

Dispersal: a matter of scale

ELISE R. MORTON ^{1,7} MICHAEL J. MCGRADY,² IAN NEWTON,³ CHRIS J. ROLLIE,⁴
GEORGE D. SMITH,⁵ RICHARD MEARNES,⁶ AND MADAN K. OLI¹

¹*Department of Wildlife Ecology and Conservation, School of Natural Resources and Environment, University of Florida, 110 Newins-Ziegler Hall, Gainesville, Florida 32611 USA*

²*International Avian Research, Am Rosenhügel 59, 3500 Krems, Austria*

³*Centre for Ecology and Hydrology, Benson Lane, Crowmarsh Gifford, Wallingford OX10 8BB United Kingdom*

⁴*Royal Society for the Protection of Birds, (RSPB) Scotland, Dumfries and Galloway Office, The Old School, Crossmichael, Castle Douglas DG7 3AP United Kingdom*

⁵*Scottish Raptor Study Group, 58 Meadowbank Road, Kirknewton, West Lothian EH27 8BS United Kingdom*

⁶*Conansknowe, Kirkton, Dumfries DG1 1SX United Kingdom*

Abstract. Population density around the natal site is often invoked as an explanation for variation in dispersal distance, with the expectation that competition for limiting resources, coupled with increased intra-specific aggression at high densities, should drive changes in dispersal distances. However, tests of the density-dependent dispersal hypothesis in long-lived vertebrates have yielded mixed results. Furthermore, conclusions from dispersal studies may depend on the spatial and temporal scales at which density and dispersal patterns are examined, yet multi-scale studies of dispersal are rare. Here, we present the findings of a long-term study examining factors influencing natal dispersal distances for the non-migratory population of Peregrine Falcons (*Falco peregrinus*) in the British Isles across distinct spatial and temporal scales. Our smallest scale study included Peregrines ringed as nestlings and subsequently recaptured alive in south Scotland–north England, an area that was intensively studied during the time periods 1974–1982 and 2002–2016. Second, we examined dispersal patterns of birds ringed as nestlings in south Scotland–north England, but subsequently recaptured alive or recovered dead anywhere in the British Isles. Finally, we examined the natal dispersal patterns for Peregrines ringed and recaptured or recovered anywhere in the British Isles from 1964 to 2016. Consistent with prior findings, females dispersed farther than males across all scales. However, the patterns of dispersal were strongly scale dependent. Specifically, we found a lack of a discernible relationship between index of density and dispersal distance in the limited study area, but when region-wide recaptures and recoveries were included in the analyses, a negative relationship was revealed. Our results suggest that conclusions of dispersal studies may be scale dependent, highlighting the importance of spatial and temporal scales in examining and interpreting the relationship between population density and dispersal patterns.

Key words: density-dependent dispersal hypothesis; dispersal distance; natal dispersal; Peregrine Falcon; raptor; spatial scale.

INTRODUCTION

Natal dispersal, defined as the movement of pre-reproductive individuals from their place of birth to a site where they actually or potentially breed (Dobson 1982, Greenwood and Harvey 1982, Newton 2010, Armitage et al. 2011), is an important life-history trait that can profoundly influence geographical distribution, as well as the dynamics, persistence, and genetic structure of natural populations (Bowler and Benton 2005, Ronce 2007; Clobert et al. 2012). The recognition that many biological populations are spatially structured, either naturally or due to anthropogenic fragmentation of habitats (Hanski 1999, Cale 2003), has spurred many theoretical studies evaluating the influence of dispersal on the dynamics, persistence and evolution of spatially structured populations (McPeck and Holt 1992, Bowler and Benton 2005, Ronce 2007). Recent technological developments (e.g., GPS and satellite tracking) and availability of

long-term, individual-based monitoring data, have led to various empirical studies, focused on understanding the causes and dynamics of dispersal across species (Greenwood 1980, Martin et al. 2008, Armitage et al. 2011, Clutton-Brock and Lukas 2012, Matthysen 2012, Hoogland 2013).

