



Dear territory or dear partner? Causes and consequences of breeding dispersal in a highly territorial bird of prey with a strong pair bond

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Abstract

Territorial species are unlikely to show extensive movements between breeding seasons. This is especially true for long-lived species, which often have strong pair bonding and can occupy the same territory for years. However, also in such species, individuals may face situations that can lead to a territory shift. Here, we use a comprehensive dataset documenting 40 years of breeding behavior in tawny owl (*Strix aluco*) – a long-lived species with high site tenacity and mate fidelity – to examine the factors affecting the decisions whether or not to move to another breeding territory and how far, as well as the fitness consequences thereof. We found that the likelihood and distance of movement in either sexes is strongly associated with a change of partner, indicating that mate loss may cause breeding dispersal. Moreover, mate change, not movement to a new territory, had negative effects on subsequent reproductive performance: individuals that changed partner were more likely to skip reproduction in the subsequent year and, in those cases they bred, they produced smaller clutches and raised fewer offspring. Our findings indicate that tawny owls change territory almost exclusively when searching for a new partner and that mate change has profound consequences on their subsequent breeding performance. Overall, our study provides evidence that in tawny owls territoriality and monogamy are associated and strongly linked to fitness, but mate fidelity may be more important than site fidelity, likely because sexes are involved in specific tasks and their cooperation ensures breeding success and, consequently, increases fitness.

Significance statement

Breeding dispersal, the movement of individuals between breeding sites, can entail high costs for animal fitness, especially for territorial species, which display strong site fidelity. We studied the factors associated with breeding dispersal and the consequences on breeding performances in tawny owl (*Strix aluco*), a highly territorial species. We found that tawny owls moved more frequently to another breeding territory when the mate died. Either sexes showed an equal probability to move, but the effect was stronger in females than in males after a mate change. Moreover, owls that changed partner showed delayed reproduction, smaller clutch and a higher probability to skip reproduction. Our findings show that in tawny owls territoriality and monogamy are associated and strongly linked to fitness, but mate fidelity may be more important than site fidelity, likely because sexes share the costs of holding the territory.

Keywords Breeding investment · Monogamy · Movement ecology · Population dynamics · Skip breeding · Territoriality

Introduction

The factors determining variation in the dispersal of animals can have strong effects on the ecological and evolutionary dynamics of spatially structured populations (Bowler

and Benton 2005; Clobert et al. 2009; Bonte et al. 2012; Fronhofer et al. 2018). Broadly, the movement of immature individuals departing their natal area in search of their first breeding site describes natal dispersal, whereas the subsequent movements of adults between breeding seasons define breeding dispersal (Greenwood and Harvey 1982; Johnson and Gaines 1990). Although breeding dispersal can occur several times during an individual's lifetime, it is generally considered an uncommon process because the advantages of

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breeding site fidelity, the counterpart of dispersal, habitually outweigh the possible benefits of finding a new, but unfamiliar, breeding site (e.g., Bowler and Benton 2005; Bonte et al. 2012; Harts et al. 2016). This holds particularly for long-lived territorial species that can defend the same territory for years and that are unlikely to show extensive movements (Newton 2001; Sunde 2011).

Yet, the factors thought to drive individual variation in breeding dispersal are diverse and can be summarized in three main categories: individual factors (e.g., physical characteristics and/or personalities, Terraube et al. 2015; Luna et al. 2019), social factors (e.g., conspecific interactions in density-dependent contexts, Jenkins et al. 2021; Kim et al. 2009) and ecological factors (e.g., environmental conditions influencing dispersal decisions, Travis and Dytham 1999). Such drivers can either act in isolation or combined, making it often difficult to disentangle their relative contribution (Payne and Payne 1993; Haas 1998). Moreover, these factors can regulate both the propensity to move, namely the decision whether or not to change breeding site (or territory), and the distance to be travelled (Forero et al. 1999; Murrell et al. 2002; Bowler and Benton 2005; Furst et al. 2021). In this context, a further difficulty of studying breeding dispersal is to determine the scale on which it occurs, as it can involve either fine-scale movements intended to change breeding site within the same territory (Korpimäki 1993; Öst et al. 2011) or complete abandonment of the territory to occupy a new one (Forero et al. 1999; Jenkins et al. 2019). The latter entails movements on a wider scale and consequently the costs in terms of fitness are expected to be higher (Bonte et al. 2012).

Different non-mutually exclusive hypotheses have been proposed to explain variation in breeding dispersal. Movements have often been interpreted as a mean for individuals in poor-quality territories to acquire territories with higher quality (e.g., better food resources or a better access to them), which is expected to have fitness benefits (Serrano et al. 2001; Bowler and Benton 2005; Furst et al. 2021). On the other hand, the 'reproductive performance hypothesis' postulates that individuals would rely on their past breeding performance to decide whether to disperse or to remain tenacious to a breeding site. Accordingly, poor or unsuccessful breeding attempts may be the main proximate cause of dispersal (Greenwood and Harvey 1982; Pärt and Gustafsson 1989; Haas 1998). Since poor breeding performances may be linked to territory quality, the two hypotheses can be complementary (Daniels and Walters 2000). Also finding a new partner because of mate loss, for both widowhood and divorce, plays a prominent role in triggering breeding dispersal in different systems (Daniels and Walters 2000; Forsman et al. 2002; Valcu and Kempenaers 2008; van den Brink et al. 2012). With regard to individual factors, age can be an important determinant of breeding dispersal probability

and distance (e.g., Forero et al. 1999; Daniels and Walters 2000; Breton et al. 2014; Kentie et al. 2014), with younger individuals being more likely to disperse because they are less experienced and familiar with the environment. Philopatry, or site tenacity, should therefore increase with age (and experience) through the benefits of increased breeding-site familiarity (Bowler and Benton 2005). Similarly, sex-related breeding dispersal patterns often occur, with one sex tending to disperse more frequently and farther than the other. For instance, in birds, longer female-biased movements are commonly described (e.g., Greenwood and Harvey 1982; Calabuig et al. 2008; van den Brink et al. 2012; Otterbeck et al. 2022), while in mammals males tend to be the dispersing sex (Nunes 2007).

