The exploration of animal migration has entered a new era with individual-based tracking during multiple years. Here, we investigated repeated migratory journeys of a long-distance migrating bird, the marsh harrier *Circus aeruginosus*, in order to analyse the variation within and between individuals with respect to routes and timing. We found that there was a stronger individual repeatability in time than in space. Thus, the annual timing of migration varied much less between repeated journeys of the same individual than between different individuals, while there was considerable variation in the routes of the same individual on repeated journeys. The overall contrast in repeatability between time and space was unexpected and may be owing to strong endogenous control of timing, while short-term variation in environmental conditions (weather and habitat) might promote route flexibility. The individual variation in migration routes indicates that the birds navigate mainly by other means than detailed route recapitulation based on landmark recognition.

**Keywords:** avian migration; satellite-tracking; repeatability; routes; timing

1. INTRODUCTION

The study of long-distance migration is currently experiencing a rapid growth of individual-based tracking data of increasing coverage during multiple years and journeys [1]. Examples of repeated migratory journeys have recently been provided by a white stork *Ciconia ciconia* [2], a lesser spotted eagle *Aquila pomarina* [3], two black storks *Ciconia nigra* [4], five black-necked cranes *Grus nigricollis* [5] and seven ospreys *Pandion haliaetus* [6]. This opens up the possibility of analysing the spatial and temporal variability and the scope of flexibility in individual migratory behaviour. To date, repeatability estimates of migratory schedules have been based on observations and recaptures of marked individuals at breeding or wintering locations [7–14]. However, these studies only provide snapshots about repeatability throughout the annual cycle.

Here, we analyse the spatial and temporal variation of repeated migratory journeys by adult marsh harriers *Circus aeruginosus* along the whole migratory route. Our study is the first, to our knowledge, to present a strictly comparable analysis of repeatability in routes and timing of animal migration, assessing the variation within and between individuals. This allows us to explore current hypotheses about route recapitulation (as shown for homing pigeons *Columbia livia* [15]) and consistent migratory schedules (as shown for bar-tailed godwits *Limosa lapponica baueri* [13]) for a long-distance migrant.

2. MATERIAL AND METHODS

We used data from seven adult marsh harriers tracked by satellite telemetry (18 g PTT-100 or 22 g ARGOS/GPS PTT-100, Microwave Telemetry Inc.) between Sweden and West Africa during 2004–2009, which made at least one migratory round-trip (see [16,17] for further technical details). The complete dataset consists of 32 tracks, 19 autumn and 13 spring journeys (electronic supplementary material, table S1).

For each track, we determined the longitudes and dates at which latitudes between 54°N and 18°N (each 2° of latitude) were crossed. However, for the present analysis, we selected only the values corresponding to the latitudes 46°N, 36°N and 26°N. The three points are considered to represent independent measures of timing and routes for the crossing of different geographical regions: Europe, Mediterranean Sea and Sahara desert, respectively.

Longitudes and dates (expressed as the difference between the actual and the mean date of all tracks by all individuals for a given season and latitude) were explored by ANOVA with season and individual as factors. Additionally, repeatabilities (r) (intra-individual correlation coefficient) [18] of longitude and date were calculated for the three birds with at least two round-trips (12 autumn and nine spring journeys). Both analyses were repeated using the mean longitudes and dates at the three latitudes. Details of statistical results are given in the electronic supplementary material, tables S2 and S3. Repeatabilities were also determined at each 2° of latitude (54°N–18°N) in order to inspect the variation in repeatability along the entire migration corridor (electronic supplementary material, figure S1).

3. RESULTS

Migration occurred along a relatively well-defined corridor (figure 1a) (see also [16]). The individual effect on longitudinal variation was small in all main regions, and also after averaging it (table 1 and figure 2a). A strong seasonal effect was present, however, in the Mediterranean and Sahara, reflecting the loop migration observed in this population [17]. A significant interaction individual × season at Sahara suggests that different individuals made different, repeatable loops.

In contrast to space, dates differed significantly among individuals in all main regions (table 1 and figure 2b). Timing presented a seasonally distinct pattern with a larger within-individual variation in autumn than in spring (figure 1b,c).

Repeatabilities revealed a similarly clear contrast; r-values for longitudes were generally lower than for dates (table 2 and electronic supplementary material, figure S1). Closer inspection of repeatabilities along the migration corridor revealed that the highest levels of route repeatability occurred in the Mediterranean region during autumn, and that repeatability in timing was clearly reduced during the second part of spring migration, north of 34° N. Very high repeatabilities were calculated for the spring Sahara crossing, where individuals passed within the same 1–4 day period each year. Spring departure (18°N) had the same high consistency level (figure 1c).

