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Movement patterns of the White-tailed Sea Eagle (*Haliaeetus albicilla*): post-fledging behaviour, natal dispersal onset and the role of the natal environment

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Exploratory movements and natal dispersal form essential processes during early life history stages of raptors, but identifying the factors shaping individual movement decisions is challenging. Global positioning system (GPS) telemetry thereby provides a promising technique to study movement patterns on adequate spatio-temporal scales. We analysed data of juvenile White-tailed Sea Eagles *Haliaeetus albicilla* (WTSE) in north-east Germany (n = 24) derived from GPS tracking to extensively analyse movements between fledging and emigration from the natal territory. Our goal was to determine the time point of fledging, characterize pre-emigration movements and the onset of natal dispersal while investigating the influence of the natal environment. WTSE fledged at an average age of 72 days and showed strong excursive behaviour during the post-fledging period regarding the number, distance and duration of excursions, yet with high individual variability. Excursive behaviour did not differ between sexes. On average, WTSE left the parental territory 93 days after fledging. The quantity of excursive behaviour delayed the timing of emigration and WTSE tended to postpone their emigration when foraging water was accessible within the boundaries of their parental territory. The overall results suggest that young WTSE assess the quality of the natal environment via pre-emigration movements and stay in their territory of origin for as long as internal and external conditions allow for it. Our study is one of the first to characterize post-fledging and natal dispersal movements of young WTSE to such an extent and applies modern techniques to understand related movements in relation to the natal environment. The results emphasize the urgent necessity for the extension of currently existing nest protection periods and guaranteeing sustainable management of potential breeding and foraging grounds for WTSE. Ultimately, the results are relevant for all large raptor species sensitive to human-related disturbance, as they support the increasing importance of regulations with spatio-temporal specifications for breeding populations of large raptors in densely human-inhabited areas with increasing alteration of land.

Keywords: natal dispersal, post-fledging period, raptor conservation, satellite telemetry.

INTRODUCTION

Natal dispersal and related movements form a fundamental mechanism for mobile organisms because they affect their individual reproductive fitness, lead to gene flow, and therefore have non-negligible impacts on population dynamics via genetic and demographic linkage in metapopulations (Brooker *et al.* 1999, Clobert *et al.* 2001, 2012, Bowler & Benton 2005).

As movement patterns throughout the natal dispersal process are shaped by an interplay between an individual's internal state and external factors, the causality is complex and potentially comprises combinations of various underlying mechanisms

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(Lambin *et al.* 2001, Bowler & Benton 2005, Clobert *et al.* 2009, 2012, Bonte *et al.* 2012). In general, the dispersal process is accepted to consist of three distinct phases: emigration, transfer phase and immigration into a new site of reproduction (Bowler & Benton 2005). In many raptor species, the onset of natal dispersal, defined as movements between the natal site and sites of reproduction (Greenwood & Harvey 1982), is preceded by extensive exploratory behaviour in the form of excursions. Such movements during the post-fledging period and outside of the natal area but with subsequent return in a relatively short time period have been observed in multiple raptor species and should be given special consideration, e.g. when analysing the point of emigration (Walls & Kenward 1995, Kenward 2006, Cadahía *et al.* 2008, Morrison & Wood 2009, Weston *et al.* 2013).

Many raptor species are characterized by a slow life history with delayed maturity and often occupy a nesting territory over multiple successive years (Steenhof *et al.* 2017). Due to intraspecific competition, recruitment of juveniles to the parental nesting territory is therefore usually not an option and natal dispersal is deeply anchored in their life history (Serrano 2018). Underlying causes and mechanisms by which natal dispersal movements of raptors are shaped have been diversely discussed in the literature, yet identifying patterns remains difficult.

Given the fundamental complexity, much scientific work has been dedicated towards a better understanding of early dispersal movements over the past decades (Clobert *et al.* 2001, 2012, Serrano 2018). Among others, factors such as resource availability, or habitat quality as a proxy (Kenward *et al.* 1993, Kennedy & Ward 2003), sex (Kenward *et al.* 1993, Soutullo *et al.* 2006a, Whitfield *et al.* 2009b), physical and nutritional conditions (Ferrer 1992a, Kennedy & Ward 2003, Delgado *et al.* 2010, Ferrer & Morandini 2017) and weather conditions (Ferrer 1993b, Walls *et al.* 2005) have all been shown to affect early stages of the dispersal process in different large raptor species. Several studies further identified high levels of individual variation in the timing of emigration and natal dispersal distances among raptors (Soutullo *et al.* 2006a, Cadahía *et al.* 2010, Weston *et al.* 2013). With more than half of all raptor species worldwide showing declines in global populations (McClure *et al.* 2018) and high sensitivity to anthropogenic threats (Owens & Bennett 2000, Krone *et al.* 2003), a better understanding of early post-fledging and natal dispersal movements is crucial for the implementation of conservation policies (Morrison & Wood 2009, Serrano 2018). For example, species-specific regulations with spatial and temporal specifications such as nest protection zones (NPZs; e.g. 100 m) over explicit time periods aim to reduce human disturbances, e.g. forestry action or hunting activities, at the level of German states.

Tracking devices can assist in answering conservation-related questions addressing distinct phases of movement in the lifetime of an individual (Nathan *et al.* 2008, Fiedler 2009, Cadahía *et al.* 2010, Urbano *et al.* 2010). However, accurately determining the post-fledging and dispersal characteristics of raptors, e.g. detecting the onset of dispersal, still represents a fundamental challenge and is seldom straightforward, despite various approaches available in the recent literature (Soutullo *et al.* 2006b, Cadahía *et al.* 2008, Weston *et al.* 2013).

Distributed throughout the northern Palaearctic (Fischer 1984, Del Hoyo *et al.* 1994), the White-tailed Sea Eagle *Haliaeetus albicilla* (WTSE) is a large diurnal raptor that inhabits undisturbed areas in forests with access to fish-rich freshwater lakes that offer perching possibilities along the shoreline to increase foraging success (Fischer 1984, Krone *et al.* 2013, Nadjafzadeh *et al.* 2016). So far, knowledge about dispersal in WTSE is very poor, with only a few studies having addressed juvenile dispersal movements in general (Whitfield *et al.* 2009a, 2009b, Balotari-Chiebao *et al.* 2016). To our knowledge, only Balotari-Chiebao *et al.* (2016) primarily described spatial aspects of post-fledging movements of WTSE in detail, yet no quantitative assessment of excursive behaviour and related interplay with the onset of dispersal currently exists.

