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Animal behaviour

How hazardous is the Sahara Desert crossing for migratory birds? Indications from satellite tracking of raptors

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We investigated the risk associated with crossing the Sahara Desert for migrating birds by evaluating more than 90 journeys across this desert by four species of raptors (osprey Pandion haliaetus, honey buzzard Pernis apivorus, marsh harrier Circus aeruginosus and Eurasian hobby Falco subbuteo) recorded by satellite telemetry. Forty per cent of the crossings included events of aberrant behaviours, such as abrupt course changes, slow travel speeds, interruptions, aborted crossings followed by retreats from the desert and failed crossings due to death, indicating difficulties for the migrants. The mortality during the Sahara crossing was 31 per cent per crossing attempt for juveniles (first autumn migration), compared with only 2 per cent 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, demonstrating that this passage has a profound influence on survival and fitness of migrants. Aberrant behaviours resulted in late arrival at the breeding grounds and an increased probability of breeding failure (carry-over effects). This study also demonstrates that satellite tracking can be a powerful method to reveal when and where birds are exposed to enhanced risk and mortality during their annual cycles.

Keywords: avian migration; barrier crossings; carry-over effects; mortality

1. INTRODUCTION

Bird migration may be associated with considerable costs in terms of mortality and detrimental effects on body condition and seasonal timing that carry over to reduce fitness after the migratory journeys (reviewed by Newton 2008). There exist very few studies reporting estimates of migration-related mortality but these studies suggest that migration has indeed a great impact on the birds' annual survival (Sandercock & Jaramillo 2002; Sillett & Holmes 2002; Newton 2008).

The Sahara Desert is a formidable barrier in the Palaearctic-African migration systems where

thousands of millions of birds cross vast areas devoid of food resources and with a challenging climate (Moreau 1972; Newton 2008; Hahn *et al.* 2009). It covers between seven and nine million square kilometres and the shortest distance across the desert is about 1500 km (Moreau 1972). The harshness of the desert, low probability of finding prey and high risk of dehydration certainly affect survival of migrating birds. This is aggravated by strong winds, creating dust storms which have dramatically increased in frequency since the late 1950s (Goudie & Middleton 2006; Niang *et al.* 2008).

In order to investigate possible difficulties and hazards for avian migrants crossing this geographical barrier, we have evaluated migratory journeys across the Sahara Desert made by raptors recorded by satellite telemetry. In contrast to songbirds that mainly cross Sahara during night and rest during day (e.g. Biebach 1990; Schmaljohann et al. 2007), raptors migrate mainly during daytime (e.g. Hake et al. 2003; Klaassen et al. 2008; Strandberg et al. 2008). We have identified events of aberrant behaviour, aborted crossings and failed crossings due to death, for both adult and juvenile birds. The proportions of journeys with different types of aberrant behaviour and with failed crossings will indicate, when evaluated in the light of the raptors' total annual survival rate, whether the Sahara crossing has a significant impact on fitness and survival of long-distance avian migrants.

2. MATERIAL AND METHODS

We used data from four raptor species (osprey, honey buzzard, marsh harrier and hobby) tracked by satellite telemetry between Sweden and tropical Africa on autumn and spring migration during the period 1995–2009 (for methods see Hake *et al.* 2001, 2003; Klaassen *et al.* 2008; Strandberg *et al.* 2008; Strandberg *et al.* 2009). We investigated tracking segments across the Sahara Desert primarily in the latitudinal range of 17.0°–30.0°N.

We defined the following cases of aberrant behaviour:

- (1) Distinct course change. A deviation more than 45° from the overall track direction (calculated from start to end of the desert crossing), measured over a flight distance of more than 100 km and during a day or more.
- (2) Slow travel speed. Speeds less than 10 km h⁻¹ during diurnal migration, measured over a more than 5 h period between the hours of 09.00 and 17.00.
- (3) Interruption of active migration. A stop of more than 1 h (recorded within daily flight sessions) or, for tracks with few locations, a very slow speed (less than 50 km for a day or more), during diurnal hours.
- (4) Aborted crossing and retreat migration. If a bird made a return flight out of the desert area.
- (5) Failed crossing and death. When a bird most probably succumbed in association with a failed crossing attempt, either in the desert or after a retreat flight. The death of a bird was evident from the transmitter's activity sensor and from stationary locations in all cases (verified by field observations at breeding sites; see below).

Cases when birds stopped at possible feeding habitats such as oases and temporary river systems and when birds made return trips before entering the desert were not included in the analyses.

