honey Buzzard *Pernis apivorus*, Western Marsh Harrier *Circus aeruginosus*, Eurasian Hobby *Falco subbuteo*), tracked by satellite, Sweden to Africa, 1995–2009, 33 adults with 82 tracks and 13 juveniles with 13 autumn tracks, recorded by satellite telemetry (Strandberg *et al.* 2010). The combined mortality during 95 crossings of the Sahara alone was 31% per crossing for juveniles (first autumn migration), compared with only 2% for adults (autumn and spring combined). Mortality associated with the Sahara passage made up a substantial fraction (up to about half for juveniles) of the total annual mortality.

(continued)

Table 1. (continued)

Osprey *Pandion haliaetus*, Sweden to West Africa, 1995–2011, 18 adults, some tracked for more than 1 year by satellite tracking (Klaassen *et al.* 2014). Mortality during migration formed around 67% of total annual mortality, comprising 16% in autumn and 51% in spring. With 11 deaths recorded, mortality per day during autumn and spring journeys was 3.8 and 23.5 times higher than at other times.

Montagu's Harrier *Circus pygargus*, Western Europe to West Africa, 2005–11, 34 adults, some followed in more than 1 year by satellite tracking (Klaassen *et al.* 2014). Mortality during migration formed around 53% of total annual mortality, comprising 18% in autumn and 35% in spring. With 25 deaths recorded, mortality per day during autumn and spring journeys was 2.9 and 6.5 times greater than at other times.

Marsh Harrier *Circus aeruginosus*, Sweden to West Africa, 2004–11, 17 adults, some followed in more than 1 year by satellite tracking (Klaassen *et al.* 2014). Mortality during migration formed around 58% of total annual mortality, comprising 33% in autumn and 25% in spring. With 15 deaths recorded, mortality per day during autumn and spring journeys was 8.7 and 6.0 times greater than at other times.

Golden Eagle *Aquila chrysaetos*, Alaska southward to New Mexico, 1997 and 1999, 41 juveniles, followed by satellite tracking (McIntyre *et al.* 2006). During autumn migration and early winter, monthly survival was 0.88 for the 1997 cohort and 0.78 for the 1999 cohort, while in three other periods of year (one embracing spring migration) monthly survival was 0.94 in both years. Mortality during autumn migration and in the 2 months after arrival in wintering areas was therefore twice as high as during the rest of the year embracing spring migration.

Egyptian Vulture *Neophron percnopterus*, Balkan region to West Africa, 2010–14 (Oppel *et al.* 2015). Of 18 juveniles tracked on autumn migration, only nine (50%) survived to reach suitable wintering areas, and only six reached 1 year of age. However, much depended on the route taken: only one out of 10 birds that headed directly south survived the crossing of the open Mediterranean, compared with all eight birds that took a landward detour round the eastern end of the Mediterranean. No deaths were recorded in the Sahara Desert. Monthly survival during migration was 0.750, compared with 0.958 in subsequent wintering areas. Mortality rates were therefore six times higher during migration than in wintering areas, and 70% of first-year mortality occurred on autumn migration.

Egyptian Vulture *Neophron percnopterus*, Europe and Middle East to sub-Saharan Africa, 2007–20, based on satellite tracking of 220 birds (including those in the above study), 152 tagged as juveniles and 68 as immatures or adults, but many were tracked in more than 1 year as they aged (Buechley *et al.* 2021). Juveniles showed monthly survival of 0.905 on migration compared with 0.955 in the first month post-fledging. Older birds showed a monthly survival of 0.979 during migrations, compared with 0.990 in breeding areas and 0.995 in wintering areas, so in both age groups the mortality rate was at least twice as high during migration as at other times. Many juveniles drowned in the Mediterranean Sea on their first autumn migration but few were confirmed dead in the Sahara Desert.

Black Kite *Milvus migrans*, southern Spain to West Africa, 2007–14 (Sergio *et al.* 2019). Among 108 birds of known age, 53 deaths were recorded over a number of years: 43% in the Spanish breeding areas, 30% in the African wintering areas, 17% in the autumn migration and 9% in the spring migration. Allowing for the different durations of these periods, daily mortality rates averaged around five to eight times higher during each migration than at other times, depending on age and season. In total, 64% of the migration deaths occurred in the Sahara Desert, but were not clustered at specific locations. All mortality, and its distribution through the year, changed with age. Juveniles travelled only on the autumn journey and then remained in Africa for at least another year; their daily mortality was about seven times higher during migration than when stationary in Europe and about three times higher than when stationary in Africa.

Honey Buzzard *Pernis apivorus*, Germany to sub-Saharan Africa, 2001–11, 12 adults tracked by satellite, some in more than 1 year (Meyburg & Ziesemer 2023). Three died on autumn migration, four in wintering areas, two on spring migration and one in breeding areas. Allowing for the duration of these different periods, deaths per unit time emerged as four times greater during migration than during the rest of the year, and were relatively more frequent in spring than in autumn.

Himalayan Vulture *Gyps himalayensis*, Bhutan to central Asia, 18 immatures aged 1–2 years, caught on wintering areas in Bhutan, and followed for up to a year, 2014–15 (Sherub *et al.* 2017). Five individuals (28%) died on their northward migration, the only deaths recorded.

