

When and where does mortality occur in migratory birds? Direct evidence from long-term satellite tracking of raptors

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Summary

1. Information about when and where animals die is important to understand population regulation. In migratory animals, mortality might occur not only during the stationary periods (e.g. breeding and wintering) but also during the migration seasons. However, the relative importance of population limiting factors during different periods of the year remains poorly understood, and previous studies mainly relied on indirect evidence.

2. Here, we provide direct evidence about when and where migrants die by identifying cases of confirmed and probable deaths in three species of long-distance migratory raptors tracked by satellite telemetry.

3. We show that mortality rate was about six times higher during migration seasons than during stationary periods. However, total mortality was surprisingly similar between periods, which can be explained by the fact that risky migration periods are shorter than safer stationary periods. Nevertheless, more than half of the annual mortality occurred during migration. We also found spatiotemporal patterns in mortality: spring mortality occurred mainly in Africa in association with the crossing of the Sahara desert, while most mortality during autumn took place in Europe.

4. Our results strongly suggest that events during the migration seasons have an important impact on the population dynamics of long-distance migrants. We speculate that mortality during spring migration may account for short-term annual variation in survival and population sizes, while mortality during autumn migration may be more important for long-term population regulation (through density-dependent effects).

Key-words: animal migration, annual survival, ecology of death, long-distance migration, satellite radio-telemetry

Introduction

The annual cycle of migrating animals differs fundamentally from that of resident animals by the fact that migrants use different widely dispersed sites during different times of the year (Newton 2008). The latter makes it complex to study population regulation, and hence, it is poorly understood which are the critical phases for

population limitation in the annual cycle of migrants (reviewed by Sherry & Holmes 1995; Holmes 2007; Newton 2008; Faaborg *et al.* 2010). Furthermore, as it is difficult to follow individual migrants throughout the year, most of the evidence on mortality in migrants is indirect (Sillett & Holmes 2002). Understanding the relative importance of population limiting factors during different periods of the year is important as migrants generally are in decline (Sanderson *et al.* 2006; Thaxter *et al.* 2010), and it is thus essential to identify these bottlenecks in order to know where to direct conservation measures (Wilcove & Wikelski 2008).

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Tracking histories of individual birds.

An early suggestion was that population sizes of many migratory birds are primarily determined by the availability of food on the wintering grounds, where there may be strong competition for food and where the main mortality may occur (Lack 1954, 1968). The 'buffer effect', the phenomenon that individuals increasingly spread to inferior wintering sites with an increasing population size, might be a major mechanism for density-dependent population regulation during the wintering period, as for example demonstrated for Icelandic Black-tailed Godwits *Limosa limosa* (Gill *et al.* 2001; see also Studds & Marra 2005). In addition, there are convincing correlations between annual survival of several migratory species in the European-African migration system and rainfall in African wintering areas, indicating that conditions in the winter quarters indeed have a strong influence on the breeding populations of migrants (reviewed by Newton 2008; Zwartz *et al.* 2010; see also Sherry, Johnson & Strong 2005). On the other hand, also many examples of population limitation during the breeding season exist, like the density-dependent variation in fecundity and yearling recruitment in the Black-throated Blue Warbler *Dendroica caerulescens* which has a strong impact on population regulation of this migratory bird population (Rodenhouse *et al.* 2003; Sillett & Holmes 2005).

One may expect that the relative importance of population regulating processes during breeding and wintering differs between species that are adapted to contrasting ecological conditions of resource availability in summer and winter, respectively (Alerstam & Högstedt 1982). Whether populations are limited by processes during the breeding or wintering season depends on the relative strength of density-dependent processes in these periods (Sherry & Holmes 1995; Sutherland 1996), and the strength of these processes might vary between years or over time (Newton 1998). For example, reduced winter hunting pressure on Pink-footed Goose *Anser brachyrhynchus* has resulted in a reduced summer survival among adults, indicating that there has been a shift from population limitation during winter towards population limitation during summer (Madsen, Frederiksen & Ganter 2002).

