

Article

The potential function of post-fledging dispersal behavior in first breeding territory selection for males of a migratory bird

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Abstract

One possible hypothesis for the function of post-fledging dispersal is to locate a suitable future breeding area. This post-fledging period may be particularly important in migratory species because they have a limited period to gather information prior to autumn migration, and in protandrous species, males must quickly acquire a territory after returning from spring migration to maximize their fitness. Here we use color-ring resightings to investigate how the post-fledging dispersal movements of the Cyprus wheatear *Oenanthe cyprica*, a small migratory passerine, relate to their first breeding territory the following year when they return from migration. We found that males established first breeding territories that were significantly closer to their post-fledging location than to their natal sites or to post-fledging locations of other conspecifics, but these patterns were not apparent in females. Our findings suggest that familiarity with potential breeding sites may be important for juveniles of migratory species, particularly for the sex that acquires and advertises breeding territories. Exploratory dispersal prior to a migrant's first autumn migration may contribute toward its breeding success the following year, further highlighting the importance of early seasonal breeding on fitness and population dynamics more generally.

Key words: dispersal, migratory bird, juvenile, territory selection.

Dispersal is a key process in population dynamics and biogeography with important consequences for evolution and gene flow, invasions, extinctions and colonization, and conservation biology (Clobert et al. 2001; Winger et al. 2019). Natal dispersal, the permanent movement of an individual from its natal site to its first breeding territory (Greenwood and Harvey 1982), is critical in our understanding of population dynamics, especially in an era of rapid environmental change (Travis et al. 2013). Despite its importance, it is difficult to study owing to the widely acknowledged challenges of tracking dispersing organisms (Tesson and Edelaar 2013; Jönsson et al. 2016).

The first dispersal event for individuals of many animal species occurs when they become independent from their parents and move

away from their natal area. These dispersal movements may influence future territory establishment through prospecting behavior (Cox and Kesler 2012) and by gaining public information relating to local productivity (Curie and Bernard 1997; Doligez et al. 2002; Betts et al. 2008). For migratory species though, post-fledging dispersal is followed by migration to nonbreeding grounds, so it may also be involved in forming a homing target for their return migration (Wiltschko and Wiltschko 1978), or in the commencement of migration itself as some species have been observed to “drift” southward prior to fattening for migration (Rappole and Ballard 1987).

Post-fledging dispersal describes the first movements of an individual away from its natal site, which can include movements where

they are dependent on adults (i.e., during the post-fledging dependency period) and movements once they gain independence from their parents (e.g., Morton et al. 1991; Anders et al. 1998). Previous work on dispersal in migratory species has predominantly focussed on the post-fledging dispersal movements prior to migration (e.g., Anders et al. 1998; Brown and Taylor 2015), natal dispersal (e.g., Forero et al. 2002), and the post-breeding territory prospecting movements of adult breeders (e.g., Arlt and Pärt 2008a) and non-breeders (e.g., Pärt et al. 2011), but few have considered how post-fledging movements influence natal dispersal in migratory species (e.g., Ciaglo et al. 2021). This is presumably because of difficulties in tracking the movements of dispersers, especially in migratory species that typically disperse further than resident species (Paradis et al. 1998). Nevertheless, post-fledging prospecting of future breeding territories is likely to be most important in migratory species, which have limited time available on the breeding ground prior to migration and must establish a territory rapidly on returning from spring migration because early breeding increases their fitness (Smith and Moore 2005; Verhulst and Nilsson 2008; Öberg et al. 2014; Hadjikyriakou et al. 2020). Selection for the use of the post-fledging period for locating a future breeding territory may, however, be stronger in males rather than females because the process of territory establishment may be sex biased (Greenwood 1980, but see Clarke et al. 1997; Li and Kokko 2019). Again, this might be particularly pronounced in migratory birds because males tend to return to the breeding grounds before females (Kokko et al. 2006; Schmaljohann et al. 2016).

