

RESEARCH ARTICLE

Orientation of native versus translocated juvenile lesser spotted eagles (*Clanga pomarina*) on the first autumn migration

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ABSTRACT

The ontogeny of migration routines used by wild birds remains unresolved. Here we investigated the migratory orientation of juvenile lesser spotted eagles (LSE; *Clanga pomarina*) based on translocation and satellite tracking. Between 2004 and 2016, 85 second-hatched juveniles (Abels) were reared in captivity for release into the declining German population, including 50 birds that were translocated 940 km from Latvia. In 2009, we tracked 12 translocated juveniles, as well as eight native juveniles and nine native adults, to determine how inexperienced birds come to use strategic migration routes. Native juveniles departed around the same time as the adults and six of eight used the eastern flyway around the Mediterranean, which was used by all adults. In contrast, translocated juveniles departed on average 6 days before native LSEs, and five travelled southward and died in the central Mediterranean region. Consequently, fewer translocated juveniles (4/12) than native juveniles (7/8) reached Africa. We conclude that juvenile LSEs have a much better chance of learning the strategic southeastern flyway if they leave at an appropriate time to connect with experienced elders upon departure. It is not clear why translocated juveniles departed so early. Regardless, by the end of the year, most juveniles had perished, whether they were translocated (10/12) or not (6/8). The small number of surviving translocated juveniles thus still represents a significant increase in the annual productivity of the German LSE population in 2009.

KEY WORDS: Bird migration, Orientation, Satellite-tracking, Translocation

INTRODUCTION

The advent of satellite telemetry and GPS tracking sparked a new age of discovery in animal ecology (Kays et al., 2015). This is especially true for the study of bird migration (Bridge et al., 2011;

Robinson et al., 2010; Wikelski et al., 2007). Tracking entire cross-continental or oceanic journeys of migrant birds has revealed that migrants often adhere to highly complex migration itineraries, which may differ greatly between individuals from the same species or population (Åkesson and Hedenström, 2007; Thorup et al., 2010; Vardanis et al., 2016). Complex migration routines, sometimes requiring accurate navigation toward crucial stop-over and staging sites, may be explained to some extent by relatively simple, genetically determined migration programs that involve one or more bouts of vector-based navigation (Berthold and Terrill, 1991; Mouritsen and Mouritsen, 2000), and some simple behavioural rules, such as aversion to crossing open water and other barriers (Erni et al., 2003; Hake et al., 2003; Kerlinger, 1985; Meyer et al., 2000; Thorup et al., 2003). Such simple mechanisms may be particularly relevant for nocturnally migrating passerines and other solitary migrants. For other migrants, however, including large diurnal migrants such as soaring birds, social learning is likely to play a much more important role. Species such as cranes (*Grus* sp.), white stork (*Ciconia ciconia*), Egyptian vulture (*Neophron percnopterus*), lesser spotted eagle (LSE; *Clanga pomarina*), short-toed eagle (*Circaetus gallicus*) and European honey buzzard (*Pernis apivorus*) all depend on guidance by elders to locate strategic flyways or important stop-over sites (Chernetsov et al., 2004; Hake et al., 2003; Mellone et al., 2011; Meyburg et al., 2016; Rotics et al., 2016; Schüz, 1950). It is likely that most birds use a combination of innate vector-based (or more complex) orientation programs and social information, as well as multiple additional cues to facilitate accurate navigation early in life (Åkesson and Hedenström, 2007; Thorup et al., 2010; Wiltschko and Wiltschko, 2015). As Thorup et al. (2010) argued: ‘how else could one account for the complex routes, such as those used by juvenile Eleonora’s falcons *Falco eleonora* travelling to a restricted wintering range in Madagascar, in the absence of experienced elders (Gschweng et al., 2008)?’ However, besides cranes and geese, most social migrants do not travel in family groups, and so it remains unclear how long after dispersal it takes for naive juveniles to encounter elder conspecifics, what they do in the absence of elder guides and how social learning affects their survival.