Therefore, the aim of this study was to analyse post-fledging movements of WTSE using movement data derived from global positioning system (GPS) trackers. We focused on (1) determining the time point of fledging and natal dispersal onset, (2) characterizing excursive behaviour during the pre-emigration period and (3) attempting to determine how both habitat quality of the natal environment and individual behaviour during the post-fledging period shape the timing of natal dispersal onset, aiming to contribute further to a species-specific understanding with respect to future conservation strategies.

METHODS

The study was carried out in North-East Germany (50°58’44.4"–54°13’15.6"N, 9°11’31.2"–14°11’31.2"E), covering the German federal states of Thuringia and Lower Saxony, Brandenburg and Mecklenburg-Western Pomerania (MWP, Fig. 1b), with the two latter areas accommodating the majority of breeding WTSE pairs in Germany (Oehme 1961, Fischer 1984, Hauff 1998).

Focal study regions included the island of Usedom, the Mecklenburg Lake Plateau and Northern Mecklenburg region; these offer highly suitable habitat for breeding and foraging grounds, as they are characterized by immediate proximity to freshwater lakes, running waters or brackish water of the South-West Baltic Sea and are dominated by undisturbed pine, beech and mixed forests.

Seven more breeding pairs were integrated outside of the focal study region in South-East Brandenburg, North-West Thuringia and central/North-East Lower Saxony.

GPS tracking

Between 2004 and 2016, 31 WTSE nestlings were equipped with GPS and global system for mobile communications satellite transmitters in North-East Germany. Devices of three different companies were used:

1 both battery- (*n* = 15) and solar-powered (*n* = 12) GPS plus 1c bird transmitter (160 g) manufactured by Vectronic (Berlin, Germany)
2 80-g bird solar universal mobile telecommunications system (UMTS) transmitters (*n* = 2) manufactured by e-obs (Gruenwald, Germany)
3 110-g GPS collar model (*n* = 2) by Biotrack (Wareham, UK).

Transmitters were partially equipped with solar panels and were attached to the eagle’s back during banding procedures using a back-pack style harness. Four Teflon ribbons were sewn together in one point above the sternum, which formed a predetermined break point (Krone *et al.* 2013).

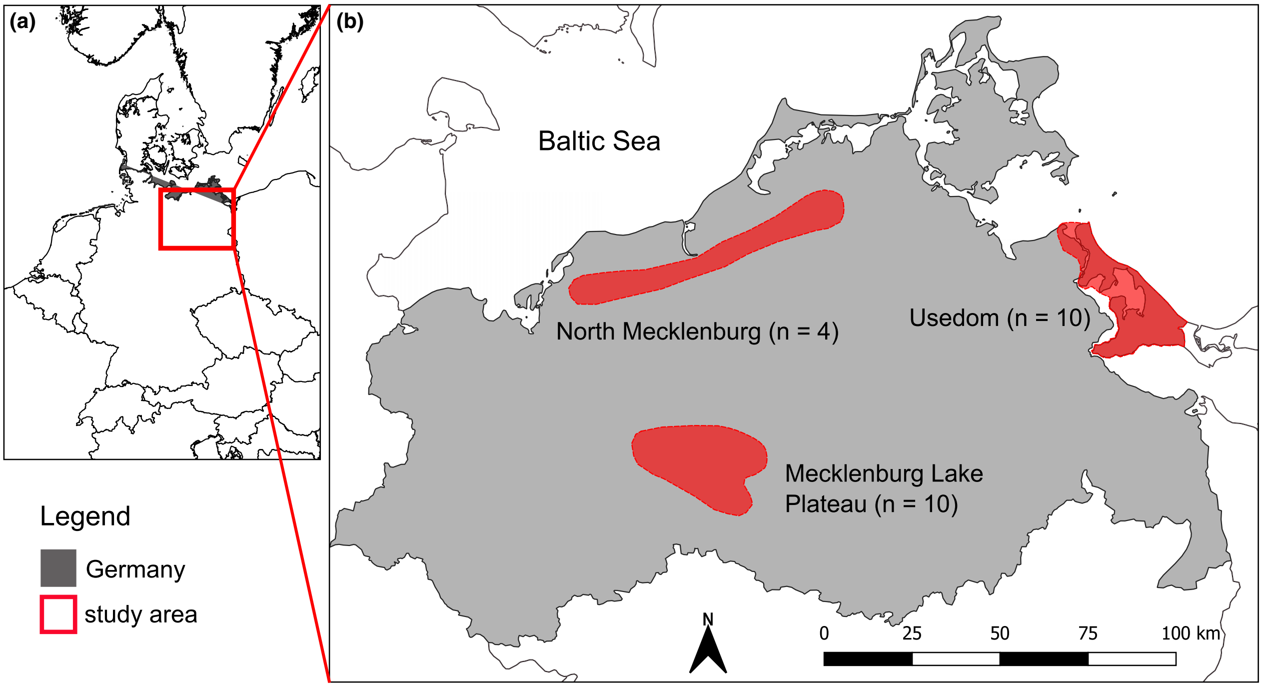

Figure 1. (a) Overview map of the study area in North-East Germany. (b) Map of the three focal study regions (red areas) in the federal state of MWP. Numbers in parentheses indicate the number of fledglings equipped with GPS-transmitters per study region. Seven individuals were located outside the focal study regions. Visualization via QGIS version 3.0 Girona. [Colour figure can be viewed at wileyonlinelibrary.com]

The transmitters' weight accounted for 3% of the eagles' bodyweight on average (3.2 ± 0.6%, $n = 31$, range: 1.3–4.1%). The individual's sex and age (days) were determined based on a combination of wing length and bodyweight. Nestlings were equipped at age between 42 and 66 days.

Transmitters were programmed to record at intervals from every 30 min to once per day between 06:00 and 20:00 h. For the sake of a constant temporal scale, GPS fixes were filtered to one location per day closest to 12:00 h, as for WTSE the acrophase of activity in a 24-h cycle is situated around midday (Krone *et al.* 2009).