Our objective was to investigate if the post-fledging dispersal period influences first territory selection in a migratory species. Here we observe the post-fledging dispersal period and subsequent first breeding site selection in Cyprus wheatear *Oenanthe cyriaca*, an obligate migratory passerine. Cyprus wheatears are a good model system to investigate post-fledging dispersal in relation to first breeding territories due to their high apparent survival in juveniles, and relatively short natal dispersal distances (Xenophontos and Cresswell 2016a). Previous work in this species found that the post-fledging dependency period, where juveniles are dependent on their parents and remain in their natal site, lasted for ~18 days after fledging before dispersing and occupying a home range of similar size to their natal site, and in suitable breeding habitat, after ~45 days (Styles et al. 2021). This suggests that the post-fledging dispersal period prior to embarking on migration may serve as a period of prospecting for a first breeding territory once individuals have returned. If the post-fledging dispersal process influences breeding territory selection for the following year, we would hypothesize that:

- a. first breeding territories of individuals would be closer to their post-fledging locations than to their natal sites and
- b. individuals' first breeding territories would be closer to their own post-fledging location than to the post-fledging locations of other juveniles in the study area.

Evidence is needed to support both of these hypotheses to determine if juveniles utilize the post-fledging dispersal period to gain familiarity with potential first breeding territories, because juveniles could cluster post-fledging in an area optimized for foraging (Streby et al. 2011), or for forming a homing target for their return migration (Wiltschko and Wiltschko 1978), which is on average closer to their subsequent first breeding location than their natal sites. We expected both patterns might be stronger in Cyprus wheatear males

than in females because males defend and advertise breeding territories (but see Patchett et al. 2021).

A key limitation of any field study aiming to observe dispersal in a natural population is the area covered by the field site (Koenig et al. 1996). In our study, we were primarily limited by the area that can be searched by fieldworkers. We acknowledge that some individuals are likely to have dispersed from the study area, and we highlight this as a key caveat to this study—we were only able to include individuals that could be observed within the field site.

Materials and Methods

Fieldwork

Cyprus wheatears migrate from their breeding range in Cyprus to eastern sub-Saharan Africa (Xenophontos et al. 2017). They arrive at Troodos during March and April, and egg laying commences in early May (median clutch initiation date was 11 May in Xenophontos and Cresswell 2016b). Eggs are incubated for ~17 days, and chicks fledge from the nest ~14 days after hatching (Xenophontos and Cresswell 2016b). This is followed by a post-fledging dependency period which lasts ~18 days and appears separate from post-fledging dispersal in this species (Styles et al. 2021). Average territory sizes were estimated to have radii of 175 ± 45 m ($N = 12$) in Styles et al. (2021) and territory centers were estimated to be separated by 88.9 ± 1.7 m ($N = 164$) in Xenophontos and Cresswell (2016a).

Our field site is located within the National Forest Park of Troodos, Cyprus (NFP of Troodos; $34^{\circ}56'11''N$, $32^{\circ}51'48''E$) and centered around the “Artemis Trail” area and has been used to study Cyprus wheatears continuously since 2009 (Xenophontos and Cresswell 2016b). Juvenile birds were captured in the breeding season (6th June to 8th August) using spring traps and mist nets during the post-fledging dependency period whilst with their respective parents and within their respective natal territories. We did not ring birds as pulli because Cyprus wheatears are ground-cavity nesters where access to the nest would have been impossible without excessive disturbance. However, we ensured that juveniles were ringed within their respective natal territories by restricting our sample to those birds that were in the post-fledging dependency period; had color-ringed parents that were on-territory; and we only attempted to capture juveniles that had parents in attendance that were observed providing parental care. Each bird was individually identified with a unique combination of 3 color rings and a metal ring provided by BirdLife Cyprus. A total of 193 juveniles from 81 broods were color-ringed in their natal territory (2017 = 91; 2018 = 49; 2019 = 53).

