

Weather-related mass-mortality events in migrants

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A major perceived cost of migration in birds is the associated mortality. This mortality has proved difficult to measure and separate from mortality during stationary periods of the annual cycle. This paper reviews some major recorded mortality incidents among migratory birds attributed to inclement weather and other factors, including: (1) in-flight losses, caused by storms and other adverse weather en route, usually over water; (2) unseasonable cold weather soon after arrival in breeding areas; and (3) unseasonable cold weather before departure from breeding areas. Cold weather often kills migrants in their breeding areas, but not the local resident species which can better withstand it at those times. For migrants, cold and snow act to cut off the food supply, and can have a major selective effect on the seasonal timing of migration. Records of in-flight weather-induced mortality, involving up to hundreds or thousands of birds at a time, have affected mainly small passerines, but also larger birds, including eagles and swans. Most occurred in conditions of mist, rain or snow storms, and some involved nocturnal collisions with illuminated masts and other tall structures. Records of post-arrival mortality in breeding areas have involved mainly small insectivores (especially hirundines), but also waders and waterfowl. Such incidents, associated with cold and snow, have reduced local breeding densities from the previous year by 25–90%, depending on species and area, with up to several years required for recovery. Records of pre-departure mortality on breeding areas have mainly affected hirundines. Two major incidents in central Europe in September 1931 and 1974 killed hundreds of thousands, or even millions, of swallows and martins. After the latter incident, House Martin *Delichon urbicum* populations in Switzerland the following year were reduced by an estimated 25–30%. Such climatic extremes that occurred in spring or late summer in particular parts of the breeding range have been recorded at approximate mean frequencies of 2–10 per century. Average daily mortality in many bird species can clearly be much greater during migration periods than during stationary periods. Despite the heavy losses of birds on migration, it may be assumed that migration persists in the long term because the fitness costs (in terms of associated mortality) are more than offset by the fitness benefits (in terms of improved overall survival and breeding success) that accrue from migration.

Despite its overall benefits, migration is often perceived as hazardous. During their seasonal journeys, migrating birds must travel through unfamiliar areas, and often through alien habitat, which may jeopardize their abilities to find food and avoid predators. Land-birds may also have to cross large stretches of water, deserts or high mountains, where they may run out of fuel, become exhausted or encounter storms which could kill them. It is a plausible assumption therefore that the mean daily mortality rate is greater during migration periods than at most other times. For understandable reasons, however,

little coherent information is available on the mortality costs of migration (but see O'Briain 1987, Owen & Black 1989, Sillett & Holmes 2002, Menu *et al.* 2005). This paper examines some scattered records of large-scale bird mortality incidents associated with migration. They establish the importance of such incidents as a frequent hazard for migratory birds, even though their effects on populations are hard to establish. Almost all such incidents have 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. Typically, those incidents that occurred in breeding areas were not matched by

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concurrent mortality among local resident species, and could have been avoided if the migrants had arrived some days later or left some days earlier. They are therefore classed here as migration-related. Any mass mortality incidents among migrants add to the ongoing but less spectacular losses that are suffered by migrants, resulting from the usual mortality causes of predation, food shortage or disease (which are not discussed here).

The risks of migration itself vary with the body sizes and other features of the birds themselves, with the length of the journey and the terrain to be crossed, and with weather at the time. In general, the risks would seem to be greater for small birds than for large ones, over long journeys than short ones, in adverse than favourable weather, and over hostile than favourable terrain. Moreover, some species may be on migration for a substantial part of each year, more than 6 months in some land-birds, so it would not be surprising if much of their annual mortality occurred within this period, and influenced year-to-year changes in breeding numbers.

METHODS

The information presented in this paper was found by systematic search of major European and North American bird journals back to 1970, and secondarily by checking any references cited in these papers, working back to the late 19th century. Most of the incidents found referred to deaths of hundreds, thousands or even millions of birds, but I have included in Table 1 any incident in which more than ten carcasses were retrieved (some were likely to have represented a small proportion of a much greater number of deaths). For inclusion in Table 1, the incidents also had to fall within the normal migration seasons of the species concerned, and involve birds actually on migration, soon after arrival in breeding areas or just before departure from breeding areas, as described above. Almost certainly, some relevant records were missed. Mortality events that occurred at other times of the year were excluded, even though some may have occurred in association with winter weather movements.

RESULTS

Weather and in-flight mortality

Migrants often encounter bad weather en route, whether rain, mist or adverse winds. Over land, birds

can usually seek shelter from storms, but this option is not available over water. Heavy rain may saturate the plumage, increase wing loading (often already high in migrants) and cause the loss of body heat. These stresses, probably coupled with disorientation, sometimes force migrants down where they may be killed by collision, drowning or chilling (Frazar 1881, Saunders 1907, Cottam 1929, Williams 1950, Woodford 1963, Kennedy 1970). Flying birds are also sometimes killed by hail (Hochbaum 1955, Roth 1976), or by electrocution in lightning storms (Glasrud 1976). Clearly, it is important for birds to avoid flight at times of adverse weather, and most of the recorded mortality incidents listed in Table 1 refer to land-birds that encountered storms over water or other terrain where they could not take shelter.