For single missing locations, we used linear interpolation between the location of the previous day and closest locations available in the future to conservatively reconstruct movement paths using the R package *imputeTS* (Moritz & Bartz-Beielstein 2017). Of 31 individuals, seven were removed from the analysis to determine the date of fledging due to early technical failure or large data gaps. This resulted in a sample size of 24 juveniles. For any other analysis, nine of the 31 juveniles, including the seven mentioned above, were removed for the same reason, yielding a sample size of 22 juveniles. All juveniles were from different nests.

We determined the individual date of fledging visually by plotting GPS positions during the first weeks while taking individual positioning errors into account. Because a distance threshold (first day at which a fledgling moves farther than twice the individual positioning error away from the nest) did not yield different results during pre-analysis, we chose a subjective approach, as it offered more flexibility for two-dimensional interpretation in single cases. The positioning error averaged 6.13 m (± 4.38 sd) across all individuals, which was in a similar range to errors (longitude: 3.96 m, latitude: 7.79 m) reported by Krone *et al.* (2009). All distances between two points were calculated as the shortest geodesic distance using the 'Vincenty ellipsoid' method in the *geosphere* R package (Hijmans 2017).

Pre-dispersal movements

As a general characterization of excursive behaviour, we determined the length and maximum distance from the nest for each excursion as well as the number of excursions before the onset of dispersal for each individual. In line with descriptions by Walls and Kenward (1995), we defined an excursion as any movement of the eagle outside the fixed circular parental territory that did not result in the onset of emigration but ended with a return to the parental territory within the next five consecutive days. We chose this particular time period because we considered it to reflect the time period at which juveniles would be capable of returning from an excursion without serious impact on their physiology, as they are still not capable of foraging on their own at that stage (O. Krone pers. comm.). Although parents might accompany juveniles outside their territory boundaries, hence potentially prolonging the duration of excursion, we considered this case to be the exception, particularly as we expected the excursion distance to increase with duration, making the presence of parents away from their territory less likely; we therefore consider a period of 5–6 days to be a reasonable threshold.

In that context, we considered parental territory sizes for individuals of the two core areas as the mean of available home-range (HR) sizes exclusively from a total of eight breeding pairs in the Mecklenburg Lake Plateau area from the recent literature (Krone *et al.* 2013, Krone & Treu 2018), giving an average HR size of 13.48 km^2 with a mean radius of 2.07 km (see Table S1). For all other breeding pairs we set the average HR size as the mean of all HR sizes for German WTSE populations available in the literature, equalling a mean HR size of 53.25 km^2 with an average radius of 3.9 km (Table S1). All parental territory sizes were considered to be circular and temporally fixed over the length of data collection. NPZs around the nesting sites were defined according to the respective conservation execution laws of MWP (NatSchAG M-V 2010, §23) and Brandenburg (BbgNatSchAG 2013, §19) as the area around the nest in which regulations apply, e.g. a radius of 100 m for NPZ1 and 300 m for NPZ2.

Onset of natal dispersal and influence of the natal environment

We determined the time point of natal dispersal onset visually by mapping relocations for every individual separately while using the fixed circular parental territory size (see section on Pre-dispersal movements) as a visual reference. We chose this method because in comparison with six different methods available in the current literature, including distance threshold and coefficient of variance methods, it offered reliable results with the highest flexibility and lowest estimate variability (Engler & Krone Pers. comm.).

To investigate how the natal environment shapes dispersal decisions of juveniles during the post-fledging period, we extracted multiple environmental variables from the study region assessing habitat quality and resource accessibility by using a digital land cover model for Germany (LBM-DE 2012), based on multitemporal RapidEye satellite imagery (5-m pixel resolution), with a minimal spatial resolution of 1 ha. Within the boundaries of the individual parental territory, we aggregated forest area from all broad-leaved, coniferous and mixed forest CORINE Land Cover (CLC) classes. Further, the water area consisted of CLC classes covering water courses, water bodies, coastal lagoons, estuaries and marine water. We determined the presence of any foraging water, the distance from the nest to the nearest foraging water, as well as the cumulative length of shoreline of all foraging waters within the boundaries of the parental territory. We defined foraging water as any stream or water body with a total area of at least 2.7 km^2, representing the smallest area sufficiently large to serve as an exclusive foraging ground for a single breeding pair of WTSE (Krone *et al.* 2013). Similarly, water bodies smaller than 0.015 km^2 were excluded, as they are not frequently used by breeding WTSE during foraging (Krone *et al.* 2013). Variables of interest were determined for each nest using an open-source geographical information system (QGIS version 3.4.11 *Madeira*).

Statistical analysis

Between-sex differences regarding the age at fledging were tested using a parametric two-sample *t*-test. We used generalized linear models (GLMs) and generalized linear mixed models (GLMMs) to test for effects of various predictors on the response variable of interest. A negative binomial GLM with log link was used to model the number of excursions as a function of sex as a single fixed effect. To predict the maximal distance of excursions, we included duration, sex and the interaction (duration/sex) as fixed effects using a negative binomial GLMM with the individual as a random effect. Further information on model structure and parameter output is given in Tables S3–S5.

The effect of various predictors on the timing of emigration was tested using a negative binomial GLM. Beforehand, we used a principal component analysis (PCA) to investigate the relationship among all continuous environmental predictor variables (see Fig. S1 and Table S2). Based on explained variance and eigenvalues interpreted according to Kaiser's criterion for component selection (Kaiser 1961), only PC1 was used for further analysis. We included the presence of foraging water, the number of excursions and PC1 as fixed effects.

We tested all main model assumptions including linearity, uniformity, serial autocorrelation and overdispersion by simulating residuals via parametric boot-strapping with 1000 repetitions using the R package *DHARMa* (Hartig 2019). Model selection of different families and link functions was based on the Akaike information criterion. The significance of fixed effects was tested by comparing the full and reduced null model using Bartlett-corrected likelihood ratio tests with parametric boot-strapping based on 200 repetitions using the R package *spaMM* (Rousset & Ferdy 2014). The significance level α was set at $P < 0.05$ for all statistical tests. The summarizing group values are presented as mean ± sd if not stated otherwise. Data processing and statistical analyses were performed in R version 3.5.1 (R Core Team 2018).