During 4 breeding seasons from 2017 to 2020 (April to August), we repeatedly searched the field site to identify and map the territories of adult Cyprus wheatears. We carried out this work alongside a parallel study focused on migration. The search routes were neither randomized, nor defined in structure, other than each marked territory was visited at least weekly. Some territories were visited more regularly because routes often started from the same point. In 2018, 2019, and 2020, we searched within an additional 500 m buffer surrounding the main field site to include first breeding territories of returning birds ringed as juveniles in the previous year that may have dispersed out of the main field site (this increased the search area from ~2 km² to 5 km²). The 500 m buffer was based on previous estimates of natal dispersal in this species at Troodos, where 90% of juveniles were found to settle in a first breeding territory

around 3 territories (i.e., a few hundred meters) from their natal site (Xenophontos and Cresswell 2016a), and note that increasing the search area further was also constrained by the area that could be effectively covered by fieldworkers. We covered the extended field site at least weekly, and recorded the date, time, and location of every color-ringed bird we observed. Locations were recorded using a map of the field site that included all territories and with reference to the observer's current location using GPS and landmarks. Breeding territory locations were defined by territory centers. Natal sites were defined by the nest location of the color-ringed parent birds seen feeding the fledglings where possible, otherwise we used the respective territory center estimated from territory mapping.

Distance calculations

To analyze the relationship between a bird's natal site, where it dispersed to during the post-fledging dispersal period, and its subsequent first breeding territory, we needed to have observed individuals at each of these locations. Of the 193 juvenile birds that were captured in their natal territory, 35 were observed the following year, and of these 18 had been resighted during their post-fledging dispersal period at least 32 days after fledging ($N=6$ birds with a dispersal observation between 32 and 44 days since fledging and $N=12$ birds with observations 45–67 days since fledging). Styles et al. (2021) found that juvenile Cyprus wheatears with dispersal observations from 45 days after fledging were found to have distances between consecutive locations consistent with occupying a home range equivalent in size (radius 175 ± 45 m) and habitat (e.g., *Pinus nigra* and *Juniperus foetidissima* woodlands with open areas of Serpentinophilous grassland) to a breeding territory. We included the 6 birds where dispersal observations were between 32 and 44 days after fledging because dispersal was observed to be directional for each individual, that is, each individual tended to disperse in 1 main direction, and independently from other juveniles (Styles et al. 2021), and by this point they are likely to be moving toward their final post-fledging location (In Styles et al. (2021), juveniles were estimated to have moved 355–518 m from their natal site between Days 32 and 44 after fledging, compared with 526–556 m between Days 45 and 50). This left a sample size of 18 birds for analysis (13 males and 5 females) of which 6 were also tracked using radio telemetry for a single season parallel study that described post-fledging dispersal but that could not determine its functional significance in terms of territory selection the following year (see Styles et al. 2021). We used the final locations of these 6 birds as their dispersal locations in our analyses. The 6 birds still retained their radio tags, but we assume that dispersal was unhindered because they successfully migrated with the tags. Note that the tags were only active during the post-fledging period so were not used in locating them the following year. The 18 birds were from $N=12$ broods (1 brood contributed $N=3$ individuals, 4 broods $N=2$ individuals, and 7 broods $N=1$ individual). In cases where we observed an individual multiple times during the post-fledging dispersal period ($N=10$), we used its final location for analysis. Four individuals were observed more than once >45 days from fledging. We repeated the analyses using the centroid of these observations instead of the location of the final observation and found that it made no difference to our results.

Statistical analyses

To test if a bird's first breeding territory was closer to its post-fledging location from the previous year than its natal site, we

compared the difference in distance between its post-fledging location and first breeding territory, and between its natal site and first breeding territory. If the post-fledging dispersal process influences subsequent breeding territory selection, then we expect the first breeding territory to be closer on average to the post-fledging location than the natal site. We tested this hypothesis statistically by fitting a linear mixed model (LMM) using the lme4 R package (Bates et al. 2014). This model included distance as a response variable and a 2-level factor that categorized whether distance was between post-fledging locations and first breeding territories, or between natal sites and first breeding territories, with sex as an interaction term. We included "individual" as a random intercept because we calculated 2 distance values per bird, so these data are paired at the individual level. We log-transformed the response variable "distance" to ensure normally distributed residuals.