However, among migratory birds, significant mortality may occur not only during stationary periods in the breeding range or winter quarters but also during the migration seasons when the birds are actually travelling or are at stopover sites along the migratory routes. Migratory journeys may be associated with enhanced risks of predation, diseases, exhaustion, food shortage at critical stopover sites and mass mortality (often associated with adverse weather and wind conditions), which may have at least short-term effects on population sizes (reviewed by Newton 2008). Obviously, migratory seasons could also constitute important bottle-necks for migratory populations and potentially might be more important for population regulation than processes during breeding and wintering periods.

There is as yet only one study where the levels of mortality during the three main annual periods of breeding, wintering and migration have been compared in detail for a migratory bird species (Sillett & Holmes 2002). Seasonal survival of the Black-throated Blue Warbler during the 3 months stationary breeding period in North America as well as during the 6 month stationary winter period in Jamaica was estimated from re-sightings of colour-ringed individuals (Sillett & Holmes 2002). Combining these seasonal survival estimates with the estimated total annual survival made it possible to calculate survival during the spring and autumn periods covering the remaining 3 months of the year. The results showed a remarkably high mortality during migration. While survival during stationary periods was high both in summer (0.99) and winter (0.93), it was much lower during the two migration periods combined (0.5). This meant that more than 85% of apparent annual mortality occurred during migration, and mortality rate during migration was at least 15 times higher than during the stationary periods (Sillett & Holmes 2002). A few other studies have demonstrated significant seasonal variation in mortality rate of migratory birds more broadly during the year. For example, among three species of geese, the highest mortality occurred during that part of the year that included summer as well as migration periods (Clausen *et al.* 2001; Madsen, Frederiksen & Ganter 2002; Hupp, Schmutz & Ely 2008), while the highest mortality occurred during winter in one goose and one bustard species, and in both cases, this mortality was related to hunting (Combreau, Launay & Lawrence 2001; Gauthier *et al.* 2001). Another example is the variation in survival at an autumn staging area which has a major impact on population dynamics of White Storks *Ciconia ciconia* migrating between Europe and South Africa (Schaub, Kania & Köppen 2005). The scarcity of evidence for the importance of migration-related mortality in relation to the overall annual mortality most likely should be attributed to the difficulty in studying this phenomenon.

In this study, we will present results from a large satellite tracking program of three species of migratory raptors, Osprey *Pandion haliaetus*, Marsh Harrier *Circus aeruginosus* and Montagu's Harrier *Circus pygargus*, migrating between breeding grounds in Europe (mainly Sweden and the Netherlands) and winter quarters in tropical West Africa (Hake, Kjellén & Alerstam 2001; Kjellén, Hake & Alerstam 2001; Alerstam, Hake & Kjellén 2006; Strandberg *et al.* 2008; Trierweiler & Koks 2009; Klaassen *et al.* 2010), in order to investigate seasonal and geographical patterns of mortality of adult birds. Close inspection of tracking data in combination with field monitoring of returns to breeding sites of transmitter birds allowed us to identify cases of (probable) deaths, and we could distinguish these from cases of transmitter/battery failure as most probable cause of terminated tracking (cf. Combreau, Launay & Lawrence 2001; Hupp, Schmutz & Ely 2008). The main aim of this study was to

compare the occurrence of mortality between the four seasonal periods of breeding, autumn migration, wintering and spring migration. Specifically, we wished to investigate whether mortality rates were enhanced during migration compared with stationary seasons and, if so, to compare the geographical patterns of mortality during autumn and spring migration. In this study, we provide the first direct evidence about when and where natural mortality occurs, which is essential to understand the relative importance of migration-related mortality for the population dynamics of migrants.

Materials and methods

TRACKING DATA AND FIELD OBSERVATIONS

A total of 69 adult raptors were tracked using satellite transmitters (ARGOS PTT-100, Solar ARGOS PTT-100, Solar ARGOS/GPS- PTT-100; Microwave Telemetry Inc., Columbia, MD, USA): 18 Ospreys between 1995 and 2011 (Hake, Kjellén & Alerstam 2001; Kjellén, Hake & Alerstam 2001; Alerstam, Hake & Kjellén 2006), 17 Marsh Harriers between 2004 and 2011 (Strandberg *et al.* 2008; Klaassen *et al.* 2010) and 34 Montagu's Harriers between 2005 and 2011 (Trierweiler & Koks 2009). During 1995–1997, we used battery-driven transmitters for the Ospreys and batteries did not last much longer than one annual cycle; hence, some birds returned with an already expired transmitter. Four of these birds were fitted with a new transmitter. Since 1998, the birds were equipped with transmitters with solar panels making it possible to obtain continuous tracking records during several years (e.g. Alerstam, Hake & Kjellén 2006; Trierweiler & Koks 2009; Vardanis *et al.* 2011). We have used all tracking data up to and including August 2011, when nine individuals were still alive.