Migrant land-birds caught by mist or storms over water must often be lost without trace, being consumed by gulls and other predators, or washed onto remote shorelines. Nevertheless, reports of mass deaths of migrants caught in bad weather (Table 1), and of birds arriving exhausted and emaciated, are fairly frequent (Dick & Pienkowski 1979, Morse 1980, Evans & Pienkowski 1984, Pienkowski & Evans 1985, Spindelow 1985). Examples include the large numbers of Common Quail *Coturnix coturnix* found drowned during a spell of sea fog off North Africa (Moreau 1927), the large numbers of dead Common Swifts *Apus apus* and martins washed up on a beach in North Africa (Perrins *et al.* 1985), or the hundreds of Garden Warblers *Sylvia borin* and other species washed ashore in Spain following a night of heavy rainstorms (Mead 1991).

The greatest over-water losses have been recorded in the New World (Table 1). A massive kill, estimated at 40 000 migrants of 45 species, occurred during a tornado and storm on 8 April 1993 off Louisiana. The storm occurred when large numbers of birds were arriving at the coast after an overnight sea crossing (Wiedenfeld & Wiedenfeld 1995). Other mortality events in the Gulf of Mexico included one of 10 000 birds (half of which were Magnolia Warblers *Dendroica magnolia*) washed up on Padre Island, Texas, in May 1951 (James 1956), and another of 5000 birds on Galveston Island, Texas, in May 1974 (Webster 1974, King 1976).

Lapland Longspurs *Calcarius lapponicus* seem to be frequent victims of spring storms. While migrating northward at night, large numbers have sometimes been grounded by storms of wet, clinging snow. In March 1904, an estimated 750 000 were found dead on the ice of two lakes in Minnesota, each about one

Table 1. Some large-scale mortality incidents associated with migration. Within categories, incidents are listed in date order.

Species	Date	Location	Conditions	Numbers	Source
(a) Mortality during spring migration					
Various species (> 23 species)	April 1881	Off Louisiana coast*	Gale	'Many thousands'	Frazar (1881)
Lapland Longspurs <i>Calcarius lapponicus</i>	March 1904	Minnesota-Iowa	Snowstorm	1.5 million	Roberts (1907a, 1907b)
Mainly Lapland Longspurs <i>Calcarius lapponicus</i>	February 1922	Nebraska	Snowstorm	'Thousands'	Reed (1922), Swenk (1922)
Magnolia Warblers <i>Dendroica magnolia</i> and others (39 species)	May 1951	Off Texas coast*	Rainstorm	> 10 000	James (1956)
Ducks, geese and swans	April 1954	Wisconsin	Hailstorm	'Many'	Hochbaum (1955)
Various (> 14 species)	May 1954	Minnesota	Snowstorm	> 175	Frenzell and Marshall (1954)
Hirundines (4 species)	May 1956	Saskatchewan	Snow and cold	74	Sealy (1966)
Snow Geese <i>Anser caerulescens</i>	May 1959	North Dakota	Hail	100	Krause (1959)
Various (43 species)	May 1962	Minnesota*	Mist and rain	5500	Green (1962)
Various (56 species)	April 1960	Michigan*	Gale, hail	3636	Segal (1960)
White-throated Sparrows <i>Zonotrichia albicollis</i> and many others (> 9 species)	April 1963	Georgian Bay, Ontario*	Rainstorm	'Thousands'	Woodford (1963)
Barn Swallows <i>Hirundo rustica</i> and others	April 1965	Morocco	Cold and rain	> 30	Ash (1969)
Various (> 32) species	May 1974	Off Texas coast*	Rainstorm	5000	Webster (1974), King (1976)
Various (32) species	April-May 1975	Utah	Cold and snow	569	Whitmore <i>et al.</i> (1977)
Warblers	May 1974	Lake Manitoba*	Cold	'Thousands'	Houston and Shadick (1974)
Scarlet Tanagers <i>Piranga olivacea</i> and others	May 1974	NE Maritime Region	Cold and wet	Many thousands	Finch (1975)
Turnstone <i>Arenaria interpres</i> and Knot <i>Calidris alpina</i>	June 1974	Ellesmere Island, Canada	'Bad weather'	24	Morrison (1975)
Jays, thrushes, warblers Michigan*	May 1976	Lake Huron	Rainstorm	200 000	Janssen (1976)
Swifts <i>Apus apus</i> and martin species	April 1982	Off Tunisia coast*	Rainstorm	Large numbers	Perrins <i>et al.</i> (1985)
Raptors, and others (> 12 species)	April 1980	Off Israel coast	Wind	> 1300	Zu-Aretz and Leshem (1983)
Mainly Rooks <i>Corvus frugilegus</i> and many others (20 species)	April 1985	Off Swedish coast	Dense fog	> 20 000	Alerstam (1988)

Table 1. Continued.