Direct mortality has been shown to be a prominent cost associated with dispersal (Bowman and Robel 1977, Van Vuren and Armitage 1994, Matthysen 2005, Wiens et al. 2006, Bonte et al. 2012). One of the most frequently asked questions regarding dispersal is why some individuals incur the presumed costs of long-distance travel in order to breed (Rousset and Gandon 2002, Bonte et al. 2012). Population density around the natal site has been proposed as a proximate cause of dispersal (Travis et al. 1999, Bowler and Benton 2005, Matthysen 2005). High densities around natal sites can potentially reduce individual fitness via exploitative competition (i.e., competition for resources such as prey and nest sites) or interference competition (e.g., intra-specific aggression; Denno and Peterson 1995, Bowler and Benton 2005). By moving away from high-density natal areas, conditional dispersers can avoid adverse effects of competition and improve their individual fitness prospects. This idea, dubbed density-dependent dispersal, predicts a positive relationship

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⁷E-mail: elisemorton@ufl.edu

between population density around natal sites and dispersal distances (or a negative relationship between fidelity rates and population density). In contrast, several studies have shown the opposite relationship between density at natal sites and dispersal as high population density can signify high-quality habitat (Baguette et al. 2011) or low population density can be associated with a decreased ability to find mates (Loe et al. 2009). Both empirical and theoretical studies demonstrate how both positive and negative density-dependent dispersal can have adaptive value, particularly in spatially and temporally varying environments (Gadgil 1971, McPeck and Holt 1992, Rodrigues and Johnstone 2014).

Although the majority of observational and experimental studies have reported positive relationships between population density and dispersal distances in various taxa (Otronen and Hanski 1983, Denno and Peterson 1995, Fonseca and Hart 1996, Wolff 1997, Léna et al. 1998), the direction of density-dependence can vary in response to ecological factors (Rodrigues and Johnstone 2014) and can also exhibit a U-shaped pattern with the highest dispersal distance at both high and low population densities (Kim et al. 2009). The relationship between population density and dispersal parameters can also vary across spatial and temporal scales, sometimes leading to contrasting results for the same population at different scales (Bowler and Benton 2005, Kim et al. 2009, Rodrigues and Johnstone 2014). However, studies of dispersal across different spatial scales are logistically challenging, and consequently, rare. As such, our understanding of how spatial and temporal scales might influence the conclusions of dispersal studies remains limited.

We studied dispersal in a non-migratory population of Peregrine Falcons (*Falco peregrinus*) in the British Isles at different spatial and temporal scales: south Scotland and north England (hereafter, the limited study area) from 1974 to 1982 and 2002 to 2016, and the entire British Isles (hereafter, the extended study area) from 1964 to 2016. The extended study area encompassed the entire breeding range of Peregrine Falcons in the British Isles, and covered a wide spectrum of Peregrine density conditions (Fig. 1). During the 1960s and 1970s, Peregrines occurred in low numbers, suffering the effects of organochlorine pesticides, which were still in use during that period (Ratcliffe 1970, Newton and Mearns 1988, Smith et al. 2015). Through the 1980s and 1990s, following restrictions on the use of these compounds, the population recovered as the direct and residual effects of organochlorines subsided. More recently, the Peregrine population of the British Isles is thought to have fully recovered and stabilized around equilibrium densities, except in grouse-moor areas where the species is illegally persecuted (Banks et al. 2010, Amar et al. 2012, Smith et al. 2015, McGrady et al. 2017).

Theoretically, as population density increases, competition for resources and breeding territories should increase, and dispersers would have to travel further, on average, to find a potentially suitable territory with a mate and an adequate prey base. Thus, we expected a positive relationship between population density and dispersal distance, with distances increasing in later years when the population rebounded following restrictions on organochlorine pesticide use. We could directly test this hypothesis with estimates of population density for the intensively surveyed limited study area. Although rigorous estimates of absolute or relative abundance of