For every deployment, we determined the probable cause of termination of tracking (death of the bird or transmitter/battery failure), using very similar criteria (cf. below) as in earlier studies of the mortality of Houbara Bustards *Chlamydotis macqueenii* (Combreau, Launay & Lawrence 2001) and Emperor Geese *Chen canagica* (Hupp, Schmutz & Ely 2008). In addition, field searches were made in the breeding area during all years to find returning birds with non-functional transmitters. Long-term studies show that the adults of these species normally return to breed within the same area from year to year, in which they often use the same nest or breed in the same territory (e.g. Poole 1989; Strandberg *et al.* 2008; Trierweiler *et al.* 2008). Female Montagu's Harriers are the only group that more or less regularly switch breeding sites between years (30–50% of females switches breeding site between years, unpublished data Ben Koks; Trierweiler *et al.* 2008).

For each individual, we recorded the number of months when tracking data showed the individual to be alive, including the month of capture/start of tracking if this occurred on date ≤ 15 of that month (if capture/start of tracking occurred later, this month was excluded from survival time). We included only months of active transmission in survival time, disregarding survival time of birds with non-functional transmitters. We also recorded the date and place when tracking was terminated and assessed the probable cause according to the following criteria (number of cases in parentheses):

- Probable transmission failure ($n = 4$): Loss of radio contact was preceded by poor transmission performance and/or low battery voltage.
- Confirmed transmission failure ($n = 9$): Loss of radio contact as described above, and the bird was furthermore observed and identified by field observations when returning at the breeding site with a non-functional transmitter.
- Probable death of bird ($n = 41$): Loss of radio contact occurred abruptly and in spite of preceding good transmission and/or battery performance, or transmitter was continuously sending from the same position without indicating movement (activity counter stopped). Number of deaths may have been overestimated if birds did not die but just lost their transmitters, but we have not recorded any case of suspected harness failure, as we never observed birds returning without transmitters despite the fact that we annually check the identity of all breeding birds in our study areas (great majority of birds applied with satellite transmitters can be recognized by their colour rings). Thus, this potential bias is probably very small or non-existent.
- Confirmed death of bird ($n = 10$): Tracking data indicated mortality (cf. 'Probable death of bird'), and this was confirmed by additional observations: transmitter transported into a town, probably related to hunting ($n = 1$), killed by people, confirmed by local contacts ($n = 1$), killed by mammalian predator, confirmed by finding leftovers ($n = 1$), collision with power-line, confirmed by finding carcass under power-line ($n = 1$) or confirmed by series of GPS-positions directly under a power-line as judged from Google Earth (earth.google.com; $n = 2$), exhaustion at sea, confirmed by very slow final movement indicating floating at surface ($n = 1$), exhaustion after retreat migration; birds died after aborted Sahara crossing attempts, cf. Strandberg *et al.* 2010 ($n = 2$), and death close to breeding site, bird died after fast sprint migration after a delay, cf. Strandberg *et al.* 2010 ($n = 1$). On four of these occasions, the transmitter was collected from the dead bird.

SURVIVAL RATES

Monthly survival rates were calculated as the number of months survived by the individuals divided by the total number of months (survival and mortality months) that have been monitored. The annual survival was calculated as the product of monthly survival rates. A corresponding calculation of survival during four main periods of the year – summer/breeding, autumn migration, winter, spring migration – was also made.