To understand breeding dispersal it is important to study not only the potential causes, but also the adaptive significance of dispersal with focus on costs and benefits. Indeed, the consequences of dispersal are shaped by the balance between the costs and the benefits linked to the decision to leave or to stay, and a species' life-history strategies can influence this costs-benefits balance (Danchin and Cam 2002; Pasinelli et al. 2007). In non-territorial species, the benefits can outweigh the costs of breeding dispersal. Indeed, if the local conditions cease to be good enough to reproduce, these species can leave to find better places where to breed and thus improve their breeding success (Eeva et al. 2008). Conversely, in territorial species with strong site-tenacity the abandonment of the territory is uncommon and the fitness costs of dispersal are expected to be higher. In fact, movements have been found to negatively covary with breeding success (i.e., lower offspring production; Korpimäki 1987) and even lead to skipping reproduction after movement (Danchin and Cam 2002). These apparent negative effects of breeding dispersal may arise as a consequence of a lack of familiarity with local food sources, the effort to find new mates and/or simply as a cost in terms of time and energy to acquire a new site (i.e., movement distance) (Danchin and Cam 2002; Bowler and Benton 2005).

However, the costs (and benefits) of breeding dispersal might not be directly connected to the movement itself but rather to the factors implied in breeding dispersal. While site choice, mate loss, breeding experience and success have been widely considered in the study of the causes of breeding dispersal, their relative contribution to variation in fitness is rarely taken into account (Warkentin et al. 1991; Forero et al. 1999). If movement were the main cause of a decrease in fitness, one would expect to regularly find a negative relationship between any estimates of dispersal and breeding parameters. However, the decrease in breeding performances after dispersing seems not to be always coupled with movement (Öst et al. 2011; Terraube et al. 2015), suggesting that the negative effects on fitness might be instead linked to the circumstances triggering breeding dispersal. For instance, both in lesser kestrels

(Calabuig et al. 2008) and in common kestrels (Terraube et al. 2015) breeding success after movement was more influenced respectively by colony characteristics and local food abundance, rather than by probability to disperse or distance travelled. Disentangling the effects of the movement and the main drivers of breeding dispersal would thus be critical to understand if the evolutionary constraints of breeding dispersal may reside in the effects produced by the factors associated with it.

The purpose of this paper is to examine the factors associated with movement and the possible consequences of breeding dispersal in the tawny owl (*Strix aluco*), a long-lived species with high site tenacity and mate fidelity (Southern 1970; Hirons 1985; Jedrzejewski et al. 1996; Sunde 2011). We used a long-term dataset spanning more than 40 years to study both the probability to change breeding territory and the distances travelled by adult tawny owls between breeding seasons. Moreover, we analyzed the possible consequences on fitness by considering jointly the decision to move and the main factors underlying breeding dispersal to disentangle their relative role on successive breeding performances. We hypothesize that mate loss may result in increased breeding dispersal, where individuals that changed mate would show higher probability to move (and possibly longer displacements). Secondly, in line with previous results in other species (e.g., Forero et al. 1999; Jenkins et al. 2019), we expect that younger and less experienced breeders would move more frequently. Moreover, since this species is characterized by a highly heritable melanin-based color polymorphism (Brommer et al. 2005; Karell et al. 2011a; Morosinotto et al. 2020) with a context-dependent morph-specific pattern in natal dispersal (Passarotto et al. 2022), we also tested the potential existence of morph-specific strategies for breeding dispersal. Adult tawny owl color morphs have been found to differ in their physiological and behavioral profiles (Karell et al. 2011b, 2017; Emaresi et al. 2014) likely because of pleiotropic effects (Ducrest et al. 2008). We can thus expect that morphs might differ in the decision-making concerning moving or not to a different breeding territory because of differences in behavior and reproductive decision-making. In particular, the more pheomelanic brown morph has been found to defend the nest more aggressively than the grey one (Da Silva et al. 2013) and to invest more in current reproduction at a cost of residual reproduction (Emaresi et al. 2014), which suggests that brown tawny owls might be more territorial (i.e., more prone to defend their territory all-year around) and hence less prone to move to another territory.

Material and methods

Study system

We studied breeding dispersal in tawny owls in two adjacent almost equally sized areas in western Uusimaa, Southern

Finland (60°15' N, 24°15' E). The two localities extend over a total area of approximately 500 km² and both are equipped with about 150 nest-boxes each (for description of the study areas, see Brommer et al. 2015; Morosinotto et al. 2020; Passarotto et al. 2022), although local breeding density is overall quite low (on average, 25 nests occupied per year, SD ± 12.21). One part of the population was monitored from 1978 to 2021 and the other between 1987 and 2021. Nest boxes are associated to geographical coordinates, enabling us to compute linear distances between them. It was not possible to record data blind because our study involved focal animals in the field.