Outside of the laboratory, the best way to empirically study the role of innate versus external influences on migratory behaviour is through displacement or delayed-release experiments (Perdeck, 1958; Schüz, 1950). Few migratory behaviour studies of displaced birds have been performed using tracking devices (Chernetsov et al., 2004; Thorup et al., 2010; Wikelski et al., 2015; Willemoes et al., 2015). Moreover, very few tracking studies have been conducted on juvenile migrants because naturally higher juvenile mortality rates mean that young birds are likely to die shortly after they are fitted with an expensive transmitter, and also because transmitters may affect juveniles relatively more than adults. So far, juvenile tracking studies have mostly been conducted on large soaring birds, and

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although in some species juveniles travel faster than adults (Rus et al., 2017), juveniles from wild populations are usually outperformed by adults (Rotics et al., 2016; Sergio et al., 2014), migratory performance improves with age (Sergio et al., 2014) and juveniles are often guided by elders to migrate (Mueller et al., 2013; Oppel et al., 2015; Rotics et al., 2016; Sergio et al., 2014). In the absence of displacement or delayed-release experiments on juvenile birds, however, it is impossible to disentangle the relative influence of innate behaviours from social information in the development of migratory repertoires in individual birds from natural populations (Muriel et al., 2016; Senner et al., 2015). This knowledge gap must be addressed to develop a comprehensive ontogenetic perspective on migratory orientation (Guilford et al., 2011; Senner et al., 2015; Thorup et al., 2010) and concomitant patterns of migratory connectivity (Cresswell, 2014; Trierweiler et al., 2014), in addition to determining how migration affects population numbers (Hewson et al., 2016; Newton, 2006). A better understanding of migratory development could also help to identify conservation priorities in the annual cycle and life cycle of migrant birds (Hostetler et al., 2015; Vickery et al., 2014).

The present study aimed to determine how translocation affects the route choice of juvenile LSEs (*Clanga pomarina* Brehm 1831) (Lerner et al., 2017) during the first autumn migration. In 2009, 20 solar-powered Argos GPS platform transmitter terminals (PTTs, 22 g) were deployed on juvenile eagles. Twelve of these juveniles were second-hatched juveniles from Latvia that were reared in captivity (hereafter ‘hacked’, see Materials and methods) and translocated approximately 940 km southwestward to supplement the declining population in Brandenburg, Germany. The other eight juveniles were reared in the wild in northeastern Germany. Moreover, of 48 adult LSEs that were tracked since 1994 (Meyburg et al., 1995, 2004a), 10 adults that bred in Germany were still transmitting in 2009. Consequently, for that year, we were able to compare the migration timing and route choice of translocated juveniles, native juveniles and native adults. The eagles were tracked primarily to monitor the effectiveness of hacking and translocation as a conservation measure (Graszynski et al., 2011; Meyburg et al., 2008). Our focus here, however, is to derive fundamental insights from this quasi-experimental study into the factors driving decision-making in a juvenile soaring migrant.

Being among the largest Palearctic soaring migrants, LSEs are especially vulnerable to exhaustion when forced to travel by flapping flight, such as during long overwater flights (Bildstein et al., 2009; Oppel et al., 2015). Consequently, most of the LSE population avoids sea crossings, and migrates over land by thermal soaring (Kerlinger, 1985; Meyburg et al., 2002). Most LSEs that make successful autumn migrations travel along the eastern Mediterranean flyway, from the Bosphorus to Suez and along the Great Rift Valley into central and southern Africa (Bijlsma, 1983; Leshem and YomTov, 1996; Meyburg et al., 1995, 2008; Michev et al., 2011). The use of this eastern migration route is a highly conserved trait in the migration of the LSE, as evidenced by the fact that all adult LSEs that have ever been tracked for more than 1 year (48 individuals), including individuals that were tracked for up to 11 consecutive years (Meyburg et al., 2004a, 2015), used the eastern route every autumn and spring. A small number of adult and juvenile LSEs do migrate along southwestern and southern flyways via the Strait of Gibraltar (Onrubia et al., 2011) or the Strait of Sicily between Italy and Tunisia (Thiollay, 1975; Dejonghe, 1980; Giordano, 1991).