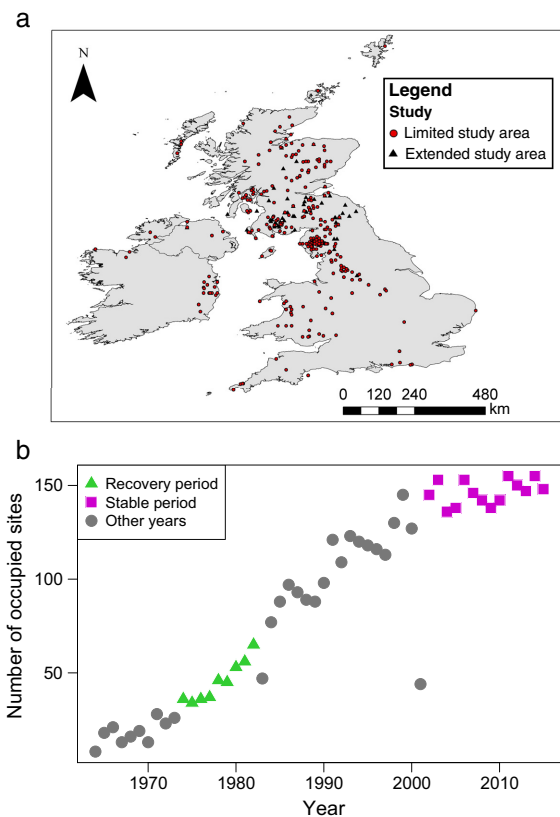


FIG. 1. (a) Map showing Peregrine Falcon ringing sites. (b) The number of occupied nest sites across years relevant for this study (1964–2016). Triangles (green) and squares (purple) indicate years during which the more intensive local-scale study took place, the recovery (1974–1982) and stable (2002–2016) periods, respectively. Circles (gray) reflect years only relevant for the regional-scale study.

Peregrines for the extended study area are not available, periodic surveys have shown that the British Peregrine population went through a period of recovery as described above (Ratcliffe 1990) and is now relatively stable (Banks et al. 2010, Smith et al. 2015, McGrady et al. 2017). Thus, we expected a monotonically increasing linear or quadratic temporal trend in Peregrine dispersal distances over time, corresponding to Peregrine population recovery.

MATERIALS AND METHODS

Study area and population monitoring

This study was conducted across two temporal and three spatial scales within the British Isles. The smallest, yet most intensive study, was carried out in south Scotland and north England (local) (Fig. 1; see McGrady et al. [2017] for a detailed description of the study area). The fieldwork was conducted during two time periods: (1) from 1974 to 1982, when the Peregrine population was recovering from near-extinction due mainly to effects of organochlorine pesticides, and (2) from 2002 to 2016, during which the population was more or less stable around a presumed equilibrium level (Banks et al. 2010, Smith et al. 2015). Every year during each study period, established and potential Peregrine

breeding sites were visited during the nesting season. Fledglings, and breeding adults, were ringed under the British Trust for Ornithology (BTO) ringing scheme. Identity and breeding status were recorded for previously marked birds upon subsequent encounters. During the latter study period, some nestlings were fitted with passive integrated transponder (PIT) rings, and since 2003, PIT-tagged birds have been electronically “recaptured” using PIT-tag readers placed in the birds’ nests (Mearns and Newton 1984, Smith et al. 2015). In our analyses, we first considered only birds that were recaptured within the intensively surveyed study area. However, to examine the impact of the spatial constraints imposed at this scale, we also analyzed natal dispersal patterns of birds ringed in the south Scotland–north England study area but recaptured or recovered anywhere in the British Isles (local extended). This information was obtained from the BTO database.

Our largest regional scale study included the entire breeding range of Peregrines in the British Isles and spanned five decades (1964 to 2016) (regional). These data were collected by ornithologists, experienced volunteers, and members of the public who have been contributing information to the BTO ringing scheme (Baillie et al. 1999) since the early 20th century. These data included recaptures and recoveries (meeting specified criteria) for birds ringed in south Scotland and north England during the intensive studies described above, as well as those ringed and recaptured or recovered elsewhere within the British Isles. Information included sex, natal location, and finding location (GPS coordinates), date of ringing, and finding condition. For birds that were first captured as fledglings or in their first year of independent life, exact ages were known.

BTO data were filtered according to each bird’s finding condition (coded with integers 0–9, 20–22, 27, 79, and 89) to distinguish between types of recaptures and recoveries (EURING, The European Union for Bird Ringing 2010). Recaptures included birds that were previously ringed and either recaptured or re-sighted alive (BTO codes 4–8, 20, 27, 79, and 89). Recoveries included birds that were found dead (with or without detailed information; codes 1–3, 21, and 22). Birds for which finding condition or fate was unknown (codes 0 and 9, respectively) were excluded from analyses.

Dispersal distance and direction

We defined natal dispersal distance as the distance between the site where an individual was hatched and the location of first recapture or re-sight as a breeder or the location of recovery if found dead as a potential breeder. Because juvenile Peregrines do not disperse prior to six weeks after fledging (Hardey et al. 2009), and then require some time to find a place to settle, we only considered recaptures/recoveries that occurred at least 60 d post-ringing. Prior examination of the data showed no general increase in dispersal distances after this age, implying that the dispersal period had ended by then. We calculated dispersal distance as the shortest distance between the natal and initial recapture sites. Dispersal direction (azimuth) was the direction from the natal site to the site of first recapture as breeder or recovery at more than 60 d of age. Both dispersal distance

and direction were calculated using the geosphere package (Hijmans et al. 2016) in R version 3.2.3 (R Development Core Team 2012).