DAILY MORTALITY RATES

Survival during four main periods of the year – summer/breeding, autumn migration, winter and spring migration – were calculated as the number of periods survived by the individuals divided by the total number of periods monitored (survival and mortality periods). Daily mortality rates (μ) were calculated by taking the mean duration (number of days, d) of each period into account as

$$\mu = 1 - s^{\frac{1}{d}}$$

where s is the total survival during the period. The average duration of the four main periods as given in Table 2 was determined from Hake, Kjellén & Alerstam (2001), Kjellén, Hake & Alerstam (2001) and Alerstam, Hake & Kjellén 2006 for Osprey, from Strandberg *et al.* (2008) for Marsh Harrier and from Trierweiler & Koks (2009) for Montagu's Harrier. Average durations for the three species were used in calculations where the three species were combined.

STATISTICAL TESTS

Data are presented for each species separately, but in statistical tests, data were combined for all three species due to small sample sizes and similarities in mortality patterns in space and time (see Results). It is not unreasonable to expect that these three raptor species will be exposed to similar seasonal and geographical patterns of mortality risk during the annual cycle, given similarities in routes (same flyway between breeding sites in Europe and wintering sites in West Africa) and migration habits (all are diurnal migrants depending on soaring flight). Distributions of mortality in different months and different periods of the year were tested in relation to expected distributions (assuming a constant mortality rate) calculated from the number of months or days that the birds were monitored (chi-square tests). Latitudinal distributions of places where mortality occurred during spring and autumn migration were compared by Mann-Whitney U -test (Sokal & Rohlf 1995).

Results

We identified 51 cases of deaths and probable deaths in our sample of 69 adult raptors monitored by satellite tracking during a total time of 1135 individual months. The monthly distribution of mortality indicated two annual peaks, during spring (March-May) and summer/

autumn (July-October), respectively (Table 1, Fig. 1a). This seasonal pattern differed from a uniform distribution of mortality events (bimonthly periods, species combined, chi-square = 15.7, d.f. = 5, $P < 0.01$).

Daily mortality rates during migratory periods were on average six times higher than during stationary periods (mean for migration periods combined = 0.0044, mean for stationary periods combined = 0.00075, Table 2, Fig. 1b). Comparing the observed number of deaths per period with the expected number of deaths per period assuming a constant daily mortality rate throughout the year ($\mu = 0.0014$, taking into account the durations of the four different periods and correcting for the number of periods monitored) showed that mortality rates differ significantly between periods (species combined, chi-square = 53.7, d.f. = 3, $P < 0.001$). The highest daily mortality rate occurred during spring migration for two of the three species, and there was a tendency of a higher daily mortality rate during spring compared with autumn (species combined, chi-square = 3.3, d.f. = 1, $P = 0.07$). The lowest daily mortality rate occurred during the stationary wintering season in Africa (Fig. 1b, Table 2).

Although daily mortality rate was strongly enhanced during migration periods (cf. above) only about 55% of the total annual mortality losses occurred during migration (Table 2). Significant mortality took place during all four main periods of the year, with estimated losses in the range 9–17% in each period (Table 2), and the observed number of deaths did not differ from the expected number of deaths per period when only considering the number of periods monitored (i.e. not corrected for the length of the periods; chi-square = 2.9, d.f. = 3, $P = 0.41$; Fig. 1c).

Table 1. Survival and mortality of adult migratory raptors during different months of the year

	Osprey ($N = 18$)			Marsh harrier ($N = 17$)			Montagu's harrier ($N = 34$)			Species combined ($N = 69$)		
	N surv	N mort	Surv	N surv	N mort	Surv	N surv	N mort	Surv	N surv	N mort	Surv
January	26	0	1.00	21	1	0.95	45	0	1.00	92	1	0.99
February	25	0	1.00	21	0	1.00	44	1	0.98	90	1	0.99
March	23	0	1.00	19	2	0.90	41	3	0.93	83	5	0.94
April	19	4	0.83	19	0	1.00	35	6	0.85	73	10	0.88
May	16	1	0.94	18	1	0.95	31	2	0.94	65	4	0.94
June	15	0	1.00	24	1	0.96	31	0	1.00	70	1	0.99
July	28	1	0.97	29	3	0.91	43	3	0.93	100	7	0.93
August	32	1	0.97	29	2	0.94	59	3	0.95	120	6	0.95
September	31	1	0.97	24	3	0.89	49	3	0.94	104	7	0.94
October	27	3	0.90	23	1	0.96	48	1	0.98	98	5	0.95
November	27	0	1.00	23	0	1.00	45	3	0.94	95	3	0.97
December	27	0	1.00	22	1	0.96	45	0	1.00	94	1	0.99
Sum	296	11		272	15		516	25		1084	51	
Product			0.63			0.54			0.56			0.57