Some juvenile migrant birds are able to compensate for extremely large displacements resulting from either natural causes, such as

extreme weather, or unnatural causes, such as experimental interventions (Thorup et al., 2011). True goal navigation, however, is far more common among adult migrants (Perdeck, 1958), and even such experienced individuals may elicit highly variable responses to displacement (Willemoes et al., 2015), in some cases failing to compensate at all (Kishkinev et al., 2016). Therefore, we did not expect translocated juveniles to compensate for their displacement either by returning to their natal site or by compensatory goal navigation towards the southeastern flyway. Instead, we expected that both translocated and native juveniles would locate the southeastern flyway using social information (Chernetsov et al., 2004; Schüz, 1950). Because Germany is situated at the western limit of the species’ range, and because very few adults breeding to the north and further east pass through this peripheral population on migration, native adults (and non-breeding immatures) should be the main providers of social information for juveniles departing from our study population (Oppel et al., 2015). Therefore, we expected that both translocated and native juveniles would be more likely to learn the eastern route if they departed simultaneously with native elders.

Juveniles that fail to synchronize their departure with elders likely rely on innate, vector-based orientation to find their way to sub-Saharan Africa (Thorup et al., 2003). Although LSEs frequently migrate in mixed-age groups, they do not seem to migrate in family groups (Meyburg and Meyburg, 2007; B.-U.M. and C.M., unpublished data); family group migration is also not a characteristic of other raptor species such as the closely related greater spotted eagle (*Clanga clanga*; Meyburg et al., 2005). Consequently, to maximize the opportunities to learn the route via the Bosphorus and Suez, the juveniles should time their departure to coincide with the departure or passage of adult LSEs, and their innate departure directions should be oriented from the natal area toward the southeastern flyway. We did not expect a difference in timing of departure between native and translocated juvenile LSEs, but we predicted that if translocated and native juveniles departed much earlier or later than adults, they would default to southward and eastward–southeastward departure directions, respectively. As a consequence, translocated juveniles would likely end up in the central Mediterranean flyway if they failed to connect with native adults upon departure (Meyburg et al., 1995, 2008). Given that heavy soaring birds often perish when they attempt long sea crossings (Bildstein et al., 2009; Mellone et al., 2011; Oppel et al., 2015), the failure of translocated juveniles to locate and follow elder guides using the southeastern flyway could constrain the effectiveness of translocation and hacking in reinforcing the declining LSE populations in Germany and elsewhere.

MATERIALS AND METHODS

Lesser spotted eagles in Germany

The LSE is a large soaring raptor and long-distance migrant that breeds in moist woodlands from central Europe to western Russia (Ferguson-Lees and Christie, 2006; Meyburg et al., 2001, 2016). Since 1992, we have tracked 95 LSEs via satellite. The large majority of tracked LSEs leave Europe in September, and all adults use the eastern Mediterranean flyway via the Bosphorus and Suez en route to Africa. A few thousand adults and immatures breeding in the eastern part of the range migrate along the eastern Black Sea flyway. These two routes converge over Turkey and Syria as LSEs travel toward Suez. Few LSEs cross the Mediterranean through the Straits of Gibraltar and via Sicily (Agostini et al., 2004; Onrubia et al., 2011; Giordano, 1991); these flyways are clearly of minor importance compared with the southeastern flyway.

Saving Abel: nestling management for conservation

The western limit of the species' breeding range lies in Germany, where a small population persists despite a major population decline from the 1990s to the 2000s (133 pairs in 1993 to 107 pairs in 2007, 23% decline; Meyburg et al., 2004b, 2008). Since 2001, the breeding population of LSE in the main German stronghold in Mecklenburg-Vorpommern has declined from 92 to 87 breeding pairs (LUNG, 2016). Because the LSE is red-listed in Germany (Grüneberg et al., 2015; Vökler et al., 2014), an action plan was developed to conserve it nationally, including habitat protection measures complemented by a population recovery program (Meyburg et al., 2004b; MLUV, 2005).