RESULTS

Pre-dispersal movements

Juvenile WTSE ($n = 24$) fledged between 29 May and 22 July with a mean fledging date of 25 June (± 13 days). The age at fledging averaged 72 days (± 6) and did not differ between males ($n = 13$) and females ($n = 11$, two-sample *t*-test, $t = 0.743$, df = 23, $P = 0.47$). WTSE showed extensive excursive behaviour during the post-fledging period before emigrating from their parental territory. Of 22 individuals, 18 (82%, Fig. 2a,b) undertook at least one excursion during the post-fledging period. Four individuals dispersed without having been recorded outside of the parental territory (Fig. 2c). Juveniles undertook up to 19 excursions with an average number of 6.3 (± 5.2) and no difference was found between sexes (negative binomial GLM, likelihood ratio test: $\chi^2 = 1.578$, df = 20, $P = 0.209$, $n = 22$). Over 90% ($n = 99$) of all excursions lasted fewer than 5 days, with the

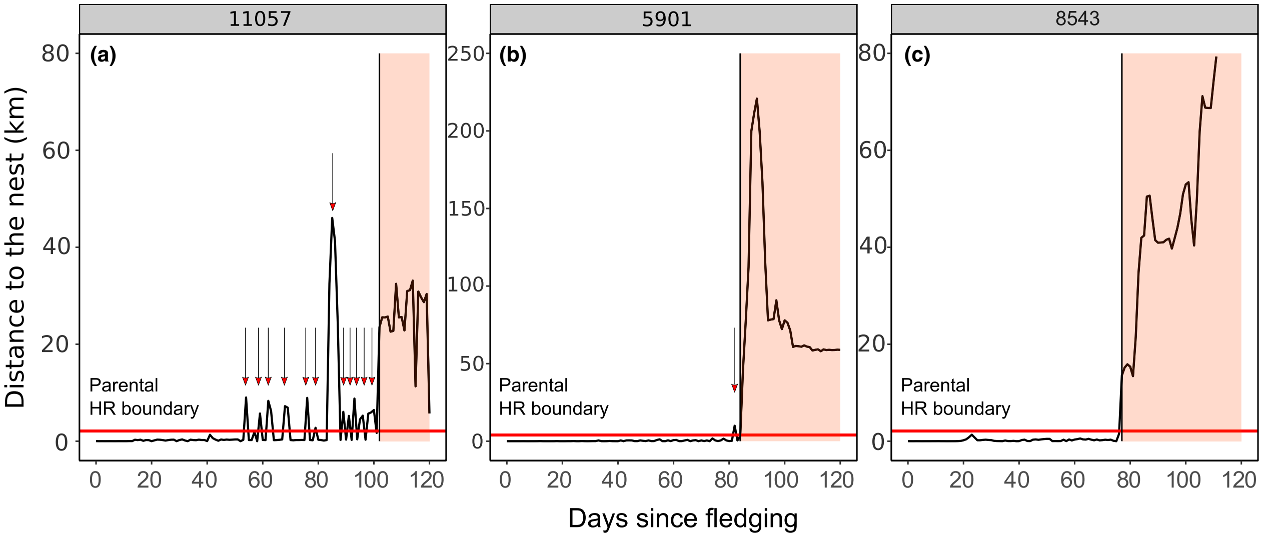

Figure 2. Examples of excursive behaviour for three juvenile WTSE. (a) Individual with multiple excursions (arrows) prior to emigration (vertical line + shaded area). (b) Individual with a single excursion just before emigration. (c) Individual with no excursive behaviour. [Colour figure can be viewed at wileyonlinelibrary.com]

mean duration of excursions averaging 2.25 days (± 1.96). However, a few extreme excursions lasted up to 10 days and outside the predefined excursion length (see section on *Pre-dispersal movements* under Methods), yet with a clear indication that the actual point of emigration took place later. Again, no difference between the sexes was found (two-sample *t*-test, $t = 1.209$, df = 15, $P = 0.245$).

Lastly, juveniles covered distances during excursions of up to 68 km, with an overall mean of all excursions averaging 8.74 km (± 10.6, $n = 107$). In 88% ($n = 94$) of all excursions, individuals stayed within 10 km of their nest, and individuals returned to their parental territory within the first 2 days in approximately 70% ($n = 75$) of all excursions.

The maximal distance individuals covered during excursions was positively related to the duration of the excursion (GLMM, likelihood ratio test, $\chi^2 = 28.99$, df = 2, $P < 0.001$, $n = 107$) and showed no difference between sexes (GLMM, likelihood ratio test, $\chi^2 = 4.61$, df = 2, $P = 0.1$, $n = 107$). The effect of excursion duration differed between sexes (interaction effect), with females increasing maximal distance over excursion duration by a factor of 0.865 compared with males (GLMM, likelihood ratio test, $\chi^2 = 4.605$, df = 1, $P = 0.032$, $n = 107$).

Onset of natal dispersal and influence of the natal environment

Juveniles initiated dispersal between early August and mid-December at an average of 92.8 days after fledging (± 30.2 sd, range 46–160). At that point, the age of the birds averaged 148 (± 30.7) days.

The timing of dispersal onset was delayed by the number of excursions an individual undertook during the pre-emigration phase (GLM, likelihood ratio test, $\chi^2 = 8.145$, df = 1, $P = 0.004$, $n = 21$), with juveniles staying in their parental territory for an increasingly prolonged time period with the more excursions they undertook previously (Fig. 3a). Additionally, the presence of at least one main foraging water body within the territory boundaries showed a distinct trend to delaying the onset of dispersal (negative binomial GLM, likelihood ratio test, $\chi^2 = 3.178$, df = 1, $P = 0.075$, $n = 21$). Juveniles of breeding pairs with foraging water access dispersed at an average of 105 days (± 29) after fledging, whereas those lacking of any main foraging water initiated dispersal onset on average 26 days earlier, at 79 days (± 26) after fledging (Fig. 3b). Dispersal onset was not affected by a gradient of water area and distance to the next foraging water (see Fig. S1), as reflected by PC1 (GLM, likelihood ratio test, $\chi^2 = 2.04$, df = 1, $P = 0.153$, $n = 21$).