We also conducted field studies at the breeding sites to verify the return or failure to return and to record whether breeding was successful or not for all ospreys and marsh harriers after their annual journeys by visiting nest sites regularly in summer. Breeding site fidelity is very high among adult ospreys and marsh harriers (M. Hake & R. Strandberg 1995–2009, unpublished data), and field observations (independent of tracking data) at breeding sites confirmed the survival of all birds returning with active transmitters and also of several birds whose transmitters had stopped working under circumstances which did not indicate death.



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Table 1. Occurrence of aberrant behaviours, retreat migration and deaths of raptors during migration across the Sahara Desert, as recorded by satellite telemetry. For definitions of cat. 1–5, see §2. Figures show number of tracks, with number of individuals given in parentheses (several adult individuals were recorded on repeated autumn and spring migration).

	age	n tracks (birds)	mean track direction (degrees)	n without aberrations	n with aberrations cat. $1-4$	course change cat. 1	slow speed cat. 2	interruption cat. 3	retreat	death cat. 5
autumn										
osprey	adult	24(14)	200	18(13)	6(4)	5(3)	3(3)	3(3)	2(1)	0
	juv	4(4)	191	2(2)	2(2)	2(2)	1(1)	0	1(1)	1
honey buzzard	adult	6(6)	189	4(4)	2(2)	0	2(2)	2(2)	0	0
	juv	7(7)	200	4(4)	3(3)	1(1)	3(3)	2(2)	0	1
marsh harrier	adult	16(9)	206	6(5)	10(7)	9(7)	7(6)	7(6)	0	0
hobby	adult	4(4)	197	3(3)	1(1)	1(1)	1(1)	0	0	0
	juv	2(2)	212	1(1)	1(1)	1(1)	1(1)	1(1)	0	2
total autumn		63(46)	200	38(32)	25(20)	19(15)	18(17)	15(14)	3(2)	4
spring										
osprey	adult	17(10)	17	12(9)	5(4)	3(3)	2(2)	1(1)	0	0
marsh harrier	adult	15(8)	11	7(4)	8(6)	6(5)	7(5)	6(5)	2(2)	2
total spring		32(18)	14	19(13)	13(10)	9(8)	9(7)	7(6)	2(2)	2
total		95(46)	_	57(33)	38(25)	28(18)	27(21)	22(18)	5(4)	6

3. RESULTS

The overall mean distance, duration and speed for 90 completed Sahara crossings made by 43 individuals of the four species were $1607 \pm 250 \text{ km}$ (mean \pm s.d.), 6.5 ± 2.4 days and $269 \pm 74 \text{ km d}^{-1}$, respectively (including a juvenile hobby which perished at the southern desert border).

Out of 95 tracks recorded for 46 different individuals, 25 tracks in autumn (40%) and 13 in spring (39%) showed aberrant behaviour of types 1-4 (table 1).

During five travels made by four individuals, crossings were aborted and retreat migrations occurred (figure 1). A total of six birds died in the southern parts of Sahara (figure 1). Four of these were birds on their first autumn migration, corresponding to a mortality rate of 31 per cent per crossing for juveniles. Three of these birds showed westward flights, which may have been downwind escape flights, prior to death.

The mortality rate was much lower for adults with only two fatal cases out of 82 crossings (2% mortality). The difference in mortality rate between juveniles and adults was statistically significant (Fisher exact test: p = 0.003). The two cases of adult mortality occurred on spring migration which may indicate that this is the most critical season for adults. However, sample sizes are too small to allow any firm conclusions (Fisher exact test: p = 0.15).

Breeding success of returning birds indicate that difficulties associated with the Sahara crossing may have carry-over effects. Combining the results of breeding success for ospreys (14 cases) and marsh harriers (13 cases), we recorded a breeding success rate of only 10 per cent for birds that showed aberrant behaviour during spring migration (10 cases), compared with 53 per cent success for birds without aberrations (17 cases, Fisher exact test: p = 0.031). Part of this difference may be associated with delayed arrival

among birds showing aberrant behaviour during the Sahara crossing, with 70 per cent (seven cases) arriving after the species-specific median arrival date (9 April for marsh harriers and 15 April for ospreys), while only 29 per cent (five cases) of birds not showing any aberrations arriving after the median arrival date (Fisher exact test: p = 0.049).

4. DISCUSSION

(a) Difficulties during the Sahara crossings

Our results show that migrating raptors often encountered difficulties during the Sahara crossings, causing abrupt changes in flight courses or very slow progress. Some of the birds even interrupted their crossings during diurnal hours. According to where these events occurred, it seems unlikely that interruptions were related to foraging events (cf. §2 and Klaassen et al. 2008). Instead, the aberrant behaviours may have been caused by adverse weather conditions, in particular severe headwinds and dust storms. Retreat migration out of the desert seems to be an extreme response to difficulties during crossings (recorded at six occasions, on five trackings, figure 1, table 1). It is nevertheless a behaviour that may cause delayed arrival at the wintering and breeding grounds and even exhaustion and death.