LSEs typically lay two eggs, both of which usually hatch. Under natural conditions, however, the second-hatched juvenile is killed by the first-hatched, a process referred to as obligate siblicide or 'Cainism' (after the biblical Cain and Abel struggle; Meyburg, 1974, 2002). Removing the second-hatched chicks before they are killed, rearing them in captivity and then releasing them can be a way of supplementing native productivity, and may help to halt population declines (Meyburg, 1978). Such a program of conservation-focused nest management has been implemented by the 'Saving Abel' project in Germany since 2004 (Meyburg et al., 2008; Graszynski et al., 2011), and between 2004 and 2016, 85 Abels were released in the German state of Brandenburg (Graszynski et al., 2011; B.-U.M. and C.M., unpublished data). This intervention increased the number of birds that fledged from the Brandenburg population by 55.9%, during a time period when only 144 juveniles fledged in the wild. Of these 85 birds, 35 individuals were taken from eyries in Brandenburg, and 50 were translocated from eyries in the core breeding range of LSE in Latvia, some 940 km to the northeast. Most Abels were sourced from populations in Latvia owing to the limited size of the Brandenburg population (ca. 20 pairs; Langgemach et al., 2010).

Translocating and releasing juvenile eagles

The Abels taken from Latvian eyries were initially reared near their natal sites, then transferred to the Riga Zoo until they reached approximately 5 weeks of age, and then flown to Berlin and taken to a release station (53°N, 13°30' E) in the UNESCO-biosphere reserve of Schorfheide-Chorin in Brandenburg. Until 2008, the Abels were captive-reared until they were old and fit enough to compete for food with a nest mate, then fostered to wild breeding parents. In 2009, so as to avoid potential problems with food provisioning and losses owing to predation, the fostering method of releasing birds was replaced by hacking (Sherrod, 1982; Graszynski et al., 2011; Meyburg et al., 2008). The hacking station was situated within the core breeding area of LSE in Brandenburg and within 100 km of all known nests. Release of hacked juveniles took place in late July to mid-August, 5 to 6 weeks before the onset of autumn migration. The young eagles moved around freely after release, and the vast majority remained in the vicinity of the hacking station, where plentiful food is provided, until they start to migrate (Graszynski et al., 2011; Meyburg et al., 2008).

Hatching date, date of placement in the hacking station, release date and date of departure from the hacking station were recorded for all translocated juveniles (Table S1). For comparison, we recorded fledging dates of wild juveniles in Latvia as determined from nest camera footage ($n=4$). Both translocated and native juveniles were fully grown with fully developed wings at the time that translocated juveniles were released from the hacking station, indicating no delay or advance in physical development of translocated, hacked juveniles versus native juveniles.

Tracking juvenile and adult eagles

We tracked 12 translocated juveniles (Abels) and eight native (wild) juveniles (Cains) in 2009 as they migrated from Germany (Table 1). Deployment of the transmitters took place approximately 1 week before fledging, for both the native and the translocated eagles (Table S1). To understand juvenile behaviour in the context of elder migration strategies, we used tracking data from 10 adult LSEs with active PTTs in 2009 (Table 1), seven of which had already been tracked for several years and three of which were trapped and marked in 2009. For comparison, we included satellite-tracking data of a non-translocated juvenile that fledged from an eyrie in Latvia in 1993 and an adult breeding in Latvia in 1997.

For each bird, we determined the date of departure as accurately as possible based on GPS fixes, complemented by Argos/Doppler fixes (LC 3,2,1, as well as lower quality fixes with coordinates at a bird's nest site or at the hacking station) when there were gaps in the GPS data. Visual examination of the tracks revealed that all birds used one of the previously described flyways to Africa: the southwestern flyway (via Gibraltar), the southern/central flyway (via the central Mediterranean) or the southeastern flyway (via the Bosphorus and Israel). We recorded the longitude and date of passage at three latitudinal thresholds, chosen to reflect three distinct milestones in the first outbound migration: successful departure, completion of migration through Europe, and arrival in Africa after crossing or circumventing the Mediterranean Sea. Finally, based on expert interpretation of the GPS and Argos data, we determined the tracks that ended owing to mortality before 31 December 2009. The causes of mortality of these and other tracked young and adult birds will be discussed in another paper. Here, mortality was confirmed in the field or assumed to be highly likely when tracks ended just before or during crossing of the sea or the Sahara, at known hot-spots for illegal shooting of migrant birds, or if a bird remained stationary for a long period of time before contact was lost.