Second, we tested whether birds' first breeding territories were closer to their own post-fledging locations than to the post-fledging locations of the other juveniles in the study. If juveniles cluster in staging locations post-fledging, then we would also expect juveniles' first breeding territories to be no nearer on average to their own post-fledging locations than to those of other birds. We tested this hypothesis statistically by fitting a LMM that included distance as a response variable and a 2-level factor that categorized whether distance was between post-fledging locations and the respective first breeding territories, or the mean distance between first breeding territory of focal individuals and the post-fledging locations of the other juvenile birds, with sex as an interaction term. As with the previous model, we included "individual" as a random effect.

All analysis was carried out in R version 4.0.3 (R Core Team 2020). Results are reported as mean \pm 1 standard error unless otherwise stated and were calculated using the emmeans package (Length 2020). Note that for Model 1 the standard errors were back-transformed using the "Delta Method" within the emmeans package because the response variable was log-transformed. For both models we used the emmeans package to compare the difference in distance between the locations (i.e., the 2-level distance factor in each model) for each sex, and so we report 3 results for each model: (1) the interaction, and then the comparison of distance between the locations for (2) males and (3) females. We considered including "brood" and "year" as random intercepts but found that models were overfitted when including either of these effects. Note that in our study system, related siblings and unrelated fledglings from the adjacent territories typically move with the same degree of independence (Styles et al. 2021 unpublished data) and so we would not predict strong brood effects. We structured our models explicitly based on our hypotheses, rather than following model selection to remove terms. We expected differences between sexes in dispersal behavior (e.g., Greenwood 1980), and so our models include the interaction between distance type and sex to estimate the difference between the 2 distance types for each sex. We also repeated both models with sex excluded and presented these models as supplementary material (Supplementary Material Appendix 1).

Results

First breeding territories were closer to post-fledging locations than to natal site for 9 of 13 males and 2 of 5 females (see Figure 1 for mapped locations). First breeding territories of males were significantly closer to their post-fledging locations than natal sites, but there was no difference between the respective distances in females (LMM: males, -303 ± 99 m, $t_{28,4} = -3.06$, $P = 0.005$; females,