Species	Date	Location	Conditions	Numbers	Source
Warblers and others	April 1991	Off Spanish coast*	Rainstorm	> 677	Mead (1991)
Various (45 species)	April 1993	Off Louisiana coast*	Tornado	40 000	Wiedenfield and Wiedenfield (1995)
(b) Mortality during autumn migration					
Various (26 species)	October 1906	Lake Huron, Ontario*	Snowstorm	> 10 000	Saunders (1907)
Eared (Black-necked) Grebe <i>Podiceps nigricollis</i>	December 1928	Nevada	Snowstorm	'Thousands'	Cottam (1929)
Common Swifts <i>Apus apus</i>	July 1930	England	Rain and wind	30	Watson (1930)
Various ducks (5 species)	October 1951	South Dakota	Fog, rain, snow	c. 500	Schorger (1952)
Various, mainly warblers (37 species)	October 1964	Florida	Low cloud, heavy rain	> 4707	White (1965)
Various ducks (8 species)	November 1973	Arkansas	Thunderstorm	> 76	Roth (1976)
Mainly Song Thrush <i>Turdus philomelos</i> , Blackbird <i>T. merula</i> and others (12 species)	October 1988	Off Swedish coast	Dense fog	> 20 000	Alerstam (1990)
Eared (Black-necked) Grebe <i>Podiceps nigricollis</i>	January 1997	Utah	Snowstorm	35 000	Jehl <i>et al.</i> (1999)
(c) Mortality after arrival from spring migration†					
Mainly warblers (22 species)	May 1888	Wisconsin	Cold	> 645	Deane (1914)
Tree Swallow	May 1906	Maine	Cold	'A number'	Deane (1923)
<i>Tachycineta bicolor</i>					
Least Flycatcher	May 1907	Minnesota	Cold and snow	'Hundreds'	Wood (1908)
<i>Empidonax minimus</i> , various warblers and others					
Warblers	May 1907	Michigan	Snowstorm	'A number'	Wood (1908)
Tree Swallow	Spring 1945	New York	Cold and wet	'Many'	Dence (1946)
<i>Tachycineta bicolor</i>					
Eurasian Chiffchaff	April 1950	Wales	Cold and snow	13	Kent (1951)
<i>Phylloscopus collybita</i>					
American Coots	March 1964	Iowa	Re-freezing	'Hundreds'	Fredrickson (1969)
<i>Fulica americana</i>					
King Eider	May–June 1964	Beaufort Sea	Re-freezing	100 000	Barry (1968)
<i>Somateria spectabilis</i>					
Northern Lapwings	April 1966	Finland–Sweden	Cold and snow	'Many thousands'	Vepsäläinen (1968), Marcström and Mascher (1979)
<i>Vanellus vanellus</i>					
Hirundines and others	May 1965	Minnesota	Cold and snow	'Hundreds'	Anderson (1965)
Various (42 species)	May 1968	Finland	Cold and snow	> 3000	Ojanen (1979)
American Coots	May 1967	North Dakota	Cold and snow	> 387	Dane and Pearson (1971)
<i>Fulica americana</i>					

Table 1. Continued.

Species	Date	Location	Conditions	Numbers	Source
Scarlet Tanagers <i>Piranga olivacea</i> and others	May 1974	New Hampshire	Cold and rain	28 per hour of road travel	Zumeta and Holmes (1978)
Dusky Flycatcher <i>Empidonax</i> <i>oberholseri</i> and others (10 species)	June 1974	Colorado	Rain and snow	> 49	Eckhardt (1977)
Various (32) species	April–May 1975	Utah	Snowstorms	569	Whitmore <i>et al.</i> (1977)
Eurasian Oystercatcher <i>Haematopus ostralegus</i>	March 1979	Scotland	Cold and snow	33	Watson (1980)
Hirundines (4 species)	April 1982	California	Cold and wet	> 100	DuBow and Moore (1985)
Cliff Swallow <i>Petrochelidon pyrrhonota</i>	May 1996	Nebraska	Cold and rain	'Thousands'	Brown & Brown (1998)
(d) Mortality before departure from breeding areas†					
Brent Geese <i>Branta bernicla</i>	August 1956	Southampton Is. Canada	Water freezing	21	Barry (1962)
Barn Swallow <i>Hirundo rustica</i> Northern House Martin <i>Delichon urbicum</i>	September 1931	Germany	Cold and snow	Millions	Alexander (1933)
Sand Martin <i>Riparia riparia</i> Barn Swallow <i>Hirundo rustica</i> Northern House Martin <i>Delichon urbicum</i>	October 1974	Germany and Switzerland	Cold and snow	Many thousands	Ruge (1974) Bruderer and Muff (1979), Reid (1981)
King Eider <i>Somateria spectabilis</i>	Autumn 1960	Banks Is., Canada	Water re-freezing	50 000**	Barry (1968)
Barn Swallow <i>Hirundo rustica</i>	October– November 2000	Kazakhstan	Cold and snow	Several thousands	Berezovikov and Anisimov (2002)
Sand Martin <i>Riparia riparia</i>	October–November 2000	Kazakhstan	Cold and snow	> 1000	Berezovikov and Anisimov (2002)
Common Swift <i>Apus apus</i>	August–November 1986	Finland	Cold and rain	2000	Kolunen and Peiponen (1991)
Common Swift <i>Apus apus</i>	July 1930	England	Cold and rain	> 30	Watson (1930)

For other examples of heavy mortality in migrants after arrival, see Smith (1929), Brown and Brown (2000).

For examples of hold-ups in migration through bad weather, see Wood (1908), Williams (1950), Berthold *et al.* (2002).

†Birds classed as killed after arrival in breeding areas may have included some migrants with further to go, and those classed as killed in breeding areas before departure may have included some migrants already en route from higher latitudes (see especially the Swifts discussed by Kolunen & Peiponen 1991).

*Much or all of mortality occurred over water.