Barnacle Goose *Branta leucopsis*, Svalbard to Scotland, 1986 (Owen & Black 1989). Based on checks for colour-ringed birds just before and after migration, about 35% of 439 juveniles had disappeared (presumed dead), compared with about 5% of 1747 older birds (about half the annual total). The losses were greatest among young hatched latest in the season, which were lightest in weight at departure. This amount of mortality was probably exceptional, because severe weather on Svalbard forced the birds to leave earlier than usual and also stopped some from staging on Bear Island. Once juveniles reached their wintering areas, mortality dropped to a level equivalent to 10% per year, the same as adults. In six other years, estimated juvenile mortality during migration varied between 12 and 21%.

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Table 1. (continued)

Pacific Brant Goose *Branta bernicla nigricans*, Alaska to Baja California, 1986–93, based on colour-banding of 6219 adults at a breeding colony and re-sightings in breeding, migration and wintering areas (Ward *et al.* 1997). Annual survival did not vary among years or sexes and averaged 0.84 ($\pm$0.031 se). Mean monthly survival rate was lowest during late spring migration (15 April–1 June), the period of greatest subsistence harvest on the breeding areas, and highest in winter (1 Jan–1 March), the period of greatest sport harvest. Mean monthly survival was estimated for the nesting period at 0.988 ($\pm$0.040 se), early autumn (migration) 0.970 ($\pm$0.015 se), late autumn 0.988 ($\pm$0.010 se), winter 1.00 ($\pm$0 se), early spring 0.984 ($\pm$0.030 se) and late spring (migration) 0.908 ($\pm$0.024 se). Mortality during autumn migration was therefore three times higher than the mean in stationary periods, and during spring migration was eight times higher. Subsidence hunting contributed to mortality during the spring migration period.

Greater Snow Goose *Anser caerulescens atlantica*, Bylot Island to St Lawrence River, Quebec, 1993–97 (Menu *et al.* 2005). Based on 9460 adults and 11 975 juveniles ringed and colour-marked, the average mortality of juveniles over the autumn journey was 34% and that of adults was 1%. Most of this mortality appeared to be natural (rather than shooting). However, after this migration, juveniles survived almost as well as adults (monthly loss of juveniles 3.1% and of adults 2.8%). On these figures, the mortality of juveniles was 11 times higher on migration than in the following stationary month, and 0.3 times higher in adults. The loss of juveniles during autumn migration also varied greatly between years (range 29–88% over 5 years), and in these years migration losses formed 46–98% of the total annual mortality of juveniles. Juvenile mortality was highest 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. Apparently, conditions on breeding areas influenced subsequent mortality on migration, as a carry-over effect. Among 33 890 adult female Greater Snow Geese from the same population marked with neck-bands, no significant variation in mortality was detected in different periods through the year or between years, although none of these periods included migration alone (Gauthier *et al.* 2001).

Emperor Goose *Anser canagicus*, within Alaska, 1999–2004. Based on 53 adult females tracked by satellite (and ignoring others marked with VHF radios which were less easy to detect when they moved from search areas; Hupp *et al.* 2008). Seven of the 53 were known for certain to have died over the next year (based largely on temperature sensors), suggesting an annual mortality of at least 13%. For various reasons, including unusual hunting pressure on breeding areas, data were selected for this analysis, being limited to April (covering spring migration) and January–March (covering the period on wintering areas). The figures from satellite-tracked birds for both periods represent monthly mortality rates of 4.2% and 1.8% respectively, suggesting a rate during spring migration 2.3 times higher than the rate during the winter stationary period. Nevertheless, on the figures available, the difference was not statistically significant.

Tundra Swan *Cygnus columbianus*, five Alaskan breeding areas to various wintering areas, 2008, 50 swans (aged 2 or more years) tracked by satellite, some for more than 1 year (Ely & Meixell 2016). Of 15 platform transmitter terminal-implanted swans known to have perished during the study (based on low body temperature), seven (46.7%) died during summer (on breeding areas), five (33.3%) died during migration (three in spring and two in autumn) and three (20%) died during winter (while at terminal southern sites). These figures are small, but deaths per unit time emerged as lower in migration seasons than in stationary periods, at one per month on spring migration, 2.3 per month in breeding areas, 0.5 per month on autumn migration and 1.5 per month in wintering areas. Statistically, they showed no significant variation though the year.

Trumpeter Swan *Cygnus buccinator*, within the north-central USA, 2000–08, based on 576 encounter histories of neck-collared or colour-ringed birds (Varner & Eichholz 2012). About 90% of birds migrated short distances and 10% longer distances; annual adult mortality was 19% in both groups, but annual sub-adult mortality was 30% in short-distance birds and 14% in long-distance birds. In 91 long-distance birds examined for seasonal variation, apparent mortality was estimated at nil for sub-adults during their first winter, 0.029 for sub-adults during their first spring migration, and 0.005 for all seasons and age classes thereafter. Overall, little evidence was found for seasonal variation in mortality: the mortality estimates for both migratory and stationary seasons were very low (<3%), but may have been slightly higher during migration; long-distance migrants survived at rates that were at least equal to, but probably higher than, short-distance migrants.