Index of population density

The south Scotland–north England Peregrine Falcon population was intensively monitored. We estimated the effective sampling area as the 95% minimum convex polygon (MCP) of the entire study area (166 nest sites) within each period and calculated the mean number of breeding pairs each year relative to that area as an index of Peregrine breeding density (Southwood and Henderson 2009) (Appendix S1: Fig. S1). The number of annual recaptures was inadequate for the application of spatially explicit mark–recapture models. The number of occupied nest sites increased from 34 to 65 during the first study period (1974–1982) and fluctuated between 136 and 155 during the second study period (2002–2016; Fig. 1 and Appendix S1: Fig. S1). Ninety-five percent MCP areas were generated using the AdeHabitatHR package in R version 1.8.18 (Calange 2006). We refer to the first study period (characterized by lower population density) as the “recovery” period and the latter, higher density period, as the “stable” period.

For the extended study area, data were not available to estimate absolute or relative measures of population density. However, following restrictions on organochlorine pesticides, the British Peregrine population began to recover in the 1970s, increased through the 1990s, thereafter became relatively stable (Ratcliffe 1970, Nisbet 1988, Newton et al. 1989, Banks et al. 2010, Smith et al. 2015, McGrady et al. 2017). We therefore tested for the effect of year and year² in breeding numbers as representative indices of density across spatial scales, partially reflecting the increase in population size over the course of the study.

Statistical analyses

We used generalized linear models with Gaussian distribution to test for the additive and interactive effects of sex, year, year², and finding condition (recapture or recovery) on dispersal distance (log-transformed). For the scales of study where birds were ringed in the limited study area, we also tested for the effect of the study period (recovery vs. stable), and linear and quadratic effect of density index. The direct effect of population density could not be tested for the extended study area, owing to the lack of adequate density data. To test for spatial autocorrelation in dispersal distances, we calculated Moran’s *I* indices (Moran 1950). We used an information-theoretic approach using the Akaike’s information criterion corrected for small sample size (AIC_c) for model comparison and statistical inference (Burnham and Anderson 2002). Conditional model-averaged coefficients, standard errors, and importance were calculated and reported for all models with $\Delta\text{AIC}_c < 4$ (Appendix S1: Table S2) using the MuMIn package in R (Barton 2009). Importance values were calculated as the sum of the Akaike weights over all models where the term appears. Non-uniformity of dispersal direction within groups was tested using the Rayleigh test using the circular package in R (Lund and Agostinelli 2007).

RESULTS

Limited study area

For the local-scale study, we had dispersal data for 68 Peregrines (21 males, 47 females) that were ringed as nestlings and subsequently recaptured alive in the limited study area. The median dispersal distance for the sampled population was 56.6 km (IQR [interquartile range] 25.8–119.8), where females dispersed substantially further (85.3 km, IQR 31.3–125.0) than males (36.2 km, IQR 18.6–57.0; Fig. 2a and Appendix S1: Table S1 and Fig. S2).

Median dispersal distances were longer during the recovery (lower density) period (61.3 km, IQR 25.7–108.2) relative to the stable (higher density) period (52.4 km, IQR 29.9–120.1; Appendix S1: Fig. S3). This pattern was driven by females (100.2 km, IQR 32.5–128.0 and 67.9 km, IQR: 32.6–124.8 for the recovery and stable periods, respectively). Male dispersal distances, shorter than females', exhibited the opposite pattern (26.8 km, IQR 18.1–48.3 and 37.3 km, IQR 23.8–55.9 for the recovery and stable periods, respectively). The proportion of males dispersing distances >100 km increased from 9% during the recovery period to 20% during the stable period. The pattern was reversed for females, where the proportion of individuals dispersing >100 km decreased from 52.2% to 41.7% between periods. At this scale, the most parsimonious general linear model for dispersal distance included sex only ($\beta[\text{males}] \pm \text{SE} = -0.6 \pm 0.26$; CI $-1.11, -0.11$) indicating that none of the indices of density that we

considered substantially affected dispersal distance (Table 1 and Appendix S1: Table S2).