**Females and young, the males having already migrated.

square mile (2.6 km²) in extent. However, carcasses were reported from a much wider area, and it was estimated that at least twice that number (1.5 million) may have been killed. Some were attracted to town lights and collided with buildings and other obstacles (Roberts 1907a, 1907b).

Waterbirds probably suffer fewer losses on overseas flights than do land-birds, being more robust and able to rest on water when navigation or flying conditions become difficult (as shown for radiotagged Whooper Swans *Cygnus cygnus* on their migration between Iceland and Britain, Pennycuik *et al.* 1996). However, for some waterbirds on migration, problems arise from their being forced down onto dry land. In western North America, Eared Grebes *Podiceps nigricollis* cross hundreds of kilometres of desert with few places for a waterbird to land in emergency. Snow storms have occasionally brought hundreds or thousands of birds crashing to the ground. After one such event in December 1928, most were dead, having struck trees or buildings, but others were busy working themselves out of the snow (Cottam 1929). In January 1997, bad weather in southern Utah several times brought grebes to ground, an estimated total of 35 000, forming about 3% of the population that stages at the Great Salt Lake (Jehl *et al.* 1999).

Headwinds provide another hazard for migrants, because in effect they force the birds to fly for longer, depleting their energy reserves. This is especially important for species that cross large expanses of inhospitable habitat, such as oceans or deserts. In strong headwinds, birds exhausted over water sometimes settle on the surface, becoming soaked and unable to take off again. In addition, birds forced by headwinds to fly close to the waves become vulnerable to attacks by gulls, which drive small birds down into the water, from which they can be snatched and swallowed (Hobbs 1959). Probably many birds are lost at sea while fighting headwinds, while others die or suffer reduced breeding success after arrival (for Brent Geese *Branta bernicla* see Ebbinge 1989). Dead land-birds are often found washed up on beaches, and their remains show that many have been eaten at sea, presumably mainly by gulls (e.g. Alerstam 1988). Other individuals arrive on coastlines in an apparently exhausted state, as often witnessed by birdwatchers. Evidently, over-water migration inflicts continual and occasionally heavy losses on many land-bird species.

Sandstorms can be a particular hazard to birds moving through the Sahara and neighbouring deserts of the Middle East, and can be fatal to any

grounded migrant. Sand-induced mortality incidents involving Northern Wheatears *Oenanthe oenanthe*, Barn Swallows *Hirundo rustica*, Common Quail and White Storks *Ciconia ciconia* have been recorded (Moreau 1928, Schüz *et al.* 1971).

Storm-induced deaths over water mostly involved small birds, but have included such robust species as Rook *Corvus frugilegus*, of which 4600 carcasses were found in one incident in southern Sweden (Alerstam 1988). At least 106 species, including passerines, cuckoos, nighthawks, rails, gulls, terns, skimmers, shorebirds and waterfowl, have been washed up following storms over the Gulf of Mexico (species total calculated from all relevant papers in Table 1). In addition, one large over-water incident off Israel in April 1980 involved at least 1300 birds of prey (including eagles), presumably blown over water from their usual landward route, and other incidents involving raptors are mentioned by Kerlinger (1989). One over-land hailstorm killed many ducks and geese, and at least 35 Tundra Swans *Cygnus columbianus* (Hochbaum 1955), while another killed 100 Snow Geese *Anser caerulescens* (Krause 1959). It seems, then, that all sizes of birds are vulnerable to in-flight mortality from adverse weather of one type or another.

Unseasonable weather soon after arrival in breeding areas

Another source of loss among migrants is the unseasonable cold which may occur in some years soon after migrants have arrived in their breeding areas. Typically, such losses are restricted to migrants, local resident species being better able to withstand the cold. In each documented example, the migrants could have avoided the cold spell if they had arrived in breeding areas some days later than they did. Such losses could often have included passage migrants on route to other breeding areas, as well as migrants breeding locally. Insectivorous migrants seemed especially vulnerable at such times, because cold and snow greatly reduced their food supplies, but large-scale losses also occurred among newly arrived waterfowl and waders. Ground-feeding birds may starve when fresh snow and ice makes their food unavailable (Roseberry 1962, Vepsäläinen 1968, Bull & Dawson 1969, King 1974), and aquatic feeders are susceptible to delayed melting or re-freezing of water surfaces (Smith 1964, Barry 1968, Fredrickson 1969).

One such catastrophe affected newly arrived Cliff Swallows *Petrochelidon pyrrhonota* in Wisconsin,

when a sudden drop in temperature caused insects to become dormant. The Swallows did not fly during this period, but clung to their old nests, with one observer collecting 'a milk pail full' of the birds that had died (Buss 1942). Another unusual period of cold caused heavy mortality of Cliff Swallows across the north-central Great Plains in 1996, reducing a study population by about 53% (Brown & Brown 1998, 2000). When short of food in cold weather, swallows and swifts often seek shelter in buildings, huddle together for warmth, and may suffer from hypothermia and starvation (Koskimies 1950, Smith 1968, Keskpaik 1972, Lyuleeva 1973, Brown & Brown 2000). Other migratory insectivores also die in such conditions, but less conspicuously (Table 1; Ligon 1968, Eckhardt 1977, Tramer & Tramer 1977, Whitmore *et al.* 1977, Zumeta & Holmes 1978, Mead 1979).