Northern Gannet *Morus bassanus*, Bass Rock, Scotland to West Africa, 2018/19. Juvenile Gannets become independent on leaving the nest, and begin their first migration within days. Over the 2 years, 38 juveniles were fitted with GPS-platform transmitter terminal tags and tracked by satellite; 11 (29%) died in their first 2 months before they had completed their first migration (Lane *et al.* 2021). Total first year mortality was estimated from large chicks ringed at the same colony in previous years at 45.8% (Wanless *et al.* 2006). Comparison of the two figures suggests that 63% of all first-year mortality occurred during autumn migration. The annual mortality of adults ringed at the same colony in previous years was 8.4%; it was not known what proportion of this mortality occurred during migration, but it was clearly much lower than that of juveniles.

mortality during migration and during stationary periods, which form the core of this review (Tables 1 & 3, Fig. 1); and (2) other papers providing no such comparison, but other information relevant to migration mortality (Table 2 and text). All papers were found initially by the
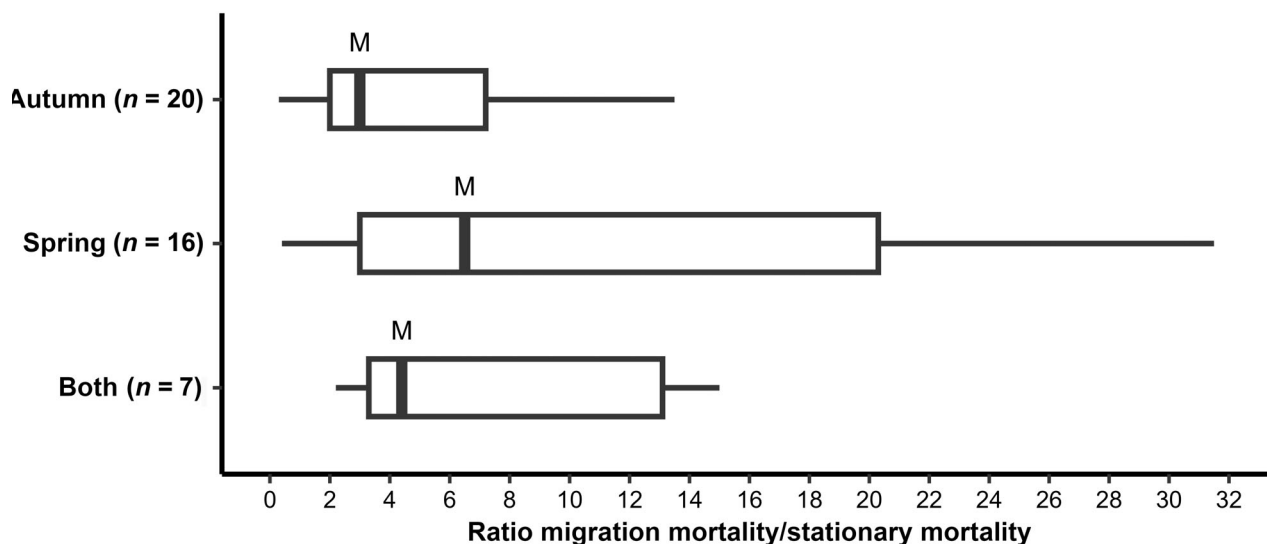
Figure 1. Ratio of migration mortality/stationary mortality per unit time in different studies, as measured during autumn journeys ($n = 20$), spring journeys ($n = 16$) or both journeys together ($n = 7$). M = median value, blocks indicate 25% of studies above and below the median, and lines show the full range of values. Where available, data from adults and juveniles from the same population are treated as separate values. Details in Table 3.

Table 2. Other studies (involving more than 10 individuals) which calculated mortality only during migration periods.

Swainson's Thrush *Catharus ustulatus*, Alabama to Yucatan, 2009–14 (Ward *et al.* 2018). A total of 139 adults and juveniles tracked by automated radio-telemetry while crossing more than 1000 km of the Gulf of Mexico in autumn showed survival rates of 0.90–0.33 (that is, mortality rates of 0.10–0.67) on this part of their migration, depending on initial fat content and wind conditions at the time.

Black-tailed Godwit *Limosa limosa*, Netherlands to West Africa, 2013–18 (Loonstra *et al.* 2019). Of 53 satellite-tracked adults, none died on 71 southward crossings of the Sahara, whereas 15 (25%) birds died on 61 northward crossings. On the southward crossings, winds were more favourable and birds took about 30 h, while on the northward crossings, winds were often unfavourable and birds took around 35 h. Individuals that died made slower progress before their death than the survivors.

Black-tailed Godwit *Limosa limosa*, Netherlands to West Africa, 2016/17 (Verhoeven *et al.* 2022). Among 28 juveniles from the same population as above (2016/17), mortality on the autumn journey was substantially greater than that of adults (25% vs. 6%, $P = 0.039$), but on the return journey the difference was less and not statistically significant (20% vs. 27%, $P = 0.584$). Seven juveniles died on southward migration, eight over the non-breeding period, and three on northward migration, a different seasonal pattern to adults.

Osprey *Pandion haliaetus*, Scotland to West Africa, involved 12 adults, many tracked by satellite for more than 1 year, and 12 juveniles tracked over the first year, 2002–18 (Roy Dennis Foundation website, March 2023). Among adults, 42 autumn journeys resulted in only one death (2%), and 30 spring journeys resulted in two (7%) deaths, and among juveniles, 12 autumn journeys resulted in five (11%) deaths. Only one juvenile attempted to return in its first year and died on route; the others stayed in Africa to return in a later year.

Honey Buzzard *Pernis apivorus*, Scotland to Africa, 2001–11, one adult and 10 juveniles tracked by satellite (Roy Dennis Foundation website, March 2023). The one adult survived the autumn journey, while two out of 10 juveniles died on route and two others either died or were lost through radio failure, giving an autumn mortality over the migration period in this small sample of juveniles of 20–40%.