Number of individuals (N inds), number of individual months of survival (N surv) and number of individuals that have died in different months (N mort) are given for each species and for all species combined. The monthly survival rate (Surv) is calculated as the number of months survived by the individuals (N surv) divided by the total number of months that have been monitored (N surv + N mort). The annual survival is calculated as the product of the monthly survival rate.

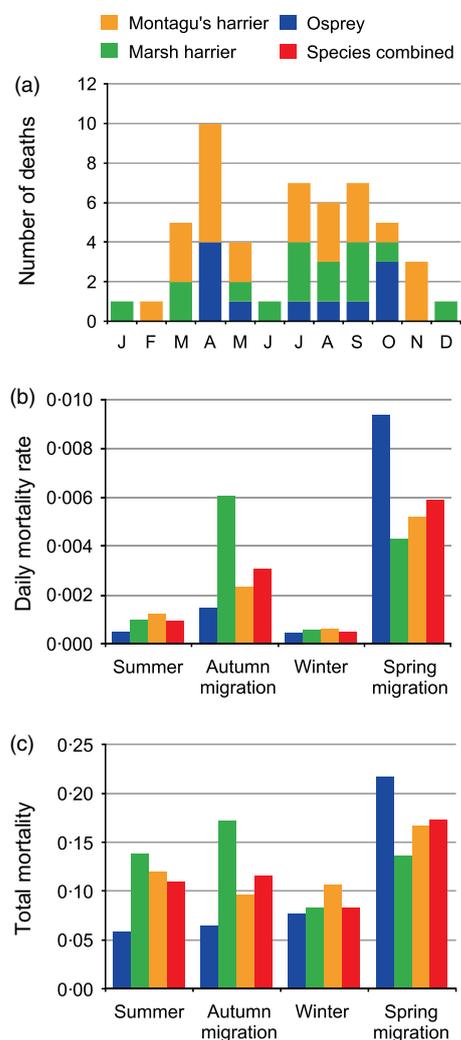


Fig. 1. (a) Monthly distribution of observed deaths among adult raptors. (b) Daily mortality rates during four main periods of the year for adult raptors. (c) Total mortality during four main periods of the year for adult raptors. For detailed information see Tables 1 and 2.

The geographical distribution of places where mortality occurred differed significantly between spring and autumn migration (Fig. 2; species combined, latitudinal distributions, Mann–Whitney $U = 43$, $n_{\text{autumn}} = 12$, $n_{\text{spring}} = 15$, $P = 0.02$). Spring mortality occurred mainly in Africa in association with the crossing of the Sahara desert, while most mortality during autumn took place in Europe (Fig. 2).

Discussion

Our analysis of long-term satellite tracking data of three species of raptors has revealed that significant mortality occurred during all four main periods of the year, but mortality rate during migration was about six times higher than during stationary periods. The total mortality was surprisingly similar between the four different periods, which can be explained by the fact that the 'more

Table 2. Survival and mortality of adult raptors during four main periods of the year (summer/breeding, autumn migration, winter/survival, spring migration)

	<i>N</i> surv	<i>N</i> mort	Surv	Days	Daily mort
Osprey (<i>N</i> = 18)					
Summer	32	2	0.94	123	0.0005
Autumn migr	29	2	0.94	45	0.0015
Winter	24	2	0.92	171	0.0005
Spring migr	18	5	0.78	26	0.0094
Annual surv			0.64	365	0.0012
Marsh harrier (<i>N</i> = 17)					
Summer	31	5	0.86	149	0.0010
Autumn migr	24	5	0.83	31	0.0061
Winter	22	2	0.92	151	0.0006
Spring migr	19	3	0.86	34	0.0043
Annual surv			0.56	365	0.0016
Montagu's harrier (<i>N</i> = 34)					
Summer	59	8	0.88	105	0.0012
Autumn migr	47	5	0.90	43	0.0023
Winter	42	5	0.89	182	0.0006
Spring migr	35	7	0.83	35	0.0052
Annual surv			0.59	365	0.0014
Species combined (<i>N</i> = 69)					
Summer	122	15	0.89	125	0.0009
Autumn migr	99	12	0.89	40	0.0029
Winter	88	9	0.91	168	0.0006
Spring migr	72	15	0.83	32	0.0059
Annual surv			0.60	365	0.0014