In spring 1964, an estimated 100 000 King Eiders *Somateria spectabilis* – about one-tenth of the whole west Canadian population – died at migration staging areas in the Beaufort Sea. This mortality occurred when newly opened leads among sea ice re-froze, preventing the birds from feeding (Barry 1968). In a more recent event, birds found dead had lost about half of their body weight, and many survivors had insufficient body reserves for breeding, so that the effects of the freeze extended beyond the immediate mortality (Fournier & Hines 1994). Such mass starvation events in spring were documented in this species several times during the 20th century (Barry 1968, Fournier & Hines 1994), and occasionally in autumn (see later). Similar events, involving the re-freezing of open water, have also killed hundreds of American Coots *Fulica americana* and other newly arrived waterfowl in western North America (Fredrickson 1969).

In spring 1966, frost and snow on 11–17 April caused massive mortality of newly arrived Northern Lapwings *Vanellus vanellus* across southern Sweden and Finland, with reductions in local breeding populations the same year of 30–90% depending on region (Vepsäläinen 1968, Marcström & Mascher 1979). In such conditions, some birds retreated southward (on 'reverse migration'), others abandoned their territories and re-assembled in flocks, moved from mountains to valleys or from inland to sea coasts, and some females about to lay resorbed their eggs. A similar event occurred in the same region in 1927 (Kalela 1955), and a smaller event affected Eurasian Oystercatchers *Haematopus ostralegus* in Scotland in 1979 (Watson 1980).

Migrants that had died during unusual cold snaps in breeding areas had simply starved to death: carcasses were light in weight and practically devoid of fat reserves (e.g. Ligon 1968, Vepsäläinen 1968, Fredrickson 1969, Morrison 1975, Whitmore *et al.* 1977, Marcström & Mascher 1979, Watson 1980). At such times, birds were often reported in unusual places, such as roadsides or human habitation, where food of some sort was available (e.g. for Scarlet Tanager *Piranga olivacea* see Manville 1957, Zumeta & Holmes 1978, for Eurasian Oystercatcher see Watson 1980).

Again, little information is available on the importance of occasional heavy spring losses on the overall annual mortality. However, among Common Sandpipers *Actitis hypoleucos*, which migrate from Africa to breed in Britain, annual survival fluctuated in one area according to the weather in April, when they arrived. The mean survival over 13 years was 79%, but following late snowstorms in 1981 and 1989 survival fell to 39 and 50%, respectively, and breeding pairs from 21 to 14 and from 20 to 12 (equivalent to 33 and 40% reductions). After both these years, recovery in population level was slow, with annual increments of only 1–2 pairs (Holland & Yalden 1991). Similar reductions in breeding densities in cold springs were estimated for Scarlet Tanager at 33% in a study area in New Hampshire (Zumeta & Holmes 1978), at 30% for New Hampshire as a whole and 50% for Maine, for various hirundines (Tree Swallow *Tachycineta bicolor*, Sand Martin *Riparia riparia*, Barn Swallow and Cliff Swallow) at 30% for Nova Scotia, Maine and New Hampshire, together with an average decline of 25% in eight species of warblers in New Brunswick, compared with numbers in the previous year (Robbins & Erskine 1975). Hence, all these estimates of local or regional population declines, attributed to cold weather after arrival in breeding areas, fall within the range 25–90%, depending on species and area.

Unseasonable weather before departure from breeding areas

Unseasonable weather can also affect birds about to leave their breeding areas in autumn (Table 1). In central Europe in September 1931, during an early cold snap, 'immense numbers' of Barn Swallows and House Martins, and some Sand Martins, perished (Alexander 1933). The 89 000 individuals that were collected and transported by air for release in Italy 'were probably a small fraction of the total lost'. Another event in central Europe in 1974 had similar

effects, with hundreds of thousands of hirundines reported dead in Switzerland, Austria and southern Germany, and two million found alive flown by planes further south (Bruderer & Muff 1979, Reid 1981). In the next spring (1975), House Martin populations across Switzerland were reduced by 25–30%, but no overall effect was noted in Barn Swallows, despite some local reductions (Ruge 1974, Bruderer & Muff 1979).

Occasionally, Common Swifts are unable to leave their north European breeding areas because of adverse weather. They usually leave south Finland by the end of August, but in 1986 when late summer was cold and wet, around 2000 remained into November before dying (Kolunen & Peiponen 1991). Seven were found dead in their roost sites and others still alive were clearly starving. Scarcity of aerial insects prevented the birds from accumulating fat for migration, and they remained in southern Finland until their death. Similar events occurred in 1918 and 1957, but in these years delay was caused by late breeding resulting from cold weather in spring.

Autumn mortality events have also occurred among King Eiders following the freezing of sea water (Barry 1968). One in 1961 near Banks Island (Canada) involved an estimated 50 000 females and young. The males had already migrated and escaped the freeze. This event reportedly killed almost the entire Banks Island population of breeding females. Similarly, 21 Brent Geese hatched on Southampton Island (Canada) in the relatively late spring of 1956 were found frozen in shoreline ice the following spring. 'They were well preserved, and nothing could be found wrong with them except that their feather development was 4–5 days short of allowing them to fly' (Barry 1962).