Honey Buzzard *Pernis apivorus*, Finland to sub-Saharan Africa, 2011–14, tracked by satellite (Vansteelant *et al.* 2017). Of 27 juveniles that departed from Finland, 24 survived their first migration, giving 11% mortality over this partly sea-and-desert crossing.

traditional method of searching major ornithological journals, in this case back to 1990, and then checking all other papers mentioned in their individual reference lists, separating papers into the two categories above. In addition, in July 2023, systematic searches were also made using

Google Scholar and Medline, with combinations of search terms, including 'survival', 'mortality', 'migration', 'migratory', 'seasonal', 'satellite tracking', 'ringing', 'banding', and then from the resulting list selecting ornithological papers. This procedure yielded only three additional core papers, but some other relevant ones. In the selection of core papers (for Tables 1 & 3, Fig. 1), studies that included a mortality estimate for a migration period combined with a stationary period (breeding or wintering) were excluded, as were studies in which tag failures were stated as likely to have affected the findings. Also excluded were studies based on fewer than 10 tracked individuals, and studies of avian flu outbreaks or collisions with wind turbines or other infrastructure. This overall procedure produced 31 studies of 30 species from which estimates of mortality were obtained for both migratory and stationary periods (Table 1). A brief earlier review of migration mortality cited 18 studies (Robinson *et al.* 2020), four of which were excluded here on the criteria stated above.

Associated with different methods of analysis and periods of study, researchers expressed their findings on migration mortality in different ways: as a percentage of overall annual mortality (or of all deaths recorded), or as daily, weekly or monthly averages of numbers of deaths or rates of mortality during migration compared with other seasons. Studies also varied in the proportion of the lifespan of individuals that they covered. There is no easy way to tabulate or analyse all of these data uniformly, and in Tables 1 and 2, studies are listed individually, and depending on availability of information, some aspects are summarized in Table 3. The main question addressed here is whether mortality is greater (overall or per unit time) during migration than at other times. In most of the studies using satellite-tracked birds, samples are small, and seasonal differences within species are not always statistically significant. To circumvent the problem of small samples, some researchers have combined the results from different studies on the same species (Buechley *et al.* 2021) or from different closely related species making similar journeys (Strandberg *et al.* 2010, Klaassen *et al.* 2014). All the satellite-based studies listed in the tables relate to large or medium-sized birds, whereas the ringing or mark/re-sighting studies involved passerines or waterfowl. In some studies, separate mortality estimates were obtained for adults and juveniles from the same population (Tables 1 & 3).

RESULTS

In most species listed in Table 1, mortality was higher during migration than in stationary periods (Fig. 1). Per unit time, the median mortality estimate for autumn journeys was 3.0 times greater than for stationary periods ($n = 20$), for spring journeys 6.3 times greater ($n = 16$), and for both spring and autumn journeys together 4.4 times greater ($n = 7$). In different species, mortality per unit time during migration varied from about 0.3 to 31.5 times as high as in stationary periods. Extreme values included 28 times as high for some Black-tailed Godwits *Limosa limosa* and Black Kites *Milvus migrans* crossing the Sahara Desert in spring (Senner *et al.* 2019, Sergio *et al.* 2019), and 21–42 times (average 31.5 times) as high for some Hudsonian Godwits *Limosa haemastica* migrating between Chile and Alaska (Swift *et al.* 2020). In contrast to the majority findings, adults of five species – namely the Whooping Crane *Grus americana*, Sandhill Crane *Grus canadensis*, Greater Snow Goose, Tundra Swan *Cygnus columbianus* and Trumpeter Swan *Cygnus buccinator* – showed no significant variation in mortality through different periods of year, although in Trumpeter Swans the possibility of greater mortality during migration could not be eliminated (Table 1). These five were all large, long-lived species that made wholly overland journeys in North America. In 15 studies in which both total migration mortality (autumn and spring combined) and total annual mortality could be reliably calculated, migration mortality formed a median of 55% of the annual total, ranging in different species between 14 and 85% (and even 100% for 18 Himalayan Vultures *Gyps himalayensis* tracked for 1 year, Table 3).

Comparing species and taking adults alone, no relationship emerged between relative migration mortality and the mean body mass of the species concerned (percentage of annual mortality occurring during autumn migration vs. body mass, $n = 13$, $r_s = 0.145$, $P > 0.50$; percentage of annual mortality occurring during spring migration vs. body mass, $n = 2$, $r_s = -0.279$, $P = 0.50$; percentage of annual mortality occurring during both autumn and spring migration together vs. body mass, $n = 14$, $r_s = -0.321$. $P = 0.50$). With such small samples, it was not feasible to try and adjust

Table 3. Estimates of mortality on migration compared with stationary periods. Some data taken directly from the sources cited, others calculated from other data in the listed sources.