Incorporating recapture and recovery data for birds ringed in the limited study area and recaptured or recovered anywhere in the extended study area increased the number of individuals to 145 (61 males, 84 females). Median dispersal distance increased to 74.48 km overall (IQR 30.85–134.14) and in both sexes (females 102.4 km, IQR 41.0–156.4; males 47.0, IQR 23.4–92.4; Fig. 2a and Appendix S1: Table S1). The best supported general linear models for natal dispersal distance ($\Delta\text{AIC} < 2$) included additive or interactive effects of sex and either year or year², period, or density (Table 1 and Appendix S1: Table S2). Dispersal distance was strongly influenced by sex, with females dispersing further than males ($\beta[\text{males}] \pm \text{SE} = -0.50 \pm 0.24$, CI $-0.97, -0.029$; Fig. 2a and Appendix S1: Table S2). Dispersal distance declined over time (year², $\beta \pm \text{SE} = -3.6 \times 10^{-4} \pm 1.55 \times 10^{-4}$, CI $-6.63 \times 10^{-4}, -5.67 \times 10^{-5}$; year, $\beta \pm \text{SE} = -9.99 \times 10^{-3} \pm 7.63 \times 10^{-3}$, CI $-2.5 \times 10^{-2}, 4.97 \times 10^{-3}$), a pattern that was stronger for males (Appendix S1: Fig. S4). Including BTO recaptures and recoveries resulted in longer dispersal distances for the recovery period relative to the stable period ($\beta[\text{stable}] \pm \text{SE} = -0.31 \pm 0.22$, CI $-0.73, 0.12$; Table 1 and Appendix S1: Fig. S3). The proportion of individuals that dispersed more than 100 km away from their natal sites decreased from 30% to 16.1% for males and 55.8% to 48.8% for females during the recovery and stable periods, respectively. These results suggest a declining trend in natal dispersal distances as Peregrine breeding numbers increased (Appendix S1: Fig. S4).

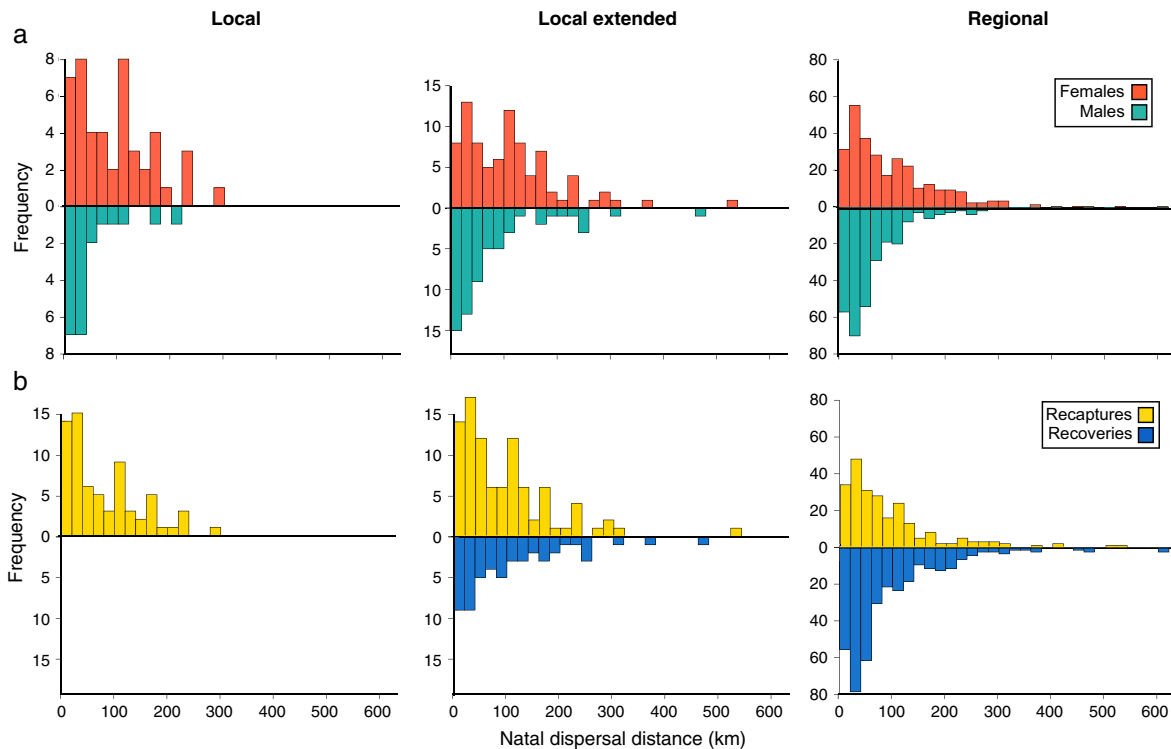


FIG. 2. Histograms showing natal dispersal distances (km) according to (a) sex and (b) finding condition (recaptures vs. recoveries) for the local-scale study where ringing and recaptures were confined to the limited study area (left column), the local extended-scale study where ringing was confined to the limited study area and recaptures and recoveries were drawn from the extended study area (middle column), and the regional-scale study where ringing, recaptures, and recoveries were drawn from the extended study area (right column).