Tawny owls are long-lived birds living up to 18 years in the wild (König and Weick 2008) and displaying strong pair bonding between the social mates, which stay together in a usually monogamous relationship for life (Southern 1970; Hirons 1985; Jedrzejewski et al. 1996; Sunde 2011). Pairs establish a territory that is defended year-round (Appleby et al. 1999) and breed early in spring, normally from March but sometimes as early as February, laying two to six eggs, which are incubated by the female alone during roughly 28–30 days (König and Weick 2008). While incubating, the female does not leave the nest and is fed by the mate. Eggs hatch asynchronously and females stay at the nest defending it and allocating the food provided by the male within the brood almost until chicks fledge (Sunde et al. 2003). Parental cares are then provided for other 2–3 months, with the young being fed by both male and female (Sunde et al. 2003).

In Finland, tawny owls live in mixed and boreal forests where they promptly breed in nest boxes. In our population, tawny owls start to lay in March–April (median laying date 31 March), laying 1–9 eggs (mean = 3.96, SD ± 1.06). All boxes were checked once from mid-April onwards to find active nests and to measure clutch size whenever possible. Females tend to be particularly protective and can stay in the nest during inspection sitting on the eggs, making it sometimes impossible to estimate clutch size. Similarly, clutch size could not be estimated if a clutch had already hatched.

Then, nests were regularly checked to establish hatching time, visiting the nests with approximately one-week interval. Tawny owls lay on average one egg every second day and incubation was assumed to start after the second egg was laid (Karell et al. 2017). Therefore, upon nest inspection, laying date was estimated retrospectively from the laying interval by back counting from hatching or by estimating the age of the chicks from their wing length if they had already hatched.

When all eggs had hatched, both parents were trapped at the nest box (see “Ethics approval”). Both sexes have similar capture probability (Brommer et al. 2005; Karell et al. 2009). Upon capture, adults were aged on the basis of plumage characteristics. Juvenile feathers can be determined by their different shape and banding pattern as compared to adult feathers:

one-year old individuals retain their juvenile plumage, while two-year old tawny owls typically moult only part of their juvenile flight feathers. In older individuals the plumage is completely moulted and feathers are distinguished as old or new on the basis of their abrasion; (for further details, see Karell et al. 2013). In addition, adults were measured and ringed (if not) with standard metal rings with unique alphanumeric codes to allow individual identification upon recapture (Karell et al. 2009). Plumage color was scored in adults using a semi-continuous score based on the degree of pheomelanin-based redness from: facial disc, back, breast and overall appearance. Then, either grey or brown morph is assigned to each individual on the basis of this general score (see details in Brommer et al. 2005). When the oldest chick in a brood was approximately 25–28 days old (shortly prior to fledge), the nest was visited for the last time and all offspring were ringed and measured (see Karell et al. 2009 for details).

This study only considered those individuals for which at least two breeding attempts were detected in the study area, which enabled to assess (a) whether there was a movement (i.e., decision to move), and (b) to estimate the distance moved between breeding sites. Therefore, in this dataset, each observation refers to two specific breeding attempts and some individuals can show multiple observations. We considered as breeding attempts all those events where individuals attempted to breed and laid at least one egg in a given nest box (territory), regardless of the final output of the reproduction. Overall, we recorded 979 observations corresponding to 403 individuals in total, 216 females and 187 males. Since tawny owls can skip reproduction in unfavourable conditions while still defending the territory (Karell et al. 2009), we also considered observations between non-consecutive years ($n=220$, ca. 22.5%), but excluding gaps greater than one year ($n=70$). This was to avoid any possible bias due to breeding events that remained potentially undetected within the study area, particularly for the study of consequences of a change in breeding site (see “Statistical analyses”). In tawny owls, breeding site choice may be influenced by the abundance and availability of multiple breeding sites within the territory and experimental research showed that small-scale movements within the territory could function as a tool to minimize predation risk (Karell et al. 2020). Here, we focused on movements on a wider scale within the study area as we are mainly interested in understanding the causes leading to a change in the territory, given that movements to new territories may have a stronger detrimental impact on breeding decision, and thereby fitness, in this highly territorial species. Tawny owls are highly sedentary and philopatric (Saurola et al. 2013) and seldom move territory (Saurola 1987). Moreover, in our study population, about 70% of the ringed individuals were recorded regularly throughout the observation period, allowing us to monitor and assess population turnover. For these reasons, we do not

expect the size of our study area to influence the detected breeding dispersal distances, and although a few individuals might have left the population to breed elsewhere, breeding dispersal is expected to mainly occur within our study area (as observed for natal dispersal, Passarotto et al. 2022).

In order to establish the threshold that may indicate a change of territory, since we have no objectively measured information about territory size in our population, we observed the distribution of distances and we found that most of the distances fell below 1 km (see Fig. S1 in supplementary material). Therefore, we considered the movements ≥ 1 km as distances potentially highlighting a territory change ($n=273$). Accordingly, we defined the decision to move as a binary variable indicating if there was or not a movement ≥ 1 km from the territory (see “Statistical analyses”).

Statistical analyses

Assessing correlates of breeding dispersal

Since we aimed to assess whether the same factors may explain both the decision to move and the distances, we run one model to assess variation in movement probability, and one to assess variation in linear movement distance. To this end, movement probability was modelled as Generalized Linear Mixed Models (GLMMs) with Binomial errors, while movement distances were modelled as Linear Mixed Models (LMMs) with Gaussian errors. These models were implemented in the package “lme4” (Bates et al. 2015) in R (R Development team 2019). The residuals in the LMMs were visually inspected to fit normality assumption and distances were log transformed to improve it. Movement probability was scored as a binary variable (0 = no movement, 1 = movement ≥ 1 km; see “Study system”). We included in the analyses mate change, which was coded as a binary variable where 0 = no change and 1 = change, indicating if an individual had a different partner in successive breeding attempts. The cases in which the identity of one of the two partners in the following breeding attempt was unknown (because the individual was not trapped) were not counted. Furthermore, we entered breeding experience to control for the effect of age on dispersal. Breeding experience is a binary variable based on the number of breeding attempts, where individuals at their first breeding attempt in the population were recorded as first breeders, while individuals with multiple breeding attempts were considered experienced (1 = first breeders, 2 = experienced breeders). We opted to use breeding experience instead of the chronological age since the latter was not estimated with the same accuracy over time. The two variables showed to be highly correlated (Pearson’s $r=0.84$, $p<0.0001$), indicating that an individual’s age corresponds well with experience since the number of breeding attempts is dependent on age (see also