Number of individuals monitored by satellite tracking is shown for each species and for the three species combined. Number of individual periods of survival (*N* surv) and number of individuals that have died in different periods (*N* mort) are given for each species and for all species combined. The survival rate (Surv) for each main period is calculated as the number of periods survived by the individuals (*N* surv) divided by the total number of periods that have been monitored (*N* surv + *N* mort). The annual survival is calculated as the product of the survival rates during the four main periods. Daily mortality rates have been calculated from survival estimates and durations (number of days) of the different periods as described in the main text.

risky migration periods' are much shorter than the 'safer stationary periods' (autumn and spring migration together covered only about 2.4 months or 20% of the year). Nevertheless, more than half of the annual mortality occurred during migration. This result is in agreement with the important role of migration for the mortality of the Black-throated Blue Warbler, as demonstrated by Sillett & Holmes (2002). However, for the warbler, mortality seems to be associated with migration to an even more extreme degree (more than 85% of annual mortality occurred on migration, see Introduction). It seems likely that raptors, which have a higher annual survival and lower fecundity than warblers, have a different balance of breeding vs. survival resources that contribute to an increased relative importance of mortality during the breeding season in comparison with the warblers (Alerstam & Högstedt 1982).

Interestingly, we also found a tendency of a higher daily mortality rate during spring compared with autumn, in

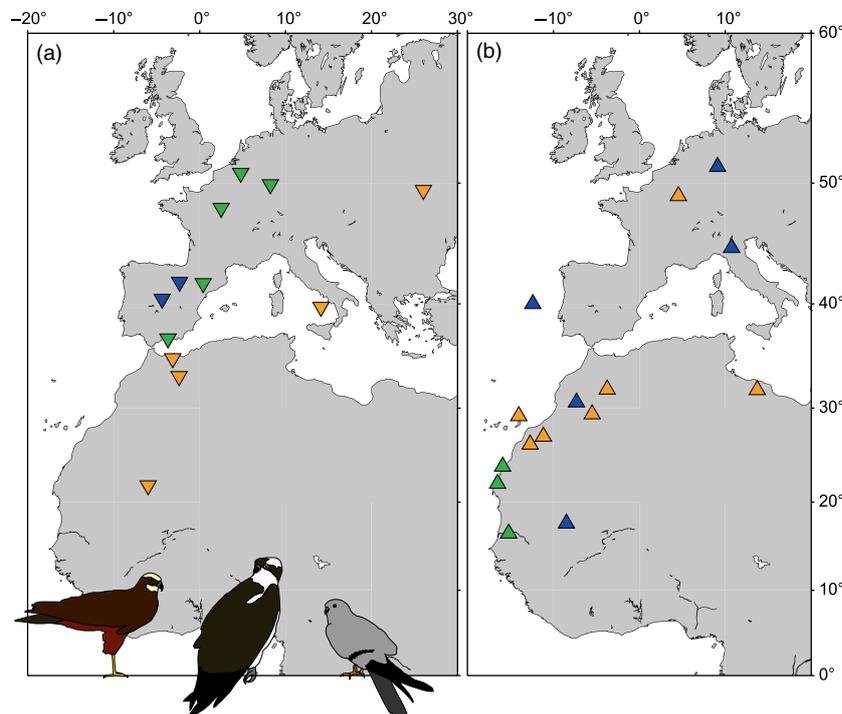


Fig. 2. Geographical distribution of cases of (probable) mortality of adult raptors during (a) autumn and (b) spring migration. Symbols show positions where birds have died according to satellite tracking information. Blue = osprey, green = marsh harrier, orange = Montagu's harrier.

which mortality events in spring occurred mainly in Africa in association with the crossing of the Sahara desert. These results fit well with recent observations on colour-ringed Eurasian Spoonbills *Platalea leucorodia*, which indicate that mortality is highest during spring migration, especially for those populations crossing the Sahara Desert (Lok, Overdijk & Piersma 2013; Lok *et al.*, in press).