TABLE 1. Model comparison statistics for generalized linear models testing for the effects of covariates of natal dispersal distance for scales of study in which (a) ringing and recaptures were confined to the limited study area (Local), (b) ringing was confined to the limited study area with recaptures and recoveries drawn from the extended study area (Local extended), and (c) ringing, recaptures, and recoveries were drawn from the extended study area (Regional).

Model	<i>K</i>	AIC _c	ΔAIC _c	Weight
a) Local				
Sex	3	191.383	0.000	0.311
Sex + period	4	193.552	2.169	0.105
Sex + density	4	193.584	2.201	0.103
Sex + year	4	193.602	2.219	0.103
Sex + year ²	4	193.610	2.228	0.102
Intercept only	2	194.964	3.581	0.052
Sex × period	5	195.443	4.060	0.041
Sex × year ²	5	195.626	4.243	0.037
Sex × year	5	195.661	4.278	0.037
Sex × density	5	195.680	4.298	0.036
b) Local extended				
Sex × year ²	5	427.607	0.000	0.106
Sex + year ²	4	427.954	0.347	0.089
Sex × year	5	428.346	0.739	0.073
Sex × year ² + recap/recov	6	428.412	0.805	0.071
Sex + year	4	428.415	0.808	0.071
Sex + period	4	428.673	1.066	0.062
Sex + density	4	428.841	1.234	0.057
Sex + year ² + recap/recov	5	428.884	1.277	0.056
Sex × period	5	429.018	1.411	0.052
Sex × density	5	429.097	1.490	0.050
c) Regional				
Sex + year ²	4	2,243.247	0.000	0.249
Sex + year	4	2,243.845	0.599	0.185
Sex + year ² × recap/recov	5	2,244.998	1.752	0.104
Sex × year ²	5	2,245.122	1.875	0.097
Sex × year	5	2,245.556	2.310	0.078
Sex + year + recap/recov	5	2,245.683	2.436	0.074
Sex × year ² + recap/recov	6	2,246.881	3.634	0.040
Sex × recap/recov + year ²	6	2,247.011	3.765	0.038
Sex × year + recap/recov	6	2,247.399	4.152	0.031
Year ²	3	2,247.693	4.446	0.027

Notes: Covariates were sex (male or female), period of study (recovery [1974–1982] and stable [2002–2016]), index of density, finding condition (recaptures [recap] or recoveries [recov]) and year or year². The number of parameters (*K*), Akaike's information criterion corrected for small sample size (AIC_c), difference in AIC_c (ΔAIC_c), and model weights (relative likelihood of models in the set) are shown. The top 10 models for each spatial scale are shown.

At this scale, recovered birds were found further away from their natal sites (78.7 km, IQR 26.5–159) relative to those that were recaptured within the study area (69.0 km, IQR 31.4–123.0; Appendix S1: Fig. S2) and finding condition was moderately important in explaining dispersal distance patterns ($\beta[\text{recoveries}] \pm \text{SE} = 0.19 \pm 0.19$; CI $-0.18, 0.57$; Table 1 and Appendix S1: Table S2). Specifically, the negative relationship between year and dispersal distance was stronger for birds that were recovered dead compared to those that were recaptured alive (Appendix S1: Figs. S4 and S5), such that removal of recovered birds from these analyses eliminated the negative relationship between dispersal distance and year. We did not find evidence for spatial autocorrelation in dispersal distances (Moran's *I*; $P = 0.59$).

Dispersal direction did not differ from a uniform distribution across sex, finding condition, study period, or overall (Rayleigh test of uniformity, $P > 0.1$; Appendix S1: Fig. S6).

Extended study area

The regional-scale study included birds ringed and recaptured or recovered anywhere in the extended study area and spanned five decades (1964 to 2016). At this scale, we had dispersal data for 589 Peregrine Falcons (290 males, 299 females), of which 233 were recaptured and 356 were recovered. Median dispersal distance was 58 km (IQR 29.7–118.7), with a more right-skewed distribution with greater kurtosis compared to the local and local extended scales of study (Fig. 2 and Appendix S1: Table S1). Dispersal distances were again longer for females (76.1 km, IQR 35.5–142.9) than for males (46.5 km, IQR 25.8–89.2; Fig. 2a and Appendix S1: Table S1 and Fig. S2), and longer for recaptured birds (62.8 km, IQR 30.9–116.5) than for recovered birds (55.1 km, IQR 29.6–119.2; Fig. 2b and Appendix S1: Fig. S2).