Karell et al. 2009). Finally, color morph (scored as 1 = grey, 2 = brown), was entered as a fixed factor to control for possible morph-specific variation in breeding dispersal. To assess the effect of sex on breeding dispersal, we included males and females jointly for their decision to move and movement distance (scored as females = 0, males = 1). Since the effect of mate change on the decision to move might be contingent to sex and/or breeding experience, we also tested the interactions between these variables. We entered ‘Year’ and ‘individual ID’ as random factors, to account for yearly variation and multiple breeding attempts of each individual, respectively. We also included ‘Nest box ID’ as a further random factor in order to control for the effect of breeding site on dispersal and for the non-independency of male and female partners sharing the same boxes. Overall, in the analyses, we considered only the observations for which we had complete information: for the decision to move, 912 observations out of 979 (ca. 93%), whereas, for distances, 256 observations out of 273 (ca. 94%).

Assessing consequences of breeding dispersal

Similarly to the analysis of the factors associated with breeding dispersal, we used a two-level analysis to explore the impact of breeding dispersal on different breeding parameters. A crucial decision an owl has to make after a breeding event, regardless if it moved or stayed in the territory, is whether to breed or not in the following breeding season. It is common that tawny owls skip breeding under particularly unfavorable conditions (e.g., poor food conditions, see Karell et al. 2009). However, here we aimed to assess whether non-consecutive reproductive attempts might be explained by territory change. To this end, we first analyzed the effect of movement (0 = no movement, 1 = movement \geq 1 km) on the probability to skip breeding relying on the same dataset used for the decision to move (912 observations out of 979 (ca. 93%)). We scored ‘skip breeding’ as a binary variable where 0 = consecutive reproduction between observations, while 1 = one-year gap between observations (see “Study system”). Secondly, we assessed the effect of movement on subsequent timing of breeding (i.e., laying date), breeding investment (i.e., clutch size) and breeding success (i.e., proportion of successful fledglings) only for those individuals that did not skip reproduction. By excluding cases where the individuals were not caught in the consecutive breeding season we avoided any bias of not detecting potential breeding events. Previous studies on tawny owl pointed out that females are the sex mainly controlling clutch size, while there is no effect on male on it. On the other hand, males can have an indirect effect on laying date (Brommer et al. 2015) since they are the main providers of food to the female and the brood during breeding. In agreement with these findings, we assessed the effect of movement on breeding investment

in consecutive years in females (308 observations out of 515 observations exclusive to females; ca. 60%), whereas we included both sexes in the model exploring the effects of movement on laying date (696 observations out of 979; ca. 71%). Breeding investment between breeding seasons was quantified as the difference in clutch size between breeding events, where negative values indicate a smaller clutch in the following year. However, to ensure a thorough estimate of the fitness costs associated with territory change, we ran further analyses considering breeding success, defined as the proportion of fledglings relative to clutch size (645 observations out of 979; ca. 66%), in subsequent breeding attempts (and therefore after a possible movement). This is because those individuals that moved to another territory might not modify their early breeding investment (i.e., clutch size), but could show a higher failure in raising their offspring. Breeding success was calculated using the function “cbind”, which allows taking into account the weight of clutch size on the proportion of successfully fledged chicks (Zuur et al. 2009). Laying date was calculated by taking the long term median March 31 as the reference value (=0) and assigning negative or positive values accordingly. In these models, we mainly aimed to disentangle the effect of movement itself. However, we further entered as fixed factors color morph (see above for scoring), to control for possible morph-specific patterns in fitness consequences of dispersal, sex, mate change and breeding experience (prior to movement) as well as the interactive effect sex by movement. Between-years breeding investment and laying date were modelled as LMMs with Gaussian errors, while ‘skip breeding’ and breeding success were modelled as GLMM (family “binomial”). In all sets of analyses, we entered ‘Year’, ‘Nest box ID’ (both considered in the following breeding attempt) and ‘individual ID’ as random factors.

Results

Correlates of breeding dispersal

Tawny owls showed clear breeding site fidelity in approximately 72% of observations considered in the analyses ($n=656/912$; Table 1). In the majority of these cases there was no movement between breeding attempts, although in ca. 16% (108/656) of cases categorized as “no movement” individuals moved less than 1 km (i.e., assumed to be movement within territory). Overall, for the 256 dispersal events we recorded, breeding dispersal distance ranged from 1 to 18 km, with a mean distance of 2.45 km (± 2.74 km SD). In rare cases, the pair moved together ($n=74$ observations of 52 pairs), but travelled on average shorter distances (mean \pm SD = 1.76 km \pm 1.96).