Birds showing aberrant behaviours in the Sahara Desert during spring migration had a significantly lower breeding success than birds that showed no aberrant behaviour, and this seemed, at least partly, to be explained by late arrival of failing birds. These carry-over effects in the complex annual cycle of migratory birds have attracted increased attention as being of critical importance for understanding the population ecology of migrants (e.g. Marra *et al.* 1998; Newton 2008), and satellite tracking may be a powerful tool to reveal the mechanisms for effects on an individual

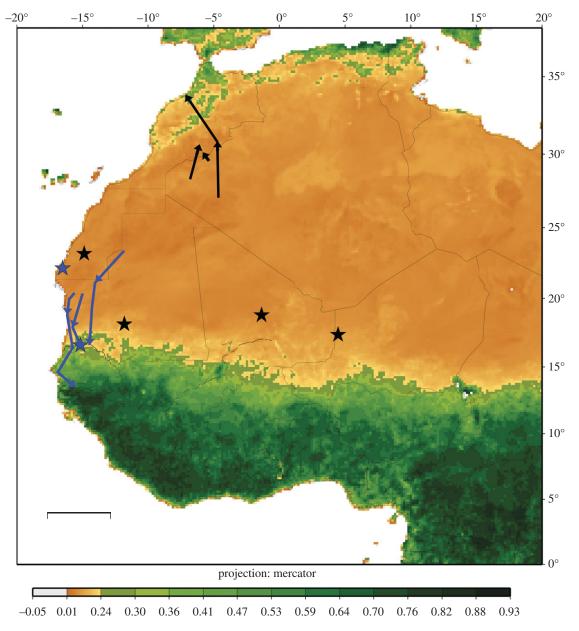


Figure 1. Retreat migration (arrows, n = 6) and locations of deaths of migrating raptors (stars, n = 6) crossing the Sahara Desert. Note that a male harrier retreated twice during the same spring (thus, number of tracks with retreats = 5). Black and blue symbols refer to autumn and spring, respectively. Map colours indicate the normalized difference vegetation index (NDVI) for October 2006 (scale bar, 500 km).

level (see also Alerstam *et al.* 2006). Such carry-over effects may have an important influence on fitness of birds, which is supported by the results obtained in this study.

Nevertheless, it is not straightforward to evaluate carry-over effects on breeding success from migration behaviour of a single bird, as we have to consider both birds in a breeding pair with different migration histories. Furthermore, there are other factors acting on the breeding result, as disturbance, predation, bird's general condition and age, weather condition and prey situation in breeding territory.

(b) Mortality

The total annual mortality rates among the raptor species in this study have been estimated at 50-60% for first year birds and 15-30% for adults (Cramp &

Simmons 1980; Fransson & Pettersson 2001). This implies that mortality associated with the Sahara crossings contributes significantly to the total annual mortality, amounting to about half of the total mortality among juveniles.

We found a significant difference in mortality between adults and juveniles during the desert crossing. This is not surprising, as juvenile raptors on their first migration journey are inexperienced and more vulnerable to weather conditions than adults (Newton 2008).

(c) Conclusion

About 5000 years ago, most of western Sahara was covered by extensive areas of Mediterranean scrub and dry woodland (Moreau 1966). The development of this area, now almost devoid of vegetation, must

have had a profound impact on the evolution of migratory strategies among *trans*-Saharan migrants to meet increasing difficulties associated with crossing of the expanding desert. The issue of desertification and climate change at the Sahara borders is controversial with contrasting indications of e.g. increasing dust storm frequencies during recent decades (Goudie & Middleton 2006) but no clear overall signs of desert expansion (Tucker *et al.* 1991). However, a further expansion of the Sahara Desert will probably have serious consequences for the *trans*-Saharan migrants given the current difficulties associated with this passage, as demonstrated in this paper.

Death in the desert is not the single most important source of mortality during migration. In fact, a similarly large proportion of travelling birds die in the Mediterranean region, partly because of illegal hunting (e.g. Panuccio 2005). This is supported by the many raptors tracked within our project disappearing in this area (Strandberg *et al.*, unpublished data). Although desertification and climate change are of great concern for migrating birds in general, reduced hunting pressure is also important for conservational work to improve the future prospects for migrating raptors as well as other birds.

The study was approved by the Ethical Committees in Uppsala (C92/6) and Malmö/Lund (204-06), with permission to capture the birds from the Swedish Environmental Protection Agency (412-429-05 Nf).

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