The four best general linear models for dispersal distance ($\Delta\text{AIC} < 2$) included additive or interactive effects of sex and either year or year² (Table 1 and Appendix S1: Table S2). Again, dispersal distance was strongly influenced by sex, with females moving further than males, ($\beta[\text{males}] \pm \text{SE} = -0.34 \pm 0.13$, CI $-0.60, -0.78$; Appendix S1: Table S2). Dispersal distance non-linearly decreased over time as the population increased (year², $\beta \pm \text{SE} = -1.73 \times 10^{-2} \pm -5.72 \times 10^{-3}$, CI $-2.85 \times 10^{-3}, -6.06 \times 10^{-3}$; year, $\beta \pm \text{SE} = -3.36 \times 10^{-4} \pm -1.08 \times 10^{-4}$, CI $-5.48 \times 10^{-4}, -1.25 \times 10^{-4}$; Appendix S1: Fig. S4). Adding finding condition (recaptures or recoveries) as a covariate did not improve the model parsimony (Table 1 and Appendix S1: Table S2). However, the negative relationship between dispersal distance and the year of recapture or recovery was stronger for recovered birds than for recaptured ones in both males and females (Appendix S1: Figs. S4 and S5). Again, we did not find evidence for spatial autocorrelation in dispersal distances (Moran's *I*, $P = 0.48$).

Dispersal direction differed from a uniform distribution (Rayleigh test, $z = 0.09$, $P = 0.006$), with the majority of birds dispersing northward (Appendix S1: Fig. S6). This pattern was largely driven by north-biased male dispersal (males, $z = 0.16$, $P = 0.0006$; females, $z = 0.07$, $P = 0.86$).

DISCUSSION

We investigated Peregrine Falcon dispersal distances across three different spatial and temporal scales, during a period when the number of occupied nest sites in the British Isles more than tripled (Fig. 1). We expected that dispersal distances would increase over time as Peregrine densities increased across spatial scales. However, at the local scale (ringing and recaptures confined to the limited study area; 1974–1982 and 2002–2016), we found that sex alone was the only meaningful predictor of dispersal distance; there was no evidence that dispersal distance of either sex was influenced by population density (Table 1 and Appendix S1: Fig. S4). In general, females moved further than males, a pattern that was consistent across scales of study (Fig. 2a and Appendix S1:

Fig. S2). This result was congruent with our expectation based on prior observations on Peregrine Falcons (Mearns and Newton 1984, Katzner et al. 2012, Dennhardt and Wakamiya 2013) and other raptor species (Newton 1979, Newton and Marquiss 1983). Female-biased dispersal and male-biased philopatry should be favored for socially monogamous species where males use territories to attract mates (Greenwood 1980, De Meester and Bonte 2010, Hovestadt et al. 2014). This is apparently the case in Peregrines, where males are primarily responsible for establishing territories and females seek unpaired males with territories (Newton and Mearns 1988, Restani and Mattox 2000). Additionally, female Peregrines are larger than males, and body size is often positively correlated with dispersal distance within and among species (Greenwood and Harvey 1982, Sutherland et al. 2000, Jenkins et al. 2007, Newton 2010).

Owing to the widespread use of organochlorine pesticides, the British population of Peregrine falcons was reduced by the 1960s to <400 breeding pairs (Ratcliffe 1990). As these pesticides were progressively restricted in use, their direct and residual effects on Peregrines waned, and the population recovered through the 1980s and 1990s, reaching apparent equilibrium densities over most of Britain in the last 10–15 yr (Banks et al. 2010, Smith et al. 2015, McGrady et al. 2017). We interpret the significant effect of year at the larger spatial and temporal scales to primarily reflect the increase in Peregrine population density observed during the study period (Fig. 1B). However, it is important to recognize that changes in other environmental factors (e.g., improved protection, improvements in habitat quality), may have also contributed to this pattern. The negative relationship between year and dispersal distance observed at larger scales (Appendix S1: Table S2 and Fig. S4) runs contrary to the pattern predicted by the density-dependent dispersal hypothesis. One explanation depends on the relative population density around natal sites compared to potential dispersal sites. Dispersal is characterized as a multi-stage process including emigration, transience, and settlement (Bowler and Benton 2005, Clobert et al. 2009, Fronhofer et al. 2015) and there is potential for environmental factors to influence dispersal decisions at each of these steps differently (Matthysen 2012, Bitume et al. 2013). If population density is higher (or increasing faster) at natal sites than at potential dispersal sites, dispersers could avoid adverse effects of high-density conditions by dispersing further away. However, if increases in population density are equivalent across both natal and potential dispersal territories, the costs of leaving familiar habitats (where birds may experience a higher probability of survival) should outweigh the benefits of dispersing further. In such cases, one would expect a negative association between population density and dispersal distance. Specifically, if density is increasing everywhere, the potential benefits of long-distance dispersal (i.e., reduced competition) disappear. This was probably the case for Peregrines in the British Isles, where population recovery began simultaneously wherever Peregrines had persisted during the period of organochlorine use (Banks et al. 2010, Smith et al. 2015). From these refugia, the birds gradually spread to areas from which they had been eliminated.