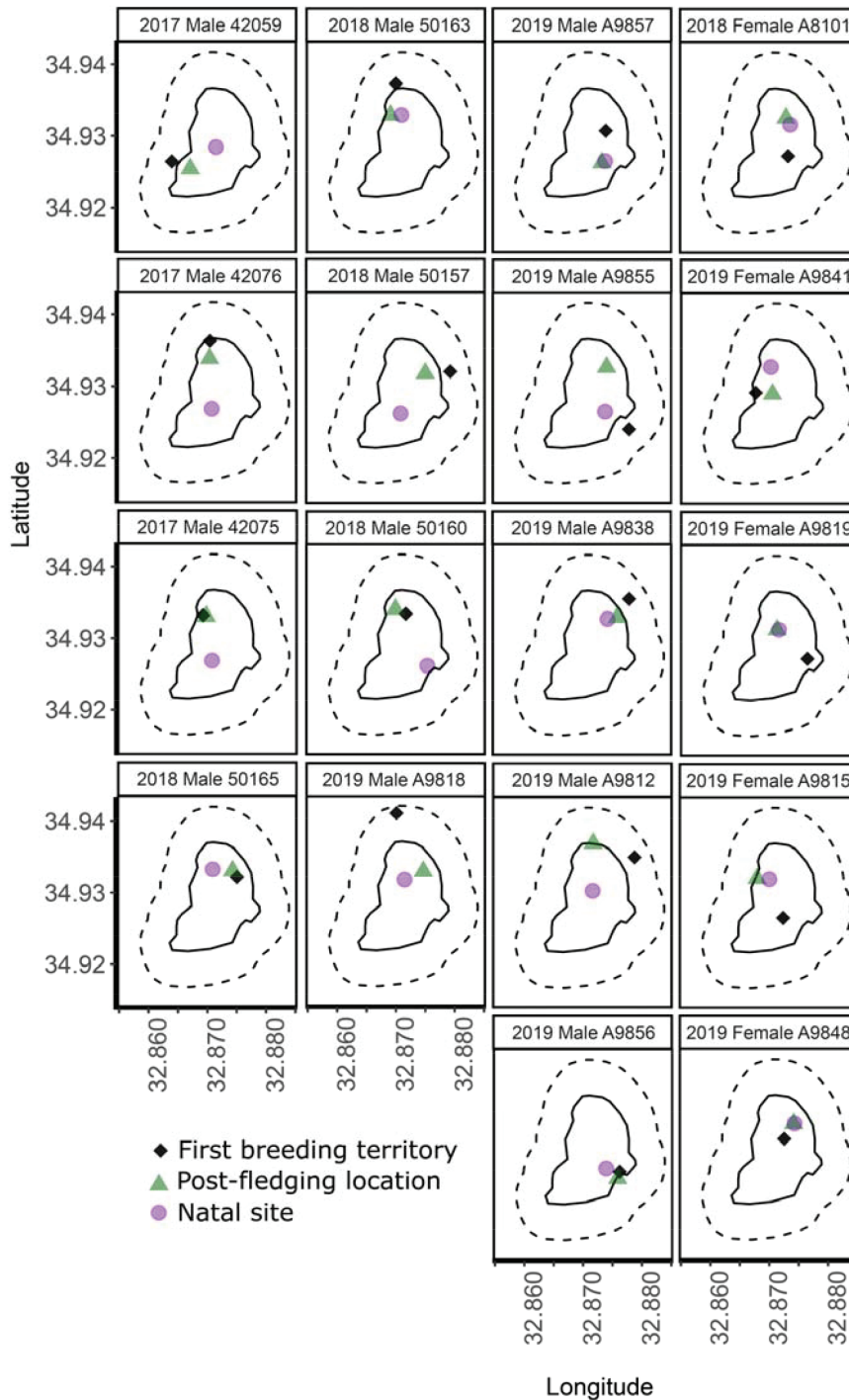


Figure 1. Natal site, post-fledging location, and first breeding territory for individual male and female Cyprus wheatears at Troodos, Cyprus. Solid line shows main field site boundary. Dashed lines show extended field site area used to search for dispersed birds. The year indicated is the year that the individual was born. Ring identification numbers are shown for each individual.

8 ± 143 m, $t_{28.4} = 0.06$, $P = 0.95$; interaction: -0.70 ± 0.37 log m, $t_{16} = -1.90$, $P = 0.08$; $R^2_{\text{marginal}} = 0.19$, $R^2_{\text{conditional}} = 0.48$; Supplementary Table S1; Figure 2(i) and (ii)).

In addition, distances between first breeding territories and post-fledging locations were significantly shorter than the mean distance between the first breeding territory and the post-fledging locations of all other birds included in the analysis for males, but not for females (LMM: males, 311 ± 63 m, $t_{16} = 4.93$, $P < 0.001$; females;

89 ± 102 , $t_{16} = 0.87$, $P = 0.40$; interaction, 223 ± 120 m $t_{16} = 1.86$, $P = 0.08$; $R^2_{\text{marginal}} = 0.24$, $R^2_{\text{conditional}} = 0.67$; Supplementary Table S3; Figure 3).