Species and age group	Numbers	Method	% of annual mortality			Ratio migration/ stationary			Reference
			B	A	S	B	A	S	
Black-throated Blue Warbler, adults	487	R	85			15.0			Sillett and Holmes (2002)
Kirtland's Warbler, adults	546	R	44			4.0			Rockwell et al. (2017)
Willow Flycatcher, adults	Unavailable	R	62			6.8			Paxton et al. (2017)
Eurasian Reed Warbler, adults	2732	R				3.3			Procházka et al. (2017)
Eurasian Reed Warbler, juveniles	3995	R				13.1			Procházka et al. (2017)
Wood Thrush, adults	1807	R	50	29	21		2.7	3.7	Rushing et al. (2017)
Wood Thrush, juveniles	227	R	60	14	46		2.7	17.0	Rushing et al. (2017)
Great Spotted Cuckoo, adults	16	ST					9.2	7.0	Ibáñez-Álamo et al. (2019)
Band-tailed Pigeon, adults	26	ST	55	22	33		1.7	1.8	Casazza et al. (2015)
Black-tailed Godwit, adults	57	ST	49	13	35	1.0	27.8[a]		Senner et al. (2019)
Hudsonian Godwit, adults	892	R				9–18[b]	21–42[b]		Swift et al. (2020)
Eurasian Whimbrel, adults	33	ST	81	48	33		5.0	5.0	Watts et al. (2019)
Eurasian Spoonbill, adults	538	R	7–20	2	5–18	2.0	3.8[c]		Lok et al. (2015)
White Stork, juveniles	169	MP					5.4		Cheng et al. (2019)
Osprey, adults	18	ST	67	16	51		3.8	23.5	Klaassen et al. (2014)
Montagu's Harrier, adults	34	ST	53	18	35		2.9	6.5	Klaassen et al. (2014)
Marsh Harrier, adults	17	ST	58	33	25		8.7	6.0	Klaassen et al. (2014)
Golden Eagle, juveniles	41	ST					2.0	1.0	McIntyre et al. (2006)
Egyptian Vulture, adults	152	ST				2.2			Buechley et al. (2021)
Egyptian Vulture, juveniles	68	ST					2.2		Buechley et al. (2021)[d]
Black Kite, adults	108	ST					6.9[e]	28.1[e]	Sergio et al. (2019)
Black Kite, juveniles	108	ST					7.4[e]		Sergio et al. (2019)
Honey Buzzard, adults	12	ST				4.0			Meyburg and Ziesemer (2023)
Himalayan Vulture, immatures	18	ST	100[e]	0	100[f]				Sherub et al. (2017)
Greater Snow Goose, adults	9460	R		1			0.3		Menu et al. (2005)
Greater Snow Goose, juveniles	11 975	R		46–98[g]			11.1		Menu et al. (2005)
Emperor Goose, adult females	53[h]	ST			32			2.3	Hupp et al. (2008)
Barnacle Goose, adults	1747	R		50					Owen and Black (1989)
Barnacle Goose, juveniles	439	R		12–21[g]					Owen and Black (1989)
Pacific Brant Goose, adults	6219	R					3.0	8.2	Ward et al. (1997)
Tundra Swan, mainly adults	50	ST	33	13	20		0.3	0.4	Ely and Meixell (2016)
Trumpeter Swan, sub-adults	91	R	24	4	20				Varner and Eichholz (2012)
Gannet, juveniles	38	ST			63				Lane et al. (2021), Wanless et al. (2006)

Key: MP – mobile phone network; R – ringing or colour marking, ST – satellite tracking. Numbers refer to individuals ringed or tracked. Ratio migration/stationary refers to mortality rates per unit time during migration and stationary periods; B – both migration seasons combined, A – autumn migration, S – spring migration. For scientific names of species see Table 1. [a]As measured over the Sahara Desert only. [b]Depending on whether annual mortality was calculated from data collected in the breeding or wintering area. [c]Range of values from birds migrating to three main areas at different distances from the breeding range (see text). [d]This study includes juveniles from the earlier study by Oppel et al. (2015). [e]Daily rate in migration vs. breeding area, adult figures are averages of values from three older age groups (Sergio et al. 2019). [f]In this study, involving the tracking of 18 winter-caught immature vultures for 1 year, five individuals died, all on spring migration. [g]In different years. [h]For various reasons, including unusual hunting pressure on breeding areas, data were selected for this analysis, being limited to birds tracked by satellite (ignoring birds tagged with VHF radios) and to the periods April (covering spring migration) and January–March (covering the period on wintering areas).

these tests for phylogenetic dependence. It seemed, however, that conditions on route (weather and food supplies) had more influence on the percentage of annual mortality that occurred during migration than did the body size of the species concerned. This finding does not of course exclude the possibility that body weight influences migration mortality within species.

Five other studies calculated mortality during migration but without comparison with periods of residency (Table 2). Like most of the other species in Table 1, these species also showed substantial losses during migration. In addition, among adult male Great Bustards *Otis tarda*, in Spain the annual mortality was 2.4–3.5 times higher in migrant than in sedentary individuals from the same breeding population (Palacín *et al.* 2016). Collision with power lines caused 37.6% of all deaths, and migrants died in this way more frequently than residents (21.3% vs. 6.3%).

Among some other large, long-lived birds, samples of satellite-tagged individuals completed their migrations without any deaths. For example, 28 adult Long-billed Curlews *Numenius americanus*, tagged on nesting areas in the northwestern USA, survived at least through their first autumn migration to the southern USA or Mexico, over distances up to 3098 km (Page *et al.* 2014). Similarly, 14 Lesser Black-backed Gulls *Larus fuscus* tagged as adults at their nests in the Netherlands completed their autumn migrations without loss, one died in the wintering area, and the remaining 13 completed their spring migrations without loss, giving 100% survival over 27 migrations extending up to 2898 km (Klaassen *et al.* 2012). Nine satellite-tracked Hooded Cranes *Grus monacha* that wintered in Japan and bred in eastern Russia survived at least two spring migrations and one autumn migration (and the intervening periods) without loss (Mi *et al.* 2018). For such species with naturally low mortality rates, year-round tracking of much larger samples would be needed to provide reliable indications of any seasonal pattern in mortality.