Alternatively, a negative relationship between dispersal distance and population density could arise if the opportunity to find a mate with a suitable breeding site increases with

population density (mate-finding Allee effect; Courchamp et al. 1999). For Peregrines, this should result in stronger negative density dependence for females, the sex that selects mates. That both males and females exhibited this pattern, suggests that the Allee effect is an unlikely explanation for the observed negative relationship between population recovery and dispersal. However, it is also possible that encounters with other Peregrines during dispersal is an indicator of suitable habitat, deterring further movement for both males and females.

At both spatial scales where recaptures and recoveries from the extended study area were included, negative density dependence was strongly influenced by recoveries (Appendix S1: Figs. S4 and S5). Although this pattern is partly determined by the nature of the data (e.g., dispersal distances at the scale of the extended study area are longer than those observed for the limited study area and 68% of the data come from birds that were recovered dead), there may be a biological mechanism driving this pattern, namely the inclusion of floaters (non-breeding, non-territorial individuals). Although floater-to-breeder ratios are not available for British Peregrines, non-breeding Peregrine Falcons may have outnumbered breeders as the population approached equilibrium densities (Newton 1988). In order to breed, these individuals must move to unoccupied habitat or displace current breeders (Newton 1979). Indeed, age of first reproduction for British Peregrines increased during population recovery (Smith et al. 2015), potentially reflecting an increase in the proportion of non-breeders in the population. It has been shown in other species that prior experience at a site improves chances of acquiring a territory (Pciman 1987, Sergio et al. 2017). It is possible that negative density dependence of dispersal distances is stronger among floaters, reflecting a strategy of staying closer to their natal sites.

A second question raised by our findings, namely why recorded dispersal distances differed across scales, is likely explained by spatial and temporal variation in density patterns. Density-determined dispersal dynamics will differ depending on the time frame at which both density and dispersal are measured (Brown and Orions 1970, Forero et al. 1999). Even when population density is changing temporally, short-term studies may fail to detect temporal change in density or its effect on dispersal distances. Similarly, if the spatial scale of a study excludes long-distance dispersers or range edges, recorded dispersal distances will be truncated and conclusions potentially biased downward. In our study, the negative relationship between dispersal distance and year at the larger scales was not reflected in longer dispersal distances for all individuals, but rather a small portion of birds dispersing further during the lower density period. Restricting years of the regional-scale study to those of the local scale (1974–1982 and 2002–2016) did not alter the observed patterns, suggesting that the primary explanation for the observed differences across studies was the spatial scale over which capture, recapture, and recovery occurred.

Dispersal is a plastic process, providing birds with the ability to adjust their behavior according to prevailing environmental conditions (Massot et al. 2002, Clobert et al. 2009). However, our understanding of how various extrinsic and intrinsic factors interact to influence natal dispersal distances remains incomplete (Bowler and Benton 2005, Matthysen 2005, Bitume et al. 2013). Studies testing for

effects of density in birds are limited in part by the narrow range of density values that are available for single populations. Matthysen (2005) reported that there was no relationship between population density around natal sites and dispersal distance for the majority of bird species included in their review. This could reflect a true absence of a pattern or the limited temporal and/or spatial scale of the studies. A U-shaped pattern has been observed in the Blue-footed Booby (*Sula nebouxii*; Kim et al. 2009) and the protist *Tetrahymena* (Fronhofer et al. 2015), suggesting that dispersal distances can be long at very low or very high population densities. In such systems, the observed relationship would depend on the temporal scale of study.

Peregrine Falcons in North America suffered the same detrimental effects of organochlorine pesticides as