Discussion

First breeding territories were closer to post-fledging dispersal locations the previous year than to natal territories in males, but not in

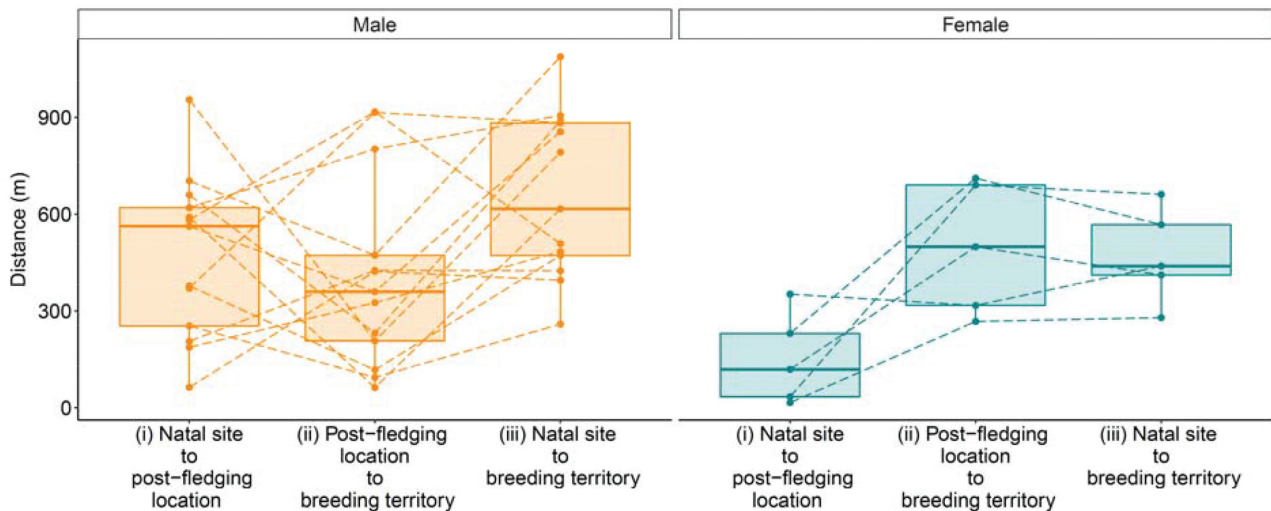


Figure 2. First breeding territories of male Cyprus wheatears were closer to their post-fledging locations than their natal territories, but this was not apparent for females. Distances between (i) Natal sites and post-fledging locations, (ii) post-fledging locations and first breeding territories, and (iii) natal sites and first breeding territories for male and female Cyprus wheatears. Points show raw data, and data for the same individual are joined by dashed lines.

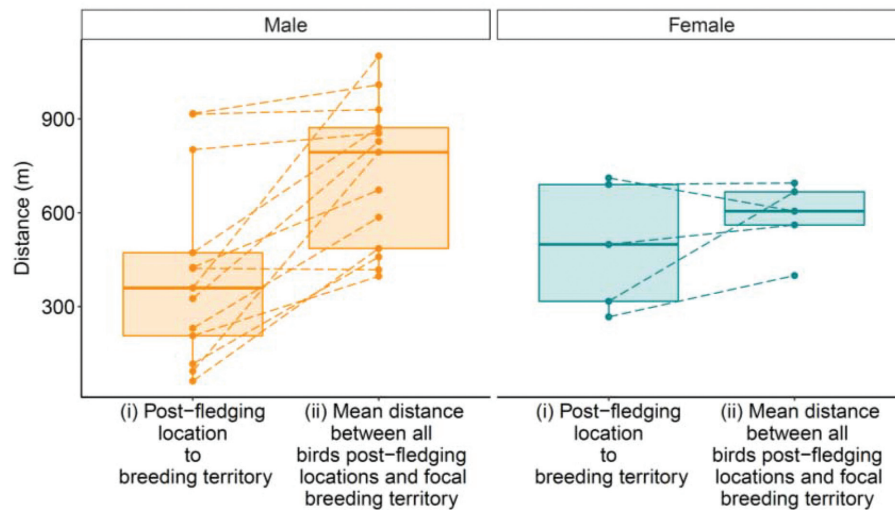


Figure 3. First breeding territories of male Cyprus wheatears were closer to their own post-fledging locations than those of other juvenile conspecifics, but this was not apparent for females. (i) Distances between post-fledging locations and first breeding territories and (ii) the mean distance between the first breeding territory of focal individuals and the post-fledging locations of the other juvenile birds for males and females. Points show raw data, and data for the same individual are joined by dashed lines.