4. DISCUSSION

Variation in routes has previously been demonstrated for individual ospreys [6], but this within-individual variation was not analysed in relation to between-individual
variation to show true repeatability. Although our dataset is rather small, such first glimpses at the degree of individuality in avian migration are worthy of attention. The marsh harriers occasionally repeated parts of their journeys, but there was a notable variation in routes within individuals, and thus no detectable general differences in routes between them. Variation in routes is also reflected in low repeatabilities for longitudes, except in the Mediterranean region, partly because individuals tended to use specific stopover sites (although not presented here) prior to sea-crossing between 40° N and 38° N (r-values peak at 40° N; electronic supplementary material, figure S1). This pattern of overall low route repeatability combined with revisited sites used on previous journeys implies that birds navigate by other means than detailed route recapitulation via landmark recognition throughout.

Figure 1. Satellite tracking data of seven adult marsh harriers with at least one migratory round-trip during 2004–2009. Dashed lines show the latitudes selected (46° N, 36° N and 26° N) to extract longitudes and dates to be used as variables. (a) Migration routes of autumn (solid lines) and spring (dotted lines) journeys; (b,c) temporal patterns of latitudinal movement for autumn and spring journeys, respectively. Autumn departure of M3 is omitted because it spends the summer in sites at 50° N. Brown lines, F1; red lines, F2; blue lines, F3; green lines, M1; yellow lines, M2; black lines, M3; orange lines, M4. F, females; M, males.

Figure 2. (a) Longitudes and (b) relative seasonal dates for spring and autumn migrations of seven adult marsh harriers. Values presented are the mean for the crossings of the latitudes 46° N, 36° N and 26° N. Blue triangles, autumn; red circles, spring.
the whole journey. The individual spatial flexibility demonstrated here contrasts with experimental evidence of route recapitulation by homing pigeons released a few kilometres away from the loft [15]. However, it should be noted that this route recapitulation only emerged after extensive training. On the other hand, the harriers had completed their journey at least once before captured and we observed no tendency towards increasing route similarity with successive journeys (Y. Vardanis 2010, unpublished MSc thesis).

We could speculate that route flexibility in long-range migration allows responses to critical factors like wind conditions, availability of suitable stopover sites and physical condition that change between years and regions. Such flexibility in route choice must be of much less potential adaptive value for movements over short distances and durations, e.g. by homing pigeons. In agreement with this idea is the suggestion that short-term environmental variability, rather than distance minimization and route fidelity, shapes the routes of the dark-bellied brent goose Branta bernicla bernicla [19].

In contrast with space, between-individual variation in timing was significant for all main regions. This supports the hypothesis that birds may have individually optimized migration schedules [13]. Battley [13] recorded a high repeatability of the spring departure date \( (r = 0.83) \) for adult bar-tailed godwits. Similarly high repeatabilities were found for the onset of spring and autumn migration in this study (see also the electronic supplementary material, figure S1), but values varied across the different geographical regions. Such variation can be expected if conditions en route (weather and habitat) affect the progress of migration. This idea has been invoked to explain different phenological patterns at different latitudes in population- [20,21] and individual-based [22] studies. A larger within-individual variation in timing in autumn is explained by variable annual breeding success [16]. Interestingly, the order in which the birds departed was approximately the same for spring and for autumn (figure 1b,c), suggesting that the individual harriers migrate according to individual time schedules [23].

Empirical evidence suggests that repeatability often reflects heritable differences [9]. However, long-lived animals can give transient positive repeatability during short-term studies [24]. Furthermore, the high repeatability of spring departure dates could be parsimoniously explained by area-specific climatic and social effects, rather than by genetic variation among individuals.

To explain why marsh harriers are more flexible in space than in time, we may have to consider the predictability of the relevant environmental cues. Efficient long-distance navigation between the fixed breeding and wintering locations may permit a high degree of adaptive route flexibility in relation to unpredictable conditions en route. By contrast, photoperiod, an entirely predictable ‘Zeitgeber’ for migration (cf. [25]), as well as favourable, area-specific ‘climatic windows’ may contribute to highly repeatable individual schedules. Focusing on the spatial and temporal variability and the ways in which it can be correlated with environmental conditions can further our understanding about the scope of flexibility in migratory behaviour.

The study was approved by the ethical committees in Uppsala (C92/6) and Malmö/Lund (204-06).

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