In the whole 40 years data set with 979 observations, we found 262 mate losses (26.7% where the partner was no

Table 1 Table showing the breakdown of the sample sizes for decision to move to another territory in relation to mate change in males ($n=461$), females ($n=451$) and overall ($n=912$)

		No mate change	Mate change	Total
Females	No movement	247 (78%)	68 (22%)	315
	Movement	74 (54%)	62 (46%)	136
Males	No movement	254 (75%)	87 (25%)	341
	Movement	74 (62%)	46 (38%)	120
Total	No movement	501 (76%)	155 (24%)	656
	Movement	148 (58%)	108 (42%)	256

longer detected in the population) and 23 divorces (2.3% where both partners were breeding in the population with different partners). Among these divorces, the partners returned to breed together later in life in 6/23 (26%) cases. In our sample, both females and males had mostly just one partner (mean \pm SD for males = 1.81 ± 0.95 , range = 1–5; mean \pm SD for females = 1.72 ± 0.83 , range = 1–4).

The probability to move to another breeding territory was greater after a mate change (Table 2A, Fig. 1a), although less so for males (Mate change * sex; Table 2A, Fig. 1b). Color morph and breeding experience were not associated with the probability to move (Table 2A). Males and females that moved showed similar breeding dispersal distances (Table 2B; mean \pm SD for males = $2.28 \text{ km} \pm 2.67$; mean \pm SD for females = $2.58 \text{ km} \pm 2.80$). Among those

who dispersed, distance travelled was positively associated with mate change (Table 2B, Fig. 2). Color morph and breeding experience were not associated with the distance moved (Table 2B).

Consequences of breeding dispersal

Among the owls that dispersed ($n=256/912$) 23.4% of them skipped breeding in the following season ($n=60/256$). The probability to skip breeding was higher if it was associated with a mate change (Table 3A, Fig. 3a). Indeed, in 42.2% of cases dispersers had changed partner ($n=108/256$) and among these cases the 40.7% skipped breeding ($n=44/108$). In addition, experienced breeders skipped reproduction less often than first-time breeders (Table 3A, Fig. 3b), but this effect was not linked to movement (Breeding experience * movement; Table 3A). Individuals that changed partner reproduced later in the following season (Table 3B, Fig. 3c). Females that changed partner produced smaller clutches (Mate change; Table 3C, Fig. 3d). However, laying date and clutch size were not associated with whether an individual had moved or not (Table 3B-C). Comparable results were yielded also when considering breeding success. Mate change, not movement, negatively affected breeding success in subsequent breeding attempts (estimate \pm SE = $-0.41 (\pm 0.16)$, $z = -2.57$, $P = 0.010$; Table S1 in supplementary material). Owls that changed their mate, raised fewer successful offspring (Table S1; Fig. S2 in supplementary material).

Table 2 Binomial GLMM analyzing variation in probability to move (A, Movement, left panel) and Gaussian LMM analyzing breeding dispersal distances (B, Distance, right panel) in adult tawny owls. Models include individual specific traits (color morph, sex, breeding

experience and mate change as fixed terms. The contrast is given in the table in brackets. 'Year', 'individual ID' and 'Nest box ID' are entered as random factors. Bold font indicates statistically significant effects ($\alpha=0.05$)

Predictors	A			B			
	Estimate	z	P	Estimate	df	t	P
Intercept	-1.50 ± 0.37	-4.01	<0.0001	0.48 ± 0.09	222.87	5.26	<0.0001
Color morph (brown)	-0.32 ± 0.26	-1.24	0.217	-0.02 ± 0.08	142.57	-0.27	0.786
Sex (male)	-0.03 ± 0.24	-0.12	0.944	-0.01 ± 0.08	60.47	-0.12	0.909
Breeding experience (older breeder)	-0.17 ± 0.30	-0.62	0.534	-0.03 ± 0.09	231.42	-0.31	0.754
Mate change (change)	1.92 ± 0.46	4.19	<0.0001	0.51 ± 0.12	246.54	4.43	<0.0001
Mate change*sex	-0.93 ± 0.45	-2.04	0.042	-0.03 ± 0.17	143.20	-0.21	0.835
Mate change*breeding experience	-0.67 ± 0.49	-1.37	0.171	-0.22 ± 0.14	244.88	-1.65	0.100
Random factors	Year: Variance 0.70, SD 0.84 Individual ID: Variance <0.0001 Nest box ID: Variance 4.49, SD 2.12			Year: Variance <0.0001 Individual ID: Variance 0.04 Nest box ID: Variance 0.07			

Fig. 1 Graphs showing **a)** the probability to move to another territory and **b)** the sex-specific effect of mate change on the decision to move to another territory in females and males. Error bars indicate 95% CI