Other mass mortality events, which sometimes occur during extreme weather in summer or winter, are not directly associated with migration, and can affect resident as well as migratory species (Newton 1998). However, it is sometimes difficult to separate migration-associated losses from other weather-induced mortality. For example, an estimated 27 000–62 000 wintering diving ducks (mainly Tufted Ducks *Aythya fuligula* and Common Pochards *Aythya ferina*) starved to death in Switzerland and Holland during a cold spell in March 1986, at a time when these birds would normally set off on spring migration (Suter & van Eerden 1992). This incident is not listed in Table 1 as migration mortality. But the authors argued that, if such weather had occurred earlier in winter, the birds would have moved further south and

escaped starvation. As it was, they were programmed to move, if at all, towards their breeding areas, which prevented their usual hard weather response.

Similarly, many large-scale mortality incidents have been recorded from time to time in seabirds (so-called wrecks), when large numbers are blown ashore, sometimes far inland (for a review see Newton 1998). It is usually unknown whether these birds were on migration at the time or in their wintering areas. However, because some seabird species seem to remain on the move for most of the time between leaving their breeding places in one year and returning there the next, migration periods cannot always be separated from other parts of the annual cycle. The same could be said for some land-bird species, which seem able to move long distances at almost any time during the course of a winter under the influence of food shortage (Berthold 1993).

The selective effect of severe weather on migration timing

The selective effect of severe weather on arrival dates was examined in a population of Cliff Swallows under study in Nebraska (Brown & Brown 2000). In May 1996, an unusual cold snap during the arrival period killed a large proportion of the early arriving birds (Brown & Brown 2000). Survivors had significantly later first capture dates (an index of arrival dates) in the years prior to the event than did those that died. Colony sites were occupied significantly later in the next and subsequent years, when first-capture dates were significantly shifted towards later arrivals. Offspring of the survivors tended to arrive later than birds of the same age before 1996. These findings implied that arrival dates were under genetic control, and had been changed by the selective effect of the cold spring, which removed many of the early-arriving birds from the population. Although in some years early arrival gave better nest success, this advantage was apparently offset by the greater risk of mortality in occasional cold years, the resulting arrival dates being a compromise between these opposing selection pressures. Likewise, bad weather in central Europe in autumn 1974 eliminated many of the late-departing migrants among hirundine populations, as many birds died (see above). The effects of this selective mortality were apparent for several subsequent years, as migration finished earlier in autumn than in the years before this event. This change was most evident in Barn Swallows, but also in House Martins and Sand Martins (Gatter 2000).

Role of tall masts and other structures

In some of the in-flight incidents mentioned above, human artefacts may have increased the losses at night, because on dark or misty nights birds were attracted to illuminated structures, resulting in collisions (Swenk 1922, Roth 1976). Such casualties have long been known from coastal and offshore lighthouses on nights of poor visibility, with low cloud or rain (e.g. Gätke 1895). In the years 1886–1939, some 500–8000 birds per year were reported as killed at lighthouses around Denmark, a total of 33 800 in autumn and 20 700 in spring (Hansen 1954). Relative to their numbers, some species were killed more often than others: for example Brambling *Fringilla montifringilla* more than Chaffinch *F. coelebs*, and Jack Snipe *Lymnocyptes minimus* more than Common Snipe *Gallinago gallinago*. At lighthouses and other structures, rails seem especially vulnerable. Such losses almost ceased where continuous beam lights were replaced by flashing on–off lights in the late 20th century.

Even greater losses have been associated with the tall masts used for radio, television and mobile phone transmission, especially in North America. Along with tall buildings and ceilometers (light beams for measuring cloud height which attract birds which then collide with nearby buildings), these towers kill many migrant birds (mainly by collision), especially those flying at night (e.g. Tordoff & Mengel 1956, Brewer & Ellis 1958, Taylor & Anderson 1973, Weir 1976, Avery *et al.* 1977, 1978, Lid 1977, Crawford 1978, 1981, Kemper 1996, Kerlinger 2000). In North America in the 1970s, an estimated 1.3 million migrants were killed in this way each year (Banks 1979). By the year 2000, tower numbers had increased roughly four-fold, as had the associated death toll, reaching an estimated 4–5 million birds per year (USFWS 2002). This is likely to be an under-estimate, because systematic recording is rare, and many birds probably die away from the point of collision or are removed by nocturnal scavengers before they can be found by people in daylight (for effects of scavenger control on numbers of carcasses found, see Crawford & Engstrom 2001). About 350 species have been recorded as casualties, the vast majority being nearctic–neotropical migrants which fly at night, such as Ovenbird *Seiurus aurocapillus*, Tennessee Warbler *Vermivora peregrina*, Black-and-white Warbler *Mniotilta varia*, Blackpoll Warbler *Dendroica striata*, Prairie Warbler *Dendroica discolor* and Magnolia Warbler. In one of the most detailed studies, at a

television tower in Florida, 44 007 victims of 186 species were found over a 29-year period. More than 94% were neotropical migrants, with Red-eyed Vireo *Vireo olivaceus* the most frequent (Crawford & Engstrom 2001). Higher totals in late summer/autumn than in spring were attributed to the greater numbers of birds migrating in autumn.