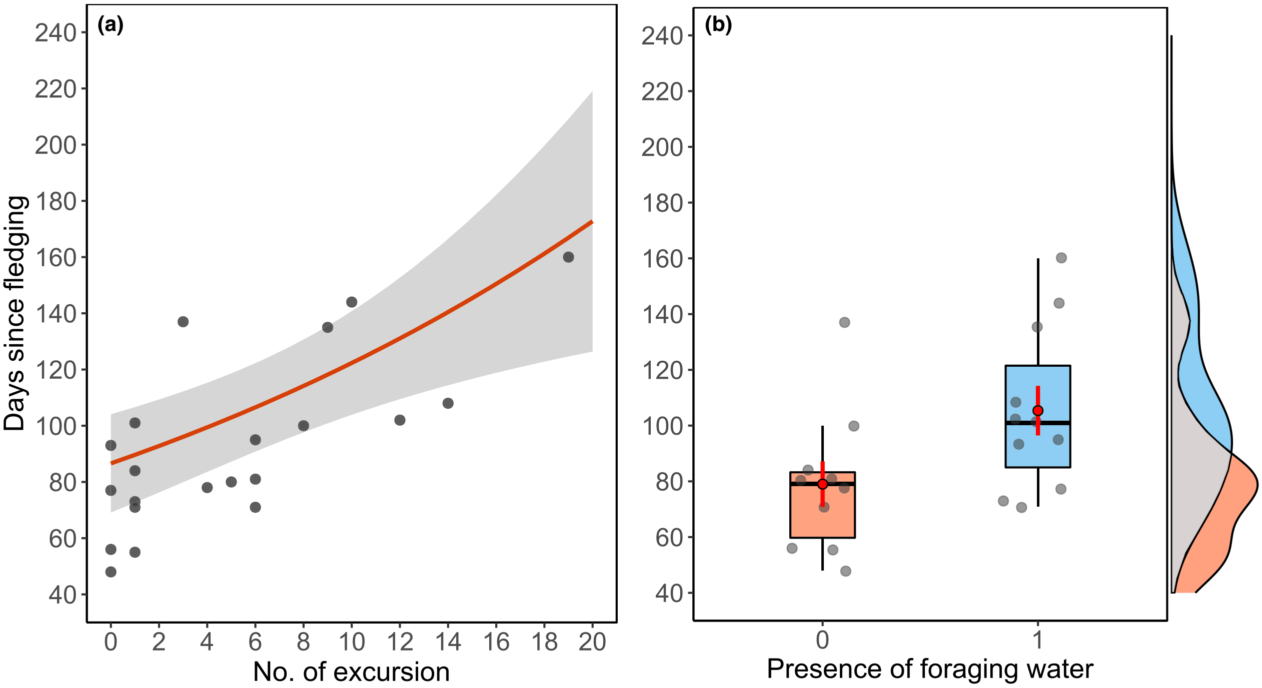

Figure 3. Timing of dispersal onset for juvenile WTSE as a function of (a) pre-emigration excursions and (b) presence of foraging water in parental territories. Red line represents predicted values based on the negative binomial GLM with 95% confidence interval. Parental territories with (1) and without (0) any foraging water present. Red dots indicate group mean, with red bars representing standard error (se). The side graph of (b) indicates the respective group density distribution. [Colour figure can be viewed at wileyonlinelibrary.com]

All 21 individuals for which the time point of emigration could be determined dispersed within the first 6 months after fledging. By 31 August, only 24% (*n* = 5) of all individuals had dispersed from their parental territory, whereas by mid-October, 80% (*n* = 17) had initiated dispersal.

The proportion of juveniles within close distance to the nest gradually decreased over the course of summer (Fig. 4). By mid-July, almost half of all juveniles still resided within 100 m (NPZ 1) of the natal nest, whereas at the end of July, 59% (*n* = 13) of all young WTSE still resided within 300 m (NPZ 2). By 31 August, *c.* 55% (*n* = 12) of juveniles had moved more than 1 km from their nest of origin, but they frequently returned to their nest area within 300 m. At that point, almost a quarter (23%, *n* = 4) still resided within 300 m of the nest. By early to mid-October, almost all individuals had left the nesting area and only a few individuals undertook occasional returns to the area close to the nest.

Over the course of the first year after fledging, the distance to the nest of origin increased steadily and with increasing variation in mean distances over time for both sexes (Fig. 5). Juveniles showed the highest variation in distance to their parental territory in the spring of the following year (*c.* 300 days since fledging) but they rapidly decreased the distance to the parental territory after around 350 days and returned to within 20 km of their area of origin (*n* = 5).

DISCUSSION

Pre-dispersal movements

The analysis of tracking data yielded new insights into post-fledging movements of young WTSE. The visually determined age at which juveniles fledged showed little variation among individuals. Although information on the age of fledging is scarce, either because many studies report different measurements (e.g. only absolute age (Nygård *et al.* 2000) or none at all (Whitfield *et al.* 2009a,