Age differences

Among 11 species in which adults and juveniles were studied over the same routes, juveniles suffered greater mortality in seven out of seven species tracked in autumn and in five out of six species tracked in spring (Table 1). The differences

between the age groups were greatest on the autumn journey, the first migration undertaken by juveniles. Extreme age-related differences on autumn journeys were shown by Barnacle Geese (35 vs. 5% for juveniles and adults), for Snow Geese (34 vs. 1%) and various raptors (31 vs. 2%). This age difference was marked in geese despite the juveniles travelling with their parents. In several raptor species, in which juvenile mortality was high on their first autumn migration, the surviving juveniles did not return to their natal areas the next spring, but only in a later spring. In other species, age differences, which were marked in autumn, had largely disappeared by the following spring journey. For example, among Black-tailed Godwits migrating between the Netherlands and West Africa, mortality of juveniles on the autumn journey was about four times higher than that of adults (25 vs. 6%, $P = 0.039$), but on the return spring journey, mortality in both groups was high and the difference between them was less and not statistically significant (20 vs. 27%, $P = 0.584$, Verhoeven *et al.* 2022). Moreover, in some species, those juveniles that fledged earliest in the season suffered less mortality on autumn migration than those that fledged later and migrated at a younger age (for Barnacle Goose see Owen & Black 1989, for Greater Snow Goose see Menu *et al.* 2005, for White Stork *Ciconia ciconia* see Cheng *et al.* 2019).

Comparing autumn and spring journeys in juvenile birds, mortality emerged as relatively higher on the autumn journey in four species for which the comparison was possible and higher on the spring journey in one species. Among adults, the equivalent figures were two in autumn against 11 in spring, giving a marginally statistically significant difference between age groups (χ^2 with Yates correction = 4.19, $P = 0.041$). The higher mortality of juveniles on the autumn journey was generally attributed to their inexperience, and the higher mortality of experienced birds in spring was attributed to more adverse winds at that season than in autumn. Poor conditions over spring migration were noted especially in Ospreys *Pandion haliaetus*, Black Kites, Eurasian Spoonbills *Platalea leucorodia*, Black-tailed Godwits and others during their spring crossings of the Sahara Desert (Klaassen *et al.* 2014, Lok *et al.* 2015, Loonstra *et al.* 2019, Sergio *et al.* 2019). In these and other species, deaths were generally more frequent over hostile than benign habitat, with many recorded

over sea or over the Sahara Desert (for the Gulf of Mexico, see Ward *et al.* 2018; for the Mediterranean Sea, see Buechley *et al.* 2021; for the Sahara Desert, see Strandberg *et al.* 2010, Sergio *et al.* 2019).

Annual mortality and migration distance

Overall, no consistency emerged within species in the relationship between migratory distance and annual mortality. From studies on two species, individuals making the longest migrations suffered the highest annual mortality. Hence, among Eurasian Spoonbills breeding in the Netherlands, birds that migrated to Mauritania showed 20% annual mortality, whereas those migrating to Iberia and France showed 8% and 7%, respectively, these differences resulting mainly from mortality on spring migration (18%, 5.5% and 5.1%, respectively) (Lok *et al.* 2015). Similarly, among White Storks tracked from Germany round the east end of the Mediterranean to Africa, six out of 54 tagged juveniles remained to winter in Europe and none died, whereas the rest went on to Africa and 62% died, another statistically significant difference (Rotics *et al.* 2017). In addition, juveniles of the Spanish White Stork population that wintered in sub-Saharan Africa showed an annual mortality of 90%, whereas juveniles from central Europe wintering in Spain or northern Morocco showed an annual mortality of 52%. The equivalent figures for second-year storks were 50% and 37%, and for older storks 10% and close to 0%, respectively (Bécares *et al.* 2019). Hence, in all these age groups of White Storks from different populations, annual mortality was greater in birds making longer journeys, although it was unclear whether the extra mortality occurred on migration or in the wintering areas (but see Cheng *et al.* 2019). Birds making longer journeys were also crossing the Sahara Desert, which may have brought risks additional to those associated merely with the length of journey. The opposite findings emerged among adult male Common Cuckoos *Cuculus canorus* migrating from Britain to tropical Africa, in which individuals taking the longer of two routes experienced lower annual mortality than those taking the shorter route (Hewson *et al.* 2016).

Greater Flamingos *Phoenicopterus roseus* breeding in southern France were unusual in that, among birds that were 1–2 years old, short-distance migrants showed lower annual mortality than long-distance migrants, whereas in older birds the long-distance migrants suffered less (Sanz-Aguilar *et al.* 2012). It seemed that long-distance migration was costly for young, inexperienced individuals, but for adults, the more distant wintering areas offered more favourable conditions for overwinter survival (Sanz-Aguilar *et al.* 2012). In some of the above species, the lower mortality of short-distance migrants may have been associated with recent climate or other man-made change, giving better conditions than previously in places nearer to breeding areas.