Spectacular slaughter has sometimes been recorded, such as the 50 000 birds of 53 species killed in one night at a ceilometer in Georgia (Johnston & Haines 1957). In general, towers taller than about 150 m kill the largest numbers of birds, and shorter towers relatively few (apart from one anomalous incident involving the deaths of 5000–10 000 Lapland Longspurs *Calcarius lapponicus* on the snowy night of 22 January 1998 at three 130-m towers in western Kansas, Kerlinger 2000). Reducing the height of some towers has greatly reduced the fatalities (Crawford & Engstrom 2001), while increasing the height of other towers has greatly increased the fatalities (Kemper 1996). As at lighthouses, mass mortalities are most frequent on nights of low cloud and fog or rain when birds are flying lower than normal.

On migration, birds normally fly too high for masts or tall buildings to represent a hazard, unless the birds are forced down by rain or snow and then dazzled by lights. I know of no evidence that windows of low buildings represent a greater hazard to birds at migration times than at other times of year.

Gas flares on oilrigs also attract birds on dark foggy nights, up to several thousand per night having been killed at individual flares (Lid 1977). The usual numbers are much lower, however, and were estimated by Bourne (1979) at a few hundreds of birds per rig per year, a small proportion of the numbers passing. Modern wind turbines are known to kill migrants by night or by day, but information is only just beginning to emerge on the scale of these losses (which generally seem small, being estimated at a total of 33 000 birds per year in the United States, USFWS 2002). The greatest losses seem to occur at wind-farms situated on narrow migration routes (with many raptors killed in southwest Spain, Barrios & Rodriguez 2004), or near wetlands, which attract large numbers of gulls and other large birds. Collision mortality at poorly sited wind-farms could have population-level effects, especially in large species, such as eagles and vultures, with low reproductive rates (Madders & Whitfield 2006). Even if the losses are small at any one turbine, the cumulative losses at multiple wind-farms could amount to population-level effects. The main problem in assessing impacts

is the shortage of systematically collected information on turbine casualties, and on the population dynamics of the most vulnerable species (Drewitt & Langston 2006).

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-tagged birds it is not usually possible to distinguish death from radio-failure. However, in a study of Black-throated Blue warblers *Dendroica caerulescens*, 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. They concluded that more than 85% of apparent annual mortality occurred during migration, giving a rate which was at least 15 times higher than the average at other times. The relative importance of weather-induced and other types of mortality to the overall migration total remained unknown.

Among Barnacle Geese *Branta leucopsis* travelling 3200 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 & 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, 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 *Branta bernicla hrota* migrating from northern Canada to Ireland was provided by O'Briain (1987). Their migration covers at least 2500 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, 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 mortality 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% per month). The loss of juveniles over the migration period also varied greatly between years (range 29–88% over five years), and most mortality appeared to be natural (rather than due to shooting). 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. These studies indicate how conditions on breeding areas can influence subsequent mortality 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, Pienkowski & Evans 1985). However, comparison of age-ratios among museum skins of Pacific Slope Flycatchers *Empidonax difficilis difficilis* obtained 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). Again, it is impossible to tell from such data how much of the additional mortality among juveniles was due to greater vulnerability of juveniles to adverse weather, as opposed to other factors.

DISCUSSION

Because mortality incidents that occur over sea or desert are usually impossible to detect, it is hard to tell whether they are of more than sporadic occurrence, let alone what proportion they form of the overall annual mortality. Losses that occur in particular storms may involve birds from wide areas of the breeding range, so have less impact on local breeding densities than the number of casualties might suggest. However, losses that occur in spring, when numbers are near their seasonal low, are more likely to affect subsequent breeding densities than are those that occur in autumn when numbers are near their highest. In populations in which over-winter mortality is density-dependent (Newton 1998, 2004), losses on autumn migration could be largely or entirely offset by reduced over-winter losses, but by

spring there is much less scope for such compensation before breeding begins. Most of the documented mortality events in Table 1 were in spring which in most northern regions tends to have more severe weather events than autumn, affecting birds on passage or soon after arrival in breeding areas.

Of the 23 spring in-flight mortality incidents listed in Table 1, eight occurred during heavy rain, five during snow, two in hail, two in dense mist, four in strong winds and two in unspecified 'bad weather'. Of eight such incidents in autumn, three occurred in heavy rain, three in snow and two in dense mist. Incidents were categorized according to the main weather factor, as mentioned by the author, but in some a combination of these factors was involved: for example rain and mist or rain and wind. Clearly, mist, rain and snow (or rain and snow associated with strong winds) were important causes of mass mortality among birds in flight. All 18 incidents that occurred soon after arrival in breeding areas were associated with a marked drop in temperature; ten also included snow, four included rain and two involved the re-freezing of lake or sea water. All eight incidents that occurred in late summer/autumn before departure were also associated with exceptional cold, including four with snow, two with rain and two with freezing lake or sea water. In none of these incidents were resident bird species mentioned as casualties. Some resident species, as well as winter-visiting migrants, suffer great mortality in hard winters, but comparisons with migration mortality are difficult because winter losses are usually spread over a longer period, and carcasses are seldom found. Their effects on local populations are easier to assess, however, from the decline in subsequent breeding numbers (Cawthorne & Marchant 1980, Newton 1998).