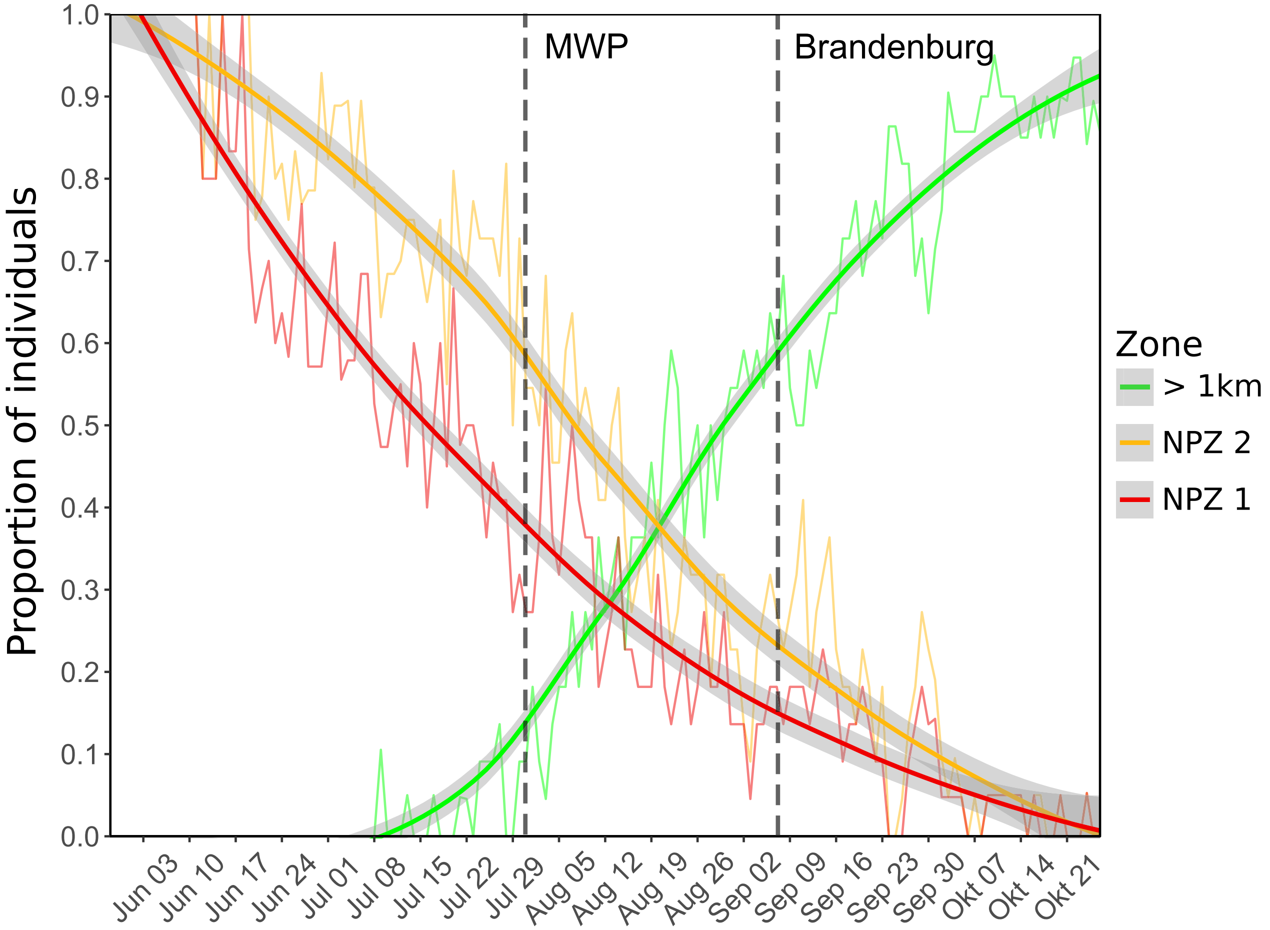

Figure 4. Proportion of individuals separated in spatial zones around the nest. NPZ 1 and NPZ 2 (nest protection zones) represent 100 and 300 m from the nest, respectively. Smoothed lines are based on local regression (LOESS), with shaded area representing 95% confidence interval. The end of nest protection period of the two main federal states in the study region is marked as vertical dashed lines according to the BbgNatSchAG (Brandenburg 2013) and the NatSchAG M-V (MWP 2010). [Colour figure can be viewed at wileyonlinelibrary.com]

2009b, Bragin *et al.* 2018)), the findings are in line with results published by Balotari-Chiebao *et al.* (2016), who reported a mean fledging age of 79 days for a WTSE population in Finland using telemetry position errors as a proxy.

The few studies addressing juvenile movements of WTSE did not report any information on excursive behaviour (Whitfield *et al.* 2009a, 2009b, Nygård *et al.* 2010), mainly because methods with suitable spatio-temporal resolution were not available. Among studies using appropriate methods such as GPS devices, the excursive behaviour of raptors during the post-fledging period has only been marginally addressed (Nygård *et al.* 2000, Balotari-Chiebao *et al.* 2016, Bragin *et al.* 2018, Miller *et al.* 2019).

Our results show that the post-fledging period of WTSE was characterized by extensive exploratory behaviour, with more than 80% of all individuals taking at least one excursion with an average duration of 2 days. Despite our predefined excursion duration, for longer excursions (>6 days) it is likely that juveniles gained access to food midway, e.g. via remaining carcasses of game mammals from hunting as well as fish from fish farms, all of which have been reported to serve as alternative sources of food for WTSE (Sulkava *et al.* 1997, Krone *et al.* 2013, Nadjafzadeh *et al.* 2016). Such freely accessible resources could allow for longer excursions despite a lack of foraging capability at that developmental stage, which in return could allow for a more thorough assessment of patch quality prior to emigration