In some other species, however, no differences in annual mortality were apparent between birds making short or longer journeys. This held among Greater Snow Geese using different breeding areas but the same wintering area (Souchay *et al.* 2015), among adult Trumpeter Swans using the same breeding area but different wintering areas (Varner & Eichholz 2012), and among Tundra Swans using different breeding and different wintering areas (Ely & Meixell 2016). Among Tundra Swans, return migration distances from five different breeding areas across Alaska varied between 1020 and 12 720 km, but birds at the two extremes of distance had the lowest annual mortality rates (Ely & Meixell 2016). Among Trumpeter Swans, although no difference in yearly mortality was found between short- and long-distance adult migrants, among immatures the long-distance birds suffered lower mortality than short-distance birds (Varner & Eichholz 2012). Other studies showing no relationship between migration distance and annual mortality (but not eligible for inclusion in the tables) involved Sanderlings *Calidris alba* (Reneerkens *et al.* 2020), Northern Gannets *Morus bassanus* (Pelletier *et al.* 2020) and Lesser Black-backed Gulls (Kentie *et al.* 2023). There was therefore no consistency in whether short- or longer-distance migrants of the same species showed the lowest annual mortality, at least over the periods covered by these studies.

DISCUSSION

In some early studies, the attachment of tracking devices was found to add to the risk of mortality (reviews: Barron *et al.* 2010, Bodey *et al.* 2018, Green *et al.* 2019). In none of the core studies cited here was any such problem explicitly reported, and most were based on tag and harness designs that had been improved in response to

earlier problems. Apart from some raptor studies, all those based on satellite tracking were post-2000. The possibility remains that in some studies cited here the equipment used may have added to the risk of mortality, and more so during migration than stationary periods. It may also have affected other aspects of performance not considered here. Nevertheless, while 20 of the 31 studies in Table 1 involved the use of harnesses and transmitters, the other 11 were based on ringing or other marking methods expected to have minimal, if any, influence on survival. Yet most of these latter studies also showed significantly higher mortality during migration than during stationary periods, and where it was examined, greater migration mortality in juveniles than older birds. Moreover, in some of the studies cited, a lack of tag impacts on survival estimates was shown using various ad hoc evaluations (for Black Kite see Sergio *et al.* 2018, for Honey Buzzard see Meyburg & Ziesemer 2023).

Satellite tracking has been used mainly on larger species, with an additional bias to certain groups, such as waders, raptors and large waterfowl. The paucity of data for pelagic seabirds can be attributed to many of the relevant tracking studies using archival geolocators, which require that birds are re-trapped to retrieve the data, usually in their nesting places (e.g. Guilford *et al.* 2009, Harris *et al.* 2009). This means that only survivors are re-caught. In addition, seabird survival is typically very high, so big samples are needed to reveal reliable mortality estimates for different times of year. Over land areas, data from some kinds of archival tags can now be downloaded via the Global System for Mobile Communication (GSM, or mobile phone network, Cheng *et al.* 2019), but receivers are lacking over oceanic and some land areas. The further development of methods to download such data from afar could change this situation in future, yielding data from pelagic birds and also from other species too small to carry satellite tags.

The studies in Tables 1–3 probably reflect mortality rates typical of most journeys in the species concerned, but mass mortality events, affecting many thousands of birds at a time, have occasionally been recorded (Newton 2007, 2008). Almost all occurred during adverse weather, either during the journey itself, soon after arrival in breeding areas in spring, or just before departure from breeding areas in late summer or autumn. Other large-scale mortalities among migrating birds have been documented in recent years in association with outbreaks of the avian influenza virus (H5N1 strain): for example, at Qinghai Lake in China where more than 5000 Bar-headed Geese *Anser indicus* died of this cause in 2005 (Chen *et al.* 2005). Yet other large-scale mortalities have often been recorded at tall lighted structures such as communication towers, high-rise buildings and wind turbines (e.g. Longcore *et al.* 2012, Loss *et al.* 2013, Elmore *et al.* 2021). However, because such migrants are drawn from large areas, it is again not normally possible to tell how much such deaths contribute to total annual mortality or to population levels.

Extreme situations aside, daily mortality rates in most of the species studied were clearly much higher during migration than at other times of year (in some species more than 20 times higher). This was shown in studies based on ringing or other marking, and also in those on other species based on satellite tracking (Table 3). Mortality rates during migration were often also higher in juveniles than in experienced adults, especially on first autumn journeys (Table 3). Adults more often showed higher mortality on spring journeys, mainly attributed to adverse winds. Mortality rates were also often higher during the crossing of significant barriers, such as the Sahara Desert or Gulf of Mexico, than over more benign terrain (Klaassen *et al.* 2014, Ward *et al.* 2018). Hence, in many species, mortality during migration periods contributed well over half the total annual mortality, up to 85% in one small songbird species and 100% in some immature vultures tracked for only 1 year. Most of the studies reported here referred to long-distance migrants, and whether similar findings hold for shorter-distance migrants remains to be seen.

In some of the larger species studied, human hunting may have influenced recorded mortality rates. Examples included Pacific Brant *Branta bernicla nigricans* and Emperor Geese *Anser canagicus* especially in spring, and perhaps also Greater Snow Geese and Eurasian Whimbrels *Numenius phaeopus* (Ward *et al.* 1997, Menu *et al.* 2005, Hupp *et al.* 2008, Watts *et al.* 2019). Other examples may have included raptors, especially those migrating to Africa where hunting of all large birds seems to have increased in recent decades (Zwarts *et al.* 2009). At the other extreme, lack of any obvious increase in mortality during migration was apparent in the adults of some long-lived species (with high annual survival) making mainly

overland journeys, and for which much larger samples of year-round tracked individuals would be needed to reveal any seasonal variations in mortality that might exist. The same constancy of mortality through the year may not have held in juveniles of these species, but no results for juveniles were presented.