In general, the survival of any bird through a difficult journey may depend not only on the weather encountered, but also on the bird's weight (and fat content) on departure, in turn influenced by the prevailing food supply, age and dominance, and levels of competition in the population. In addition, some juvenile birds may die through their inexperience, making them more vulnerable than adults to various kinds of hazard, while others could die through directional or navigational errors. Vagrants are almost all first-year birds, as are individuals that in spring 'overshoot' their normal breeding range.

Because the records in Table 1 result from incidental observations, and not from systematic study, it is impossible to estimate how often particular popula-

tions experience different types of mass mortality events. However, in the 20th century, Northern Lapwings in Finland experienced at least two mass starvation events just after arrival, Common Swifts in Finland experienced at least three such events before departure, hirundines in central Europe experienced at least two such events just before departure, and King Eiders in the Beaufort Sea experienced at least four such events at stopover sites in spring. Cliff Swallows in Nebraska experienced at least 11 spring mortality events in 123 years (including two of extreme severity), and Lapland Longspurs in Minnesota experienced three such events in 25 years. These figures give some indication of the likely frequency of major weather-induced mortality incidents, while smaller events in other years may pass without being documented. If such big events were to increase in frequency, they would presumably lead to changed migration timing or route (through selection), or eliminate altogether those populations occupying particular parts of the breeding range.

In addition to the major weather-induced catastrophes, other birds are presumed to die because they drift too far off course, or run out of fuel in places where they cannot feed. Many records exist of emaciated or dehydrated birds that have crossed seas or deserts (for records from a ship off West Africa, see Serle 1956, and from a ship off northeast Cuba, see Johnston 1968), and small islands may often attract weakened migrants from the passing stream (Spendelov 1985).

There can be no doubt therefore that many birds die from adverse weather on migration, and that in some incidents, the numbers can be very large. In some of the examples mentioned above, the daily mortality during migration, or soon after arrival in breeding areas, was almost certainly much greater than the mean daily rate at other times of year. The estimates of migration-related mortality mentioned above for the Black-throated Blue Warbler, Barnacle Goose, Brent Goose and Greater Snow Goose provide striking examples, and in other species (such as Northern Lapwing and King Eider), the losses immediately after arrival in breeding areas in unusually cold springs exceeded the normal annual mortality expected of these species. Following post-arrival losses in spring, local breeding populations of various species fell by 25–90% and following heavy pre-departure losses in autumn, breeding populations of House Martins in Switzerland fell by 25–30%. Apart from these extreme examples, it is hard to judge the importance of such major weather events in relation

to the ongoing but more diffuse losses due to food shortage, predation and other regular mortality agents. Many severe weather events are unlikely to cause mass mortalities, because birds do not normally depart on migration when conditions look bad (Lack 1960, Richardson 1990). Such losses occur when birds already aloft over water encounter storms en route. Whether their bodies reach shore, where they might be recorded, depends on many factors, such as how long they remain afloat, the direction and strength of winds and currents, proximity to land, and actions of scavengers (Bibby & Lloyd 1977).

Regarding possible effects of over-water storms on population levels, Butler (2000) pointed out that, among Nearctic–Neotropical migrants, 25 species had declined in eastern North America during the period 1966–96, compared with only three in western North America over the same period. The eastern species migrate partly over water (western Atlantic or Gulf of Mexico), while the western ones migrate entirely over land. Moreover, among the water-crossers, declines were significantly more frequent among 13 long-distance migrants, wintering in South America, than in shorter distance migrants, wintering in Central America or on Caribbean Islands. In two of the 25 eastern species (Red-breasted Grosbeak *Pheuticus ludovicianus* and Mourning Warbler *Oporornis phildelphia*), annual population levels (as measured by the Breeding Bird Survey) were related to the number of stormy days during the previous autumn migration (mean 39 stormy days, range 18–59 days in different years). Years with the lowest populations had followed autumns with the most storms. These findings do not necessarily imply causal relationships, but they do suggest that further investigation of weather effects on the population levels of over-water land-bird migrants would be worthwhile. The autumn migration of many species between North and South America coincides with the time of hurricanes, the frequency and severity of which are said to have increased in recent years in association with climate change.

Although such losses represent a major cost of migration, for the migratory habit to persist, in the long run they are presumably less than any losses that would be experienced if the birds stayed on their breeding areas year round. For many species, high-latitude breeding areas are completely uninhabitable in winter. For others, the costs of reaching distant wintering areas may be offset by improved survival there, promoted by milder weather or greater food supplies.

Migration among birds thus involves a trade-off: the fitness benefits of breeding and wintering in separate regions, set against the fitness costs of the journeys themselves. Mortality that occurs through adverse weather during the journeys presumably has an important selective influence on the birds' behaviour with respect to weather, including the route taken, while mortality that occurs soon after arrival in breeding areas, or just before departure from breeding areas, has a selective influence on the timing of migration within the annual cycle (for evidence of genetic influence on migration dates see Berthold 1993, Møller 1994, Brown & Brown 2000). That mortality events associated with migration are not more frequent is testimony to the adaptive behaviour of birds in avoiding bad weather, either by not flying then, or by circumventing it.

In conclusion, although many mass mortality events among migratory birds almost certainly go unrecorded, and most documented ones cannot be translated into population-level impacts, the sheer scale of some events must inevitably result in temporary reductions in breeding numbers over local or wider areas (as so far documented in a few studies). Almost certainly such mortality represents in some bird species a major cost of migration.

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