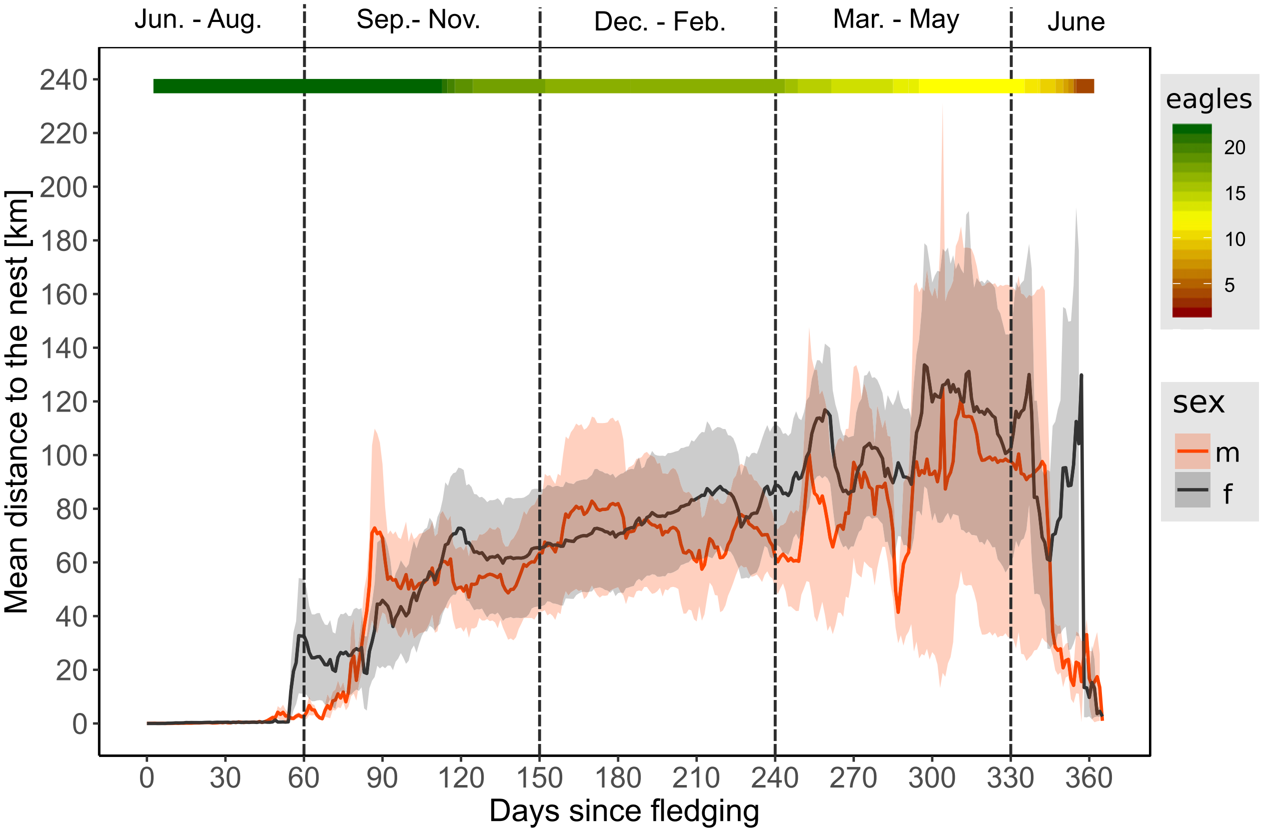

Figure 5. Mean distance of WTSE to the nest of origin in their first year after fledging. Lines represent mean distances by sex and shaded areas represent 95% confidence interval (CI). The coloured bar indicates group size over which mean and CI were calculated. [Colour figure can be viewed at wileyonlinelibrary.com]

(Clobert *et al.* 2009, 2012). In that context we point out that the classification of movements as excursions might depend on our assumptions as to parental territory size/shape and predefined excursion duration. In cases of highly asymmetrically shaped parental HRs, which greatly differ from our assumed fixed HR due to missing information on individual parental HRs, juveniles might in fact still be in close contact with their parents and benefit from their foraging, even when on excursions. If available, information on individual HR size/shape should therefore be taken into account when defining or interpreting exploratory movements.

The stronger increase in maximum excursion distance with duration for males suggests that males tend to explore their environment on a larger spatial scale compared with females, assuming that potential factors such as access to resources and physical condition allow for longer excursions. Underlying mechanisms remain unknown, yet such behaviour could potentially increase the eagles' insight into suitability of surrounding habitat and would be in concert with patterns of sex differences in dispersal distances in WTSE (Nygård *et al.* 2000, Whitfield *et al.* 2009b, Nygård *et al.* 2010), multiple raptor species (Soutullo *et al.* 2006a, 2006b) and birds in general (Greenwood 1980, Clarke *et al.* 1997).

Onset of natal dispersal and influence of the natal environment

WTSE left their parental territory approximately 92 days after fledging at an average age of 148 days, which is generally consistent with the results of two other studies (Nygård *et al.* 2010, Balotari-Chiebao *et al.* 2016).

The onset of dispersal was strongly linked to the pre-emigration behaviour, being increasingly postponed by an increasing number of excursions prior to emigration. Preliminary analysis did not indicate any correlation between the number of excursions and the extent of natal habitat quality, yet it is likely that WTSE with extensive excursive behaviour remained longer within their parental territory because they could assess the quality of their natal environment extensively (Clobert *et al.* 2012). This is in line with the Resource Competition Hypothesis (Howard 1960, Murray 1967), according to which intraspecific competition for resources or high-quality territories can cause individuals to stay longer in the parental territory if food is abundant (Balbontín & Ferrer 2005).

Juveniles showed a strong tendency to delay the onset of dispersal if they had access to foraging waters within the boundaries of the parental territory. Given that such access enables the parents to maximize foraging efficiency and increase the prey provision rate (Stephens & Krebs 1986, Nadjafzadeh *et al.* 2016), young eagles may display good physical development due to parental care during the nestling and early post-fledging period (Ferrer 1992b). Likewise, a high-quality habitat provides juveniles themselves with essential access to resources and suitable foraging grounds at a life history stage with little foraging experience and efficiency. We therefore conclude that WTSE follow the strategy to reside in the parental territory for as long as foraging conditions (Balbontín & Ferrer 2005), parent–offspring competition (Clobert *et al.* 2012), sibling competition (Kenward *et al.* 2001) or the innate drive to disperse allow for it.

These results differ from reports of early emigration from the parental territory for Spanish Imperial Eagles *Aquila adalberti* (Ferrer 1992a, 1993a), which presumably assists in gaining access to potential breeding territories (Ferrer 1993a, Massot & Clobert 1995), particularly if the costs of dispersal are already minimized due to beneficial body conditions (Balbontín & Ferrer 2005, Delgado *et al.* 2010). However, Bonelli's Eagles do not exhibit such behaviour (Balbontín & Ferrer 2005) and we assume that WTSE, which usually do not establish territories before the age of 5 years, might prioritize physical fitness and survival during the first years over the advantage of access to breeding territories in the long term (Cramp & Simmons 1980, Balbontín & Ferrer 2005).