Age differences

It is not hard to explain why juveniles suffer greater losses on migration than adults, because juveniles are inexperienced and inefficient in various ways. Typically, they feed less proficiently than adults and, being of lower dominance status, often lose out in competition for food at stopover sites (e.g. Rösner 1990, Woodrey 2000, Heise & Moore 2003). They therefore accumulate migratory fat less rapidly, often stay longer at stopover sites and migrate more slowly (review Newton 2006; see also Ellegren 1991, Morris *et al.* 1996, Woodrey 2000, Ueta & Higuchi 2002, Mellone *et al.* 2013, Péron & Grémillet 2013, McKinnon *et al.* 2014, Evens *et al.* 2017). In addition, juveniles are less skilled at avoiding predation, and on stopover have been recorded as being killed selectively compared with adults (Bijlsma 1990, van den Hout *et al.* 2008).

In soaring species, older birds have more efficient flight than juveniles, reflected in higher climb efficiency, improved soaring/flapping ratios and faster migration speeds, all leading to reduced energy expenditure on the same journeys (Weimerskirch *et al.* 2006, Harel *et al.* 2016, Rotics *et al.* 2016). In White Storks, tracked juveniles migrated alongside adults, but their inexperience led to their less efficient feeding (lower peck success), longer stopovers, less efficient flight and greater energy expenditure per distance covered (Rotics *et al.* 2016).

In general, juveniles are less good at navigating than adults, and in consequence may more often wander off route and make longer journeys (Mueller *et al.* 2013, Péron & Grémillet 2013). They are more likely to be drifted off course by crosswinds, and more likely to become concentrated in coastal areas (Murray 1966, Ralph 1971). Out-of-range vagrants that are trapped at bird observatories are almost all first-year birds, as are individuals that in spring 'overshoot' their normal breeding range (Newton 2008). Among individual Black Kites, an ability to compensate for lateral drift developed

gradually over several years, as experience was gained, and poor navigators were subject to enhanced mortality (Sergio *et al.* 2022).

Juveniles also seem less good at judging weather conditions than adults, and more often set off in suboptimal conditions. This can lead to additional energy expenditure, to off-course drift, to longer and more delayed journeys and sometimes also to deaths. For example, among Savannah Sparrows *Passerculus sandwichensis*, juveniles departed under wind conditions that were less supportive than those used by adults, resulting in juveniles taking 40% longer to complete their journeys (Mitchell *et al.* 2015). Under the same adverse weather, juveniles in several studies suffered greater mortality than adults (Owen & Black 1989, Thorup *et al.* 2003, Sergio *et al.* 2014). For all these reasons, therefore, juveniles would be expected to survive migration less well than older more experienced birds.

CONCLUDING COMMENTS AND FURTHER WORK

Although enhanced mortality represents a major cost of migration in many birds, for the migratory habit to persist, migration losses are presumably less in the long run than any losses that would occur if the birds stayed in their breeding areas all year. Migration among birds presumably involves a trade-off between the fitness benefits of breeding and wintering in separate regions and the fitness costs of the to-and-fro journeys. The fact that mortality events associated with migration are not more frequent than they are is testimony to the adaptive behaviour of birds in avoiding dangerous areas or dangerous weather, either by circumventing such areas or, in the case of weather, by not flying then.

It is hard to see how studies of migration mortality based on ringing or colour marking could be much improved in future. Ideally, they should involve studies of the same population in both breeding and wintering areas, and sampling should be undertaken in each area soon after the birds arrive and just before they depart. This potentially enables, for birds which show high fidelity to both breeding and wintering areas, separate estimates of mortality to be made for both autumn and spring migrations and for periods on breeding and wintering areas. Only for large waterfowl and cranes, with their high site fidelity, has it proved possible

to sample the same population in this way throughout the year (e.g. Owen & Black 1989, Menu *et al.* 2005, Pearse *et al.* 2019). In passerine studies, different sectors of the overall population were sampled in breeding and wintering areas (Sillett & Holmes 2002, Paxton *et al.* 2017, Rockwell *et al.* 2017).

Throughout their history, the primary aim of tracking studies on birds has been to determine migration routes, and for most of this period, it was practically impossible to separate mortality from the frequent tag failures. As equipment and harness designs have improved, gaining reliable mortality estimates over different periods of the year has become much more feasible, providing that sufficient numbers of birds can be tagged. More studies could now be designed with mortality estimation in mind from the start. In addition, other estimates may well be feasible from tracking data already in hand but where mortality estimation was not an initial objective. Some studies have provided mortality estimates for different periods of year, but not corresponding precisely with migration periods (e.g. Gauthier *et al.* 2001). Ideally, if we are to obtain a better and more representative understanding of the mortality costs of migration in birds, more studies are needed, clearly separating migration from stationary periods, and spanning a wider range of species, travelling through both benign and hostile terrain. For large, long-lived species with low annual mortality rates, large samples will be needed to demonstrate significant variation in mortality through the year. More studies on more species would enable us to better define the conditions under which migration mortality occurs, and how it impacts population levels, the species most at risk, more precisely define areas where such mortality occurs, and how it might alter under climate change. Hopefully, this brief review will help to stimulate further work along these lines.

AUTHOR CONTRIBUTIONS

Ian Newton: Conceptualization; methodology; investigation; validation; formal analysis; writing – original draft; writing – review and editing; resources.

CONFLICT OF INTEREST STATEMENT

ETHICAL NOTE

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