The low mortality during the long stationary wintering period is perhaps surprising in view of the environmental changes and variation in rainfall in sub-Saharan Africa (Zwarts *et al.* 2010) but helps to explain why, for example, Ospreys and Honey Buzzards *Pernis apivorus* remain as immatures in tropical West Africa to exploit the apparently benign and safe conditions for survival during one or more years before migrating to northerly latitudes for breeding (Strandberg *et al.* 2012). Even adult raptors occasionally remain in Africa during the summer, having a sabbatical year, as was recently revealed by an adult Honey Buzzard tracked by GPS logger (R. G. Bijlsma, J. van Diermen, W. Bouten, pers. comm.).

CAUSES OF MORTALITY

Migrants can die for many different reasons. It is extremely difficult to establish the exact cause of death from satellite tracking data only. Only in a few cases, we could be certain about the cause of death in our study, often because additional information was obtained when the transmitter was retrieved. From the limited evidence we have, we cannot rule out an important role for anthropogenic factors such as power lines and hunting (poaching), especially in Europe. Mortality in Africa, especially in the

Sahara desert, seems above all to have natural causes, although hunting is known to form a problem in some regions south of the Sahara (e.g. the Inner Niger Delta, Mali, cf. Zwarts *et al.* 2010).

CARRY-OVER EFFECTS

Judging the relative importance of different annual periods for population limitation by the amount of mortality occurring in each period may be too simplified and potentially misleading for two main reasons. (i) First, the size of a population is not only determined by mortality, but reproduction is equally important. Reproduction can be affected by circumstances during previous periods in the annual cycle (so-called carry-over effects) and in this way can a certain period have a dramatic effect on population size independently of mortality events. A classical case of a carry-over effect is the influence of winter habitat quality on the reproductive success of American Redstarts *Setophaga ruticilla* (Marra, Hobson & Holmes 1998; Norris *et al.* 2003). Importantly, virtually nothing is known about the relative importance of conditions during different periods of the year on reproduction, for example whether conditions during spring have a larger effect on subsequent reproduction than conditions during the preceding winter. Moreover, the importance of carry-over effects on mortality and reproduction could differ between seasons. For example, we could imagine that autumn migration is an important source of mortality (as shown in this paper) but that conditions during autumn migration have almost no effect on reproduction in the subsequent year.

(ii) Second, mortality itself might have indirect causes, that is, occurring as a result of delayed effects of circumstances in preceding periods. Hence, it will be important to consider whether a peak in mortality during a specific period is likely to be the result of direct causes in that period or whether it is related to preceding periods. For example, the effect of limited winter resources may carry-over to an increased mortality during spring migration, as suggested for songbirds on their northbound migration across the Sahara desert after dry wintering seasons in Africa (Zwarts *et al.* 2010). One cannot exclude that part of the spring migration mortality of the raptors in this study was indirectly caused by conditions during the preceding winter period. However, if the raptors were suffering from seriously restraining conditions in the winter quarters, we would have expected signs of enhanced mortality during the winter period in combination with a spillover of mortality to spring migration when the birds become exposed to increasing demands on performance. Instead, we found a very low mortality rate throughout the winter period, which is difficult to reconcile with limiting conditions during the winter.

DENSITY-DEPENDENT EFFECTS

It seems likely that the mortality during spring migration, which may be an important explanatory factor for annual fluctuations in survival of the raptors, is largely density independent and mainly caused by direct risk factors associated with the crossing of the Sahara desert under hazardous wind and weather conditions. We have earlier described, also on the basis of satellite tracking data, that raptors show aberrant behaviours like course changes, interruptions, slow speeds and retreat migration in association with the Sahara crossing, indicating that they encounter serious difficulties during the desert crossing (Strandberg *et al.* 2010). These difficulties do not only lead to direct mortality, as indicated in this study, but also carry over to effects of late arrival and reduced breeding success in the following breeding season (Strandberg *et al.* 2010).