Ultimately, the mutual interplay between the quality of the natal environment and the ability to assess it appears to influence the decision on timing of dispersal in WTSE (Bonte *et al.* 2012). Juveniles with good body condition, whether through parental care, habitat quality or a combination of both, were probably physically capable of taking a great number of excursions in the first place, as proposed for Northern Goshawks *Accipiter gentilis* (Kennedy & Ward 2003) and Snail Kites *Rostrhamus sociabilis* (Bennetts & Kitchens 2000). Consequently, those individuals were able to assess the quality of the surrounding habitat the best, helping them to time their emigration from the parental territory (Clobert *et al.* 2012). While we linked the timing of dispersal onset of WTSE to environmental characteristics of the parental territory and excursive behaviour during the post-fledging period, the interplay with other factors including body condition (Ferrer 1992b, Balbontín & Ferrer 2005), brood size (Ferrer 1992b, Walls & Kenward 1995) and environmental conditions (Ferrer 1993b, Walls *et al.* 2005) should still be investigated in future studies to obtain a full understanding of the process of dispersal in WTSE.

After dispersal onset, juveniles steadily increased their distance from the parental territory throughout their first year, which is consistent with the general current understanding of large-scale movements during the transfer phase after emigration (Bowler & Benton 2005, Clobert *et al.* 2009, 2012). Documentation of similar behaviour exists for the same species (Nygård *et al.* 2000) as well as other raptor species such as Golden Eagles (Soutullo *et al.* 2006a, 2006b, Nygård *et al.* 2016), Spanish Imperial Eagles (Ferrer 1993a) and Bonelli's Eagles (Cadahía *et al.* 2010).

At the end of their first year, a proportion of the eagles returned within close proximity to the parental territory. Such behaviour has been reported in a few cases for Norwegian WTSE (Nygård *et al.* 2000) but could not be detected in a population in Western Scotland (Whitfield *et al.* 2009b). Among other raptor species, natal returns indicating strong philopatry are well documented, e.g. for Common Buzzards *Buteo buteo* (Walls & Kenward 1998), Spanish Imperial Eagles (Ferrer 1993a) and Golden Eagles (Urios *et al.* 2007).

The underlying causes for such movement behaviour are complex and are still poorly understood, but knowledge about the environment collected during early life phases, specifically on breeding and foraging grounds, could influence decisions towards natal returns (Cadahía *et al.* 2010, Clobert *et al.* 2012). Consequently, knowledge gathered by extensive excursive behaviour could have led those individuals to return to their parental territory in order to exploit known available resources or to assess the current state of occupancy (Bowler & Benton 2005, Clobert *et al.* 2012).

Particularly during the breeding season, nest protection regulations with spatial and temporal specifications aim to reduce disturbances within the nesting area in the federal states of MWP and Brandenburg, which accommodate the majority of breeding WTSE pairs in Germany. Accordingly, respective conservation execution laws of MWP (NatSchAG M-V 2010, §23) and Brandenburg (BbgNatSchAG 2013, §19) currently prohibit any alteration of the environmental character within nest protection zone 1 (< 100 m from the nest, NPZ 1) as well as the execution of any vehicle-assisted forestry action, hunting activities or the erection of hunting structures within 300 m (NPZ 2) of the nesting sites until 31 August in Brandenburg and 31 July in MWP. However, the results showed that the majority of juveniles stayed within close proximity of the nest for a prolonged period of time after fledging. At the end of July, almost two-thirds of the studied population stayed within < 300 m of the nest, reducing by the end of August to a quarter of all individuals. Even by the end of September, around 15% of all juveniles frequently ventured to within the proximity of the nesting site. As a result, a reasonably high proportion of juveniles still resided within close proximity to the nest after the currently existing protection period. Particularly in the federal state of MWP, both forestry and hunting activities resume from 31 July, which could potentially affect a high proportion of young WTSE during a period in which they interact considerably with their parents and are prone to human-related disturbance (Krone *et al.* 2019). The resulting consequences remain unpredictable but could potentially enforce avoidance behaviour or trigger premature emigration and therefore affect individual survival or ultimately act on the population level.

We therefore propose that currently existing nest protection periods for the state of MWP should be extended until the end of September, when most of the individuals have left the parental territory or at least the close proximity of the nesting area. Similarly, we consider it highly advisable to delay the resumption of forestry and hunting activities in the state of Brandenburg until the end of September.

We emphasize that our findings are relevant not only for WTSE but underline the necessity of conservation regulations with spatio-temporal specifications for the protection of the reproductive sites and hence preservation of populations for all large raptor species sensitive to human-related disturbance. In the future, this will become increasingly important for breeding populations of large raptors in densely human-inhabited areas with increasing alteration of land.

This study is one of the first extensively to characterize excursive behaviour of WTSE during the post-fledging period up to the time of emigration. The results highlight the complexity of dispersal movements and the related importance of the natal environment for juvenile WTSE during the post-fledging period. Along with natural risks involved during dispersal (Bowler & Benton 2005), habitat degradation, increased human-induced disturbance and related costs could ultimately force young eagles to leave their parental territory prematurely (Kennedy & Ward 2003), reduce their fitness and competitiveness, enhance mortality rates (Kenward *et al.* 1999, Wiens *et al.* 2006) and affect the population dynamics in the long term (Clobert *et al.* 2001). It is therefore crucial to further study the factors shaping movement decisions of WTSE and raptors during natal dispersal in general and to consider sustainable management and protection of habitats suitable as foraging and breeding grounds. Species-specific conservation strategies as suggested above should be implemented to contribute further to reducing disturbance of juvenile WTSE during the post-fledging period.

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CONFLICT OF INTEREST

The authors declare that they have no conflicts of interest.

AUTHOR CONTRIBUTION

Marc Engler: Conceptualization (equal); Formal analysis (lead); Investigation (equal); Software (lead); Visualization (lead); Writing-original draft (lead). **Oliver Krone:** Conceptualization (equal); Data curation (lead); Funding acquisition (lead); Investigation (equal); Project administration (lead); Resources (lead); Supervision (lead); Writing-review & editing (lead).

Data Availability Statement

Underlying movement data includes highly sensitive information on nest and breeding locations of the study species. Therefore, we will not make raw data publicly available but are willing to share data upon request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1 Home-range sizes of WTSE

Table S2 Results of the PCA on environmental variables

Table S3 Model output of the negative binomial GLM modelling the number of excursions as a function of sex

Table S4 Model output of the negative binomial GLMM modelling the maximal distance of excursions as a function of sex and excursion duration

Table S5 Model output of the negative binomial GLM modelling the timing of emigration (days since fledging) as a function of sex, presence of foraging water and PC1

Figure S1 PCA Output.