female Cyprus wheatears (Figure 2). The proximity of male first breeding territories to their post-fledging dispersal movements suggests that post-fledging dispersal may involve prospecting for future breeding territories. Because males return earlier than females to the breeding grounds following migration, it allows them to establish territories before females arrive (Morbey and Ydenberg 2001; Arlt and Pärt 2008b; Schmaljohann et al. 2016), and early arrival can increase their breeding success (e.g., Smith and Moore 2005; Currie et al. 2000; Joos et al. 2014). Site familiarity is hypothesized to be important in initial settlement decisions (Piper 2011); familiarity with possible breeding sites gained during the post-fledging dispersal period could potentially reduce predation risk (e.g., Yoder et al. 2004), and inevitably reduce energy expenditure the following year when not having to search for a first breeding territory. These advantages are likely to be greater in migratory species that are

unable to explore the breeding grounds during most of the non-breeding season and that must establish a breeding territory immediately after an energetically costly spring migration. Male territory prospecting may operate successfully during post-fledging dispersal if territories and their quality are relatively stable between years, and so information gathered post-fledging is then likely to be useful in choosing a first territory (Ciaglo et al. 2021). Thus, first year males should increase their fitness by gaining knowledge of potential breeding sites prior to their first autumn migration.

We found that the distance of each male's first breeding territory was closer on average to their own post-fledging location than to those of other juveniles in the study (Figure 3). This result is consistent with first breeding territories being closer to the areas that each individual explored during their post-fledging dispersal period, and thus further away (on average) from the areas that other individuals

explored. It suggests that individuals prospected for their future territory during post-fledging dispersal, rather than clustering in a staging area prior to migration (Morton et al. 1991), or clustering in foraging habitat patches that were different from their typical breeding habitat (Vega Rivera et al. 1998; Streby et al. 2011), although we do not exclude the possibility that juveniles could use different foraging habitat within or near to their prospective breeding territory. This post-fledging prospecting behavior could increase the speed of territory acquisition after returning from spring migration, and because early arrival to the breeding ground is correlated with increased breeding success (e.g., Smith and Moore 2005; Hadjikyriakou et al. 2020), post-fledging prospecting may carry over to increased fitness. The advantage of post-fledging prospecting over other post-fledging strategies likely depends on the predictability of habitats between years—that is, a suitable location for a breeding territory in 1 year is also suitable the following year. The potential advantage of post-fledging prospecting may be reduced then if territory quality becomes less predictable in response to environmental change. Understanding whether the cues used to determine territory quality during post-fledging prospecting remain good indicators of territory quality the following year will likely determine the impact of environmental change on post-fledging prospecting.

In contrast to males, females did not settle closer to their post-fledging location than to their natal sites, and post-fledging dispersal distances appeared to be shorter for females than males (Figure 1). This may have emerged if juvenile females were less likely to disperse than males, or if some females stayed close to their natal territory while others dispersed further afield and were then undetected. If some females dispersed distances such that they were undetected, then these birds could potentially also have returned to a first breeding territory close to their post-fledging dispersal location. Females arrive on the breeding grounds later than males and so recruitment to their first breeding territories is likely to depend on both its availability and quality, and the quality of the male occupying it (Arlt and Pärt 2008b). This may result in females moving further from their post-fledging location because they can enhance their potential breeding success by comparing males and their resources (Greenwood 1980; Bensch and Hasselquist 1992). We caution, however, that our sample size for females was small, and that some males and females likely dispersed out of the study area so that we cannot know whether their first breeding territory was close to their post-fledging dispersal location.