Mortality during autumn migration is more likely to be density dependent. The main part of autumn migration mortality took place in Europe, where the birds forage extensively and also have longer stopover periods than during spring migration (Alerstam, Hake & Kjellén 2006; Klaassen *et al.* 2008), being under pressure to accumulate energy reserves for the impending crossing of the Sahara desert. This happens at a time when numbers of individuals are large, including yearlings on their first migration, which may lead to interference and competition at foraging sites along the migration routes. Significant mortality seemed to occur also in late summer, before the birds' departure on autumn migration (Fig. 1a), indicating that the birds may have faced important constraints during the breeding season, as expected for long-lived species for which breeding resources possibly are relatively scarce

(Alerstam & Högstedt 1982). Such a limitation during summer may well be density dependent and have consequences for the survival during the succeeding autumn migration, when individuals in poor condition may have succumbed as a delayed effect of efforts associated with breeding, as a cost of reproduction which is likely to be delayed until after the young have become independent (Williams 1966; Stearns 1992; but see Charnov 1986).

METHODOLOGICAL ISSUES

Mean annual survival for our satellite tracked birds was close to 0.6 for all three species (Table 1), which is somewhat lower than the expected adult annual survival rates (probably about 0.8 for Osprey and 0.7 for the harriers; cf. Glutz von Blotzheim, Bauer & Bezzel 1971; Cramp & Simmons 1980; Poole 1989). It is possible that the transmitters have adverse effects affecting the birds' behaviour and survival, as for example demonstrated for the Prairie Falcon *Falco mexicanus* (Steenhof *et al.* 2006). We cannot exclude that the transmitters have adverse effects on our study species, but we think that such bias is small because the weight of the transmitters was <4% of the body weight of our study species and because the Osprey and the harriers migrate to a large degree by thermal soaring flight, which is less energy demanding and probably less sensitive to added load than active flapping flight (Kenward 2001; Steenhof *et al.* 2006). A contributory possible reason for the relatively high mortality estimates for our satellite tracked birds is that we have slightly overestimated mortality because some cases of probable death have in fact been due to transmitter failures. Note that the group of 'probable deaths' has the largest sample size in our analyses (41 out of 51 cases of deaths). Even if a few cases of transmitter failure have erroneously been included among the cases of probable deaths, we believe that our results of mortality differences between seasons and regions are robust since transmitter failures are most likely randomly distributed.

Conclusions

Our study shows that satellite tracking can provide new and fascinating information about where and when mortality occurs in migrating birds. Satellite telemetry possibly is one of the best tools currently available to study patterns in mortality, not only in birds but also other animals that embark on long-distance travels such as marine turtles (e.g. Hays *et al.* 2003). Our results strongly suggest that events during the migration seasons have an important impact on population dynamics among long-distance migrants, as was earlier suggested on the basis of indirect evidence in a songbird (Sillett & Holmes 2002). In addition, our results provide support for the suggestion that mortality during spring migration may account for short-term annual variation in survival and population sizes, while mortality during autumn migration may be more

important for long-term population regulation (through density dependent effects). However, this is very speculative and further research on factors causing annual variability in mortality, and the role of density dependency and interseasonal delay effects on migration-related mortality are required in order to understand the full complexity of population regulation in long-distance migrants (cf. Ratikainen *et al.* 2008). Furthermore, it remains to be shown more generally whether the association between mortality and migration, as demonstrated for one species of songbird (Sillert & Holmes 2002) and for the three raptor species in this study, is a common pattern for migratory birds and migrating animals in general.

Further progress in this field would require data on mortality patterns for a larger variety of species (birds and other taxa). Among migratory birds, it would be particularly interesting to obtain data for species with different life-history characteristics and migration strategies than raptors, for example small nocturnal migrants such as songbirds. However, this would require the development of a smaller tag to record mortality events ('mortality tag') as current satellite transmitter models are too large to track small songbirds. In addition, smarter tags, providing information about why animals die, would be a revolution for this field as we currently have no idea about the exact causes for the observed mortality events.

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