Analyses

Adult LSEs travelled along highly similar routes, with all individuals using the southeastern flyway. Our main interest was to determine how the origin and timing of migration by juveniles affects the extent to which their migration behaviour diverges from that of the native adults. Thus, we determined the extent to which birds using each of the three flyways differed between translocated juveniles and native eagles using a Fisher's exact test (Freeman and Halton, 1951). We ran ANOVAs to determine whether the date and longitude at departure and at latitudinal milestones differed between translocated and native juveniles, between native juveniles and adults, and between translocated juveniles and native adults, while adjusting for the chosen flyway. Using a log-rank test, we compared survival between groups and between flyways.

The influence of topography and wind conditions at departure

Differences in local topography between departure locations and in weather conditions between the days that eagles departed may drive part of the observed variation in route choice. Therefore, we mapped the routes of all LSEs relative to the topography of the surrounding landscape at departure. In addition, we produced detailed maps to explore the influence of topography on route choice over eastern Europe and eastern Africa.

To detect confounding effects of westward and eastward winds on the longitudinal displacement at departure, we annotated all tracks of birds departing from Germany with the westward/eastward wind component from the NCEP-NCAR reanalysis model (Kalnay

Table 1. Overview of tracking data from 30 lesser spotted eagles in 2009, including date and longitude at departure, date and longitude at three latitudinal milestones (Fig. 2), and date of death, if this occurred in 2009

	Device	Flyway	Departure		Crossing 50°N		Crossing 40°N		Crossing 30°N		Death date (mm-dd)	
			Date (mm-dd)	Longitude (°E)	Date (mm-dd)	Longitude (°E)	Date (mm-dd)	Longitude (°E)	Date (mm-dd)	Longitude (°E)		
Native adults	B23196	SE	–	–	–	–	–	–	–	–	–	
	B36235	SE	09-19	13.98	10-01	30.76	10-01	30.764	10-07	33.48	–	
	B41861	SE	09-17	14.66	09-23	21.27	10-04	34.646	10-09	33.49	–	
	B64614	SE	09-17	15.05	09-21	23.74	09-29	30.412	–	–	10-01	
	B74996	SE	09-12	13.48	09-20	22.07	09-28	29.793	10-05	33.53	–	
	B80936	SE	09-07	13.81	09-10	20.79	09-20	30.269	09-25	32.95	–	
	B83263	SE	09-19	21.35	09-19	21.35	09-27	34.317	09-30	33.03	–	
	B83266	SE	09-19	13.60	09-23	17.96	10-09	30.582	–	–	10-12	
	B84370	SE	09-16	12.10	09-25	25.44	10-07	30.283	10-14	32.16	–	
	B94756	SE	09-26	12.87	10-03	24.35	10-14	32.743	10-24	32.92	–	
Native juveniles	B94737	SE	09-15	13.43	09-23	24.87	09-30	30.721	10-06	33.85	11-04	
	B94738	S	09-21	12.57	09-24	20.79	09-30	20.059	10-06	27.36	–	
	B94742	SW	09-14	13.69	09-18	7.83	09-26	–0.414	10-12	–5.92	10-24	
	B94743	SE	09-21	13.47	09-25	32.69	10-01	30.993	10-09	33.37	–	
	B94744	SE	09-26	13.20	10-04	26.61	10-21	26.464	11-12	33.69	11-27	
	B94747	SE	09-12	13.47	09-20	25.15	09-28	30.072	10-04	33.70	10-25	
	B94748	SE	09-16	13.40	09-21	20.70	09-29	30.159	10-05	33.14	10-27	
	B94749	SE	09-16	13.41	09-23	25.62	09-29	30.102	–	–	09-29	
	Translocated juveniles	B94732	SW	09-10	13.50	09-16	8.27	09-22	3.9488	–	–	09-23
		B94734	SE	09-17	19.57	09-20	24.63	10-06	30.001	10-13	33.70	11-22
B94735		S	09-11	13.50	09-13	15.29	09-28	15.821	–	–	10-12	
B94736		S	09-10	13.49	09-12	13.80	–	–	–	–	09-21	
B94739		SE	09-16	13.28	09-20	17.94	09-26	30.073	10-02	32.73	–	
B94740		S	09-11	13.50	09-15	16.67	–	–	–	–	10-05	
B94741		SE	09-11	13.48	09-18	15.49	09-28	29.897	10-04	33.25	–	
B94745		S	08-20	–	–	–	–	–	–	–	09-02	
B94746		SW	09-11	13.48	09-18	11.15	09-27	–0.244	10-11	–4.38	12-04	
B94750		S	09-11	13.50	09-19	12.94	09-29	16.237	–	–	10-11	
B94751	S	09-11	13.50	09-12	13.25	09-22	8.7673	–	–	09-24		
B94759	SW	09-10	13.49	09-17	8.20	09-25	–0.328	–	–	09-29		