The effects of both measurement error and the outcomes of biological processes modifying initial territory choice seem likely to explain much of the variation in distance between the post-fledging locations and first breeding territories (Figures 2 and 3). First, our estimates of post-fledging locations are likely to include some error due to both the extent of movement around the home range and the timing of the observation. With respect to the timing of observation, post-fledging dispersal is typically directional at the individual level in this species (Styles et al. 2021), so we can assume that the observed post-fledging locations are toward the final post-fledging home ranges. Second, post-migration territory establishment will depend on the presence or absence of previous incumbents of territories in the area where first year males dispersed to post-fledging (Arlt and Pärt 2008b). First year males may be forced to move to adjacent areas if the previous male occupant of that territory has returned the following year. Furthermore, competition for territories among first years is likely to further disperse some birds. It is also possible that dispersing juveniles made repeated dispersal movements to and from their natal territory (e.g., Cox and Kesler 2012)

and if this process were to happen after 32 days then it could be an additional source of error in our post-fledging locations—that is, our predicted pattern would be more difficult to detect because some post-fledging locations could be biased toward natal sites. Finally, we do not exclude the possibility that some of the sampled birds may have post-fledging strategies that do not directly involve post-fledging prospecting, indeed first breeding territories were closer to natal sites than post-fledging locations for 4 out of 13 males. For example, movements of some juveniles may be related to optimal food availability (Vitz and Rodewald 2007), but nevertheless any local scale movement has potential to inform future breeding territory selection (Piper 2011). As with similar studies, we are limited by the area that can be searched and will have missed any longer distance dispersers (>500–2,000 m depending on where the natal territory was within the field site), and whether those individuals show a similar relationship between their post-fledging dispersal and breeding territory establishment remains to be examined. In such cases, dispersers might make their long-distance movement either during the post-fledging dispersal period or on their return following migration.

Our findings overall suggest that familiarity with potential breeding sites acquired during post-fledging dispersal is likely to be important in subsequent settlement decisions in migratory species. Migrants have limited time to explore potential breeding sites prior to autumn migration, and in protandrous species males must establish a territory quickly following spring migration to maximize their fitness. Our results suggest the period prior to a bird's first autumn migration is important in its territory establishment and potentially in its breeding success the following year. Future work could investigate the relationship between breeding success and dispersal behavior: individuals that occupy territories close to areas they explored during post-fledging dispersal may increase their breeding success, and individuals that return from migration to find conditions have changed, or that their prospective territory is occupied, could continue dispersing to find a suitable territory and may be more likely to miss a breeding opportunity that year. Post-fledging dispersal might indeed play an important role in the population dynamics of migratory species more generally. Such dispersal can allow populations to adapt to environmental change (Jiguet et al. 2007) and identifying the stages and times at which dispersal occurs and their subsequent influence on fitness may be crucial in understanding how resilient species are to the current rapid changes occurring through habitat loss and shift. If the offspring of early breeders have more time to explore for a future breeding territory, there could be carry-over effects to the following year. Studies in birds have found that early breeding is associated with breeding success (e.g., Smith and Moore 2005; Hadjikyriakou et al. 2020). Our findings suggest that post-fledging dispersal could be another example of the crucial importance of phenology to fitness and population dynamics, particularly in long-distance migrant animals, because early breeding allows for earlier and more effective territory prospecting by juveniles prior to migration. This may then carry-over to higher reproductive performance in their first breeding season.

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Conflict of Interest Statement

The authors declare that they have no conflicts of interest.

Data Availability Statement

The research data supporting this publication can be accessed at <https://doi.org/10.17630/342878fe-afd2-42ed-8d45-2a4acd742580> (Patchett et al. 2022).

Supplementary Material

“Supplementary material can be found at <https://academic.oup.com/cz>”.

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