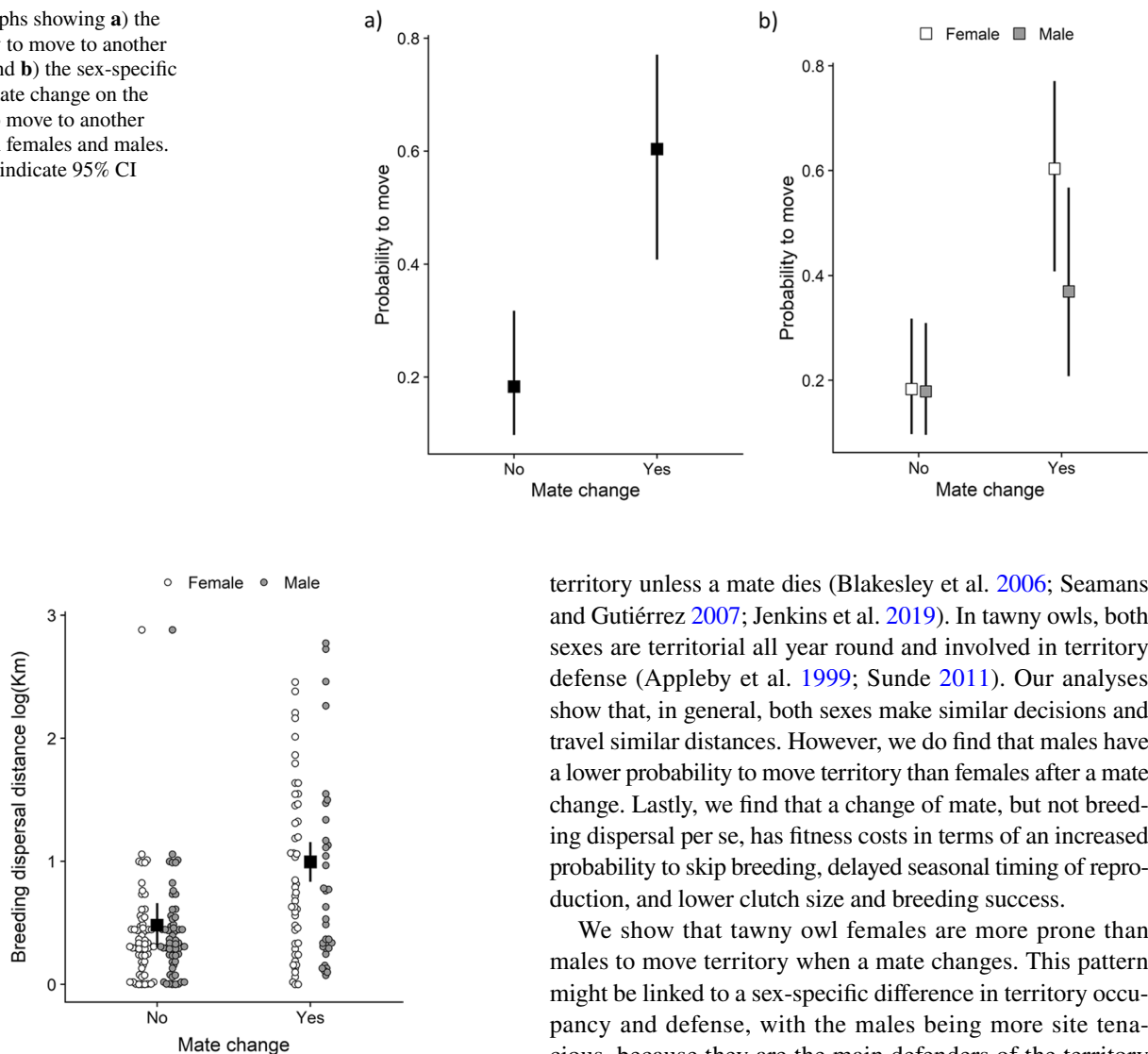


Fig. 2 Boxplot depicting the distances travelled according to mate change by both males and females. Error bars indicate 95% CI

Discussion

Our analyses indicate that breeding dispersal is rare in tawny owls and that the distances observed are way shorter than the size of the study area, indicating that movement is in most cases to the neighbouring territory and it is unlikely biased by the size of the study area. In contrast to our expectation and previous results (e.g., Forero et al. 1999), breeding experience (i.e., age) had no effect on the probability to move. On the other hand, as we hypothesized, moving territory as well as the distance moved are mainly associated with the loss of the partner in the previous year. This finding is in line with the idea that species with lasting pair bonding and marked territorial behavior are reluctant to shift to another breeding

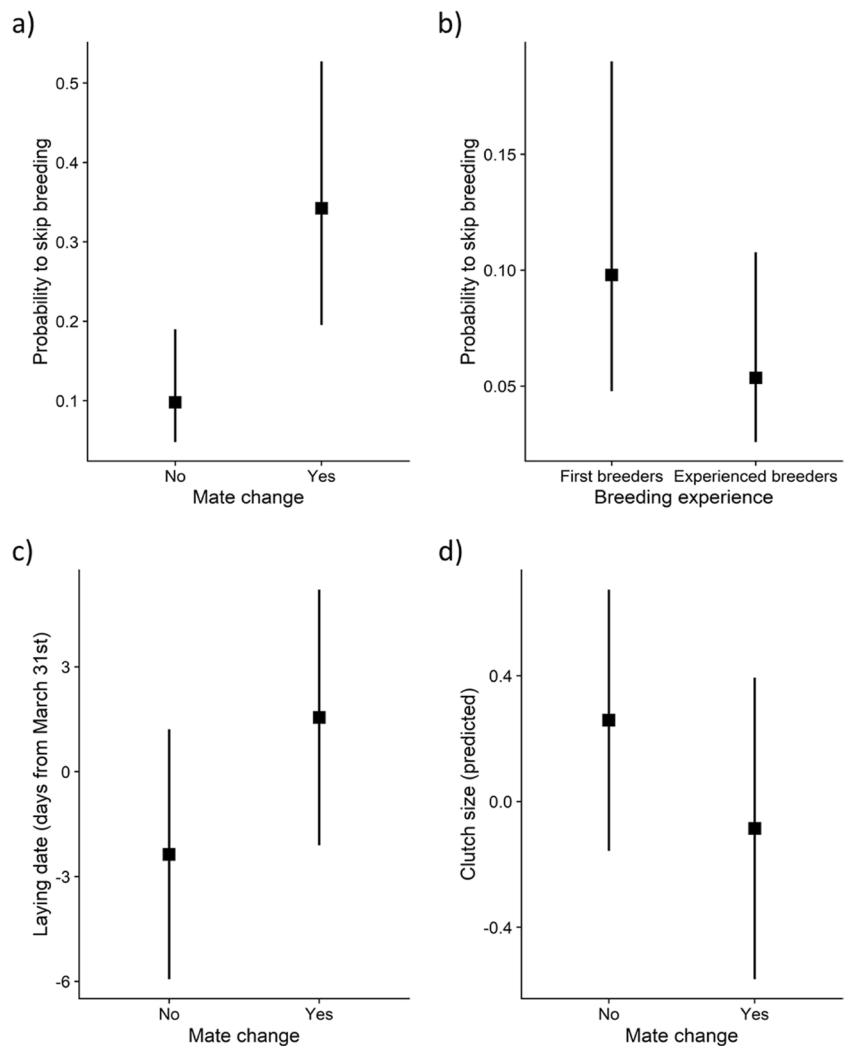
territory unless a mate dies (Blakesley et al. 2006; Seamans and Gutiérrez 2007; Jenkins et al. 2019). In tawny owls, both sexes are territorial all year round and involved in territory defense (Appleby et al. 1999; Sunde 2011). Our analyses show that, in general, both sexes make similar decisions and travel similar distances. However, we do find that males have a lower probability to move territory than females after a mate change. Lastly, we find that a change of mate, but not breeding dispersal per se, has fitness costs in terms of an increased probability to skip breeding, delayed seasonal timing of reproduction, and lower clutch size and breeding success.

We show that tawny owl females are more prone than males to move territory when a mate changes. This pattern might be linked to a sex-specific difference in territory occupancy and defense, with the males being more site tenacious, because they are the main defenders of the territory and main providers food resources during breeding in this species (Southern 1970) as has been found to be the case in other species as well (Kwon et al. 2022). The familiarity with the territory is therefore likely more important in males than females. This influence of sex roles may also be translated in differences between males and females in territory size and behavioral responses involved in territory defense. Burgos and Zuberogoitia (2020) indeed found that Tawny Owl males and females show similar home ranges (i.e., the area in which the resident individual normally moves) but that male territories were significantly larger than female ones. Furthermore, playback stimulations showed that males and females were more likely to respond to their own sex. Males, however, showed a considerable degree of aggressiveness towards intruding females, which was interpreted as an attempt to defend the reproductive value of their present mate (Appleby et al. 1999). Our finding provide support for such patterns, as in females the decision to move involved

Table 3 Binomial GLMM analyzing effects of movement on the probability to skip breeding on the left (A, Skip breeding, left panel) and Gaussian LMMs analyzing effects of movement on timing of breeding in both sexes (B, Laying date, central panel) and on breeding investment in females (C, Clutch size, right panel) in adult tawny owls. Models include individual specific traits (color morph, sex, breeding experience and mate change as fixed terms). The contrast is given in the table in brackets. 'Year', 'individual ID' and 'Nest box ID' (both in the following breeding event) are entered as random factors. Bold font indicates statistically significant effects ($\alpha=0.05$)

Predictors	A			B			C		
	Estimate	z	P	Estimate	df	P	Estimate	df	P
Intercept	-2.22 ± 0.39	-5.64	<0.0001	-2.37 ± 1.82	64.82	0.199	0.26 ± 0.21	135.90	0.223
Color morph (brown)	0.16 ± 0.24	0.65	0.515	-0.54 ± 0.61	598.25	0.380	0.005 ± 0.16	282.82	0.977
Sex (male)	0.31 ± 0.25	1.25	0.211	0.53 ± 0.54	482.30	0.323	-	-	-
Movement (yes)	-0.04 ± 0.43	-0.10	0.923	0.35 ± 1.19	654.90	0.767	0.05 ± 0.25	283.74	0.828
Mate change (change)	1.58 ± 0.25	6.23	<0.0001	3.92 ± 0.69	636.12	<0.0001	-0.35 ± 0.17	285.60	0.038
Breeding experience (older breeder)	-0.65 ± 0.27	-2.42	0.015	-0.21 ± 0.70	610.56	0.766	-0.13 ± 0.19	288.54	0.501
Sex*movement	0.01 ± 0.47	0.01	0.989	-0.60 ± 1.05	498.45	0.570	-	-	-
Breeding experience*movement	-0.15 ± 0.49	-0.31	0.754	0.25 ± 1.27	628.26	0.840	-0.17 ± 0.31	281.47	0.588
Random factors	Year: Variance 1.75, SD 1.32 Individual ID: Variance <0.0001 Nest box ID: Variance 1.25, SD 1.12	Year: Variance 106.51, SD 10.32 Individual ID: Variance <0.0001 Nest box ID: Variance 35.22, SD 5.94	Year: Variance 0.63, SD 0.79 Individual ID: Variance <0.0001 Nest box ID: Variance <0.0001						

Fig. 3 Boxplots depicting the probability to skip breeding in relation to (a) mate change and (b) breeding experience and the variation in laying date (c) and female clutch size (d) between individuals who stayed with their partner and those who changed in subsequent breeding events. Error bars indicate 95% CI



partner change more often than in males (see Table 1). This might indicate that males sometimes might aim to move to a better (closer) area bringing the female along. Regardless of the mechanism driving this pattern, territory defense is likely costly for a single individual of either sex and from an individual's success point of view moving to find a new partner (possibly already holding a territory) may be better than keep defending the territory waiting for a new mate to arrive (Danchin and Cam 2002).

Here we show that mate change is strongly associated with movement and also determines the distances the individuals travel, probably because distances can be interpreted as a function of the time an individual has to invest to find a new partner and territory (Forero et al. 1999; Bowler and Benton 2005). Site choice and partner search might be closely related as it has been suggested for the spotted owl (*Strix occidentalis*), in which the selection of new territories by breeding individuals was not correlated with habitat, but may have been associated with the presence of a mate (Seamans and Gutiérrez 2007).

Comparing breeding success between breeding events with or without movement provides an estimate of the potential costs (or benefits) of breeding dispersal. Especially in territorial species dispersal is likely costly and fitness is expected to decrease as a consequence of movement (Korpimäki 1987, 1988), a pattern frequently advocated as the reason why breeding dispersal is usually uncommon (Greenwood and Harvey 1982). Nevertheless, we found that mate change, but not movement to a new territory, had negative effects on subsequent reproductive performances, in both sexes. Indeed movement itself seemed not to have any apparent fitness consequences, whereas mate change affected the decision to skip reproduction and delayed the timing of breeding and led to smaller clutch sizes and lower breeding success in subsequent breeding events.

While in some systems individuals dispersing after a divorce showed an increase in their breeding success, likely because the individuals aimed at finding a better partner (Valcu and Kempenaers 2008), in our study system divorces were extremely rare and mate change was mainly associated

with widowhood. This may explain the higher negative effect of mate change on breeding parameters and indicate that the costs of losing and finding a new mate have a higher impact on fitness than the costs associated with losing and finding a new territory. However, since movement and mate change seem to be entwined, as mate change appears to be the major trigger of breeding dispersal in tawny owls, we are not able here to separate their relative effects.

These findings provide formal support for a connection between (social) monogamy and territoriality. One of the hypotheses for the evolution of monogamy states that it should evolve more easily in species where male assistance is indispensable for female reproductive success (Wittenberger and Tilson 1980). In addition, monogamy should evolve more frequently in territorial species given the mutual benefits for both males and females in sharing the costs of acquiring and holding good quality territory (Wittenberger and Tilson 1980; Mitani 1987). Tawny owls, as birds of prey in general, have obliged bi-parental care with a clear division of duties between sexes during the breeding season, where the males are the main food providers whereas the females defend the nest and allocate the resources within the brood (Sunde et al. 2003). Therefore, beside the benefits of sharing the costs of jointly defending a territory, pairs likely have benefits in terms of parental investment since both sexes provide parental cares but according to specific tasks. Outside the breeding season the difficulties linked to track the animals hamper the possibility of carefully studying the contribution of each sex in the territory defense. However, there is evidence suggesting that the effort of territorial defense is mainly on males as female vocal activity associated with territory defense can be negligible and focused in a core area whereas males cover a bigger area (Burgos and Zuberogoitia 2020). The biology of the species therefore, seems to support the idea that mates cooperate to increase their breeding success and therefore that being paired with a mate may have a higher impact on fitness than the territory itself.

Irrespective of the effect of mate change, we found that probability to skip breeding was also determined by the breeding experience (i.e., age) of the individuals and that younger individuals tended to skip reproduction more frequently than older (more experienced) breeders. This pattern can indicate that at the beginning of the breeding career individuals may be more affected by fluctuations in environmental conditions (e.g., lower food availability; Karell et al. 2009) and be more prone to skip breeding, whereas more experienced individuals might cope better with environmental conditions and rely on alternative mechanisms that can optimize their effort (e.g., clutch size control, use of alternative prey). Alternatively, the relationship we found might be explained by the unfamiliarity with environment that unexperienced breeders have to face at their first breeding event. Since immigrants are, by definition, unexperienced breeders, the pattern could be related somehow to social status (immigrants vs residents).

We found no association between color polymorphism and neither the causes nor the consequences of breeding dispersal. This absence of relationship might actually indicate that, contrarily to what predicted, morphs do not vary in their probability to change breeding territory. This might be due to the fact that breeding individuals are expected to become more site-tenacious over time regardless of their coloration (van den Brink et al. 2012). Alternatively, morph-specific patterns in breeding dispersal might reside in the different strategies of morphs to cope with environmental features (Karell et al. 2011a, b), as observed also for natal dispersal in this species (Passarotto et al. 2022). Therefore, we cannot fully discard that one of the phases of breeding dispersal process (i.e., departure, vagrant stage and settlement) might vary between morphs in relation to some attributes of the environment we did not account for in this study, such as local changes in habitat structure and/or food abundance.

To summarize, our study supports the idea that breeding dispersal is a rare event in territorial species. In addition, it confirms previous findings showing that mate loss is a critical factor underpinning breeding dispersal. More importantly, here we provide new important insights on the fitness consequences linked to the factors associated with dispersal, specifically to mate change, and shed light on previously overlooked sex-specific behavioral differences promoting territory change. The negative effects of mate change rather than movement on reproductive performance suggest that mate fidelity might be the constraint of breeding dispersal in territorial partner-faithful species and that individuals would be unlikely to change territory if they did not change partner. Although it is not clear if monogamy might have driven territoriality or vice versa (Wittenberger and Tilson 1980; Mitani 1987), the link between site fidelity and mate fidelity is well established and found in several species (e.g., Newton 2001; Catlin et al. 2005). However, given the different tasks in which sexes are involved, sex-specific patterns might arise when the mate is lost, revealing for example a higher site tenacity of the territory defending sex (males). Such an insight provide novel details about the complex behaviors underlying territoriality and how these can affect not only breeding dispersal movements but also subsequent breeding performances and thereby fitness.

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Authors contributions KA, TK and EA collected the long term data with help from PK, CM and JEB. PK, JEB, CM and AP conceived the study. PK performed preliminary analyses. AP, CM and PK conducted final analyses and modelling. AP and PK wrote the first draft. AP, CM, PK and JEB finalized the manuscript. All authors critically commented and approved the manuscript.

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Data accessibility Analyses reported in this article can be reproduced using the data provided in supplementary material.

Declarations

Ethics approval All applicable international, national, and institutional guidelines for the care and use of animals were followed. All birds were captured, handled, and ringed with an appropriate ringing license and no further permits were required.

Conflicts of interest The authors declare no conflicts of interest.

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