Tracking data of adult B23196 included many large gaps such that departure and passage dates could not be determined, and the bird was excluded from all analyses. Translocated juvenile B94734 left the hacking station on 25 August 2009 and stayed in eastern Poland between 30 August and 17 September 2009, when it started its long-distance migration. Translocated juvenile B94745 departed from Germany exceptionally early, died in Switzerland shortly thereafter, and was therefore excluded from our analyses as a behavioural and statistical outlier.

et al., 1996; Kemp et al., 2012). To do this, we linearly interpolated u-wind components from the 925 mB pressure level (corresponding to an average flight altitude of approximately 700 m) across the 2.5×2.5° NCEP grid to each GPS fix obtained north of latitude 50° N. We then ran generalized linear regression models to determine the relative effect of age, geographic origin (i.e. native versus displaced), and the mean amount of westward/eastward wind experienced north of latitude 50°N on the longitude at which birds crossed latitude 50°N. Next, we separately tested for the influence of westward/eastward side winds on the longitudinal displacement at departure for each group of eagles. In addition, we investigated whether selection of wind conditions could have affected departure timing by plotting departures on a graph of daily wind conditions at 12:00 UTC during September 2009 in eastern Germany (53.5°N, 13.5°E).

Fig. 1 and all analyses presented in Figs S1–S6 and Tables S4 and S5 were produced using the R Language for Statistical Programming (v3.3.0, R Foundation for Statistical Computing, Vienna, Austria). We used the ‘ggplot2’ package to produce Fig. 1 (Wickham, 2009). Figs 2–3, ANOVAs and survival analyses were produced using SAS software (v9.4, SAS Institute, Cary, NC, USA).

RESULTS

All native juveniles and adults and translocated juveniles left Germany. We excluded one adult (B23196; Table 1) from analysis

in this paper because gaps in the data prohibited accurate quantification of the departure and passage timing for this bird. Translocated juvenile B94734 left the hacking station on 25 August 2009, and stopped over in northern Poland from 30 August 2009 until 17 September 2009. We considered this initial displacement as a pre-migratory move, and used 17 September 2009 as the effective departure date (Fig. 1, Table 1). One translocated juvenile, B94745, left the hacking station on 20 August 2009 (Table S1), moved to Switzerland on 28 August 2009 and starved shortly thereafter (confirmed in the field). It is unclear whether this bird was truly in ‘migration mode’ at the time it left Germany. In any case, we excluded the data for this bird from all analyses as a statistical outlier (Fig. 1, Table 1).

Table 2 summarizes the number of birds, their timing and longitude at departure and when they crossed each latitudinal threshold per group within each flyway (see Table S2 for summary statistics across all flyways per group in and Table S3 across all groups per flyway).

Route choice of translocated and native juvenile LSEs

The majority of birds using the southern/central flyway were translocated juveniles, and a three-way Fisher’s exact test (Freeman and Halton, 1951) confirmed a highly significant difference in the proportion of translocated juveniles versus native birds (including native juveniles and native adults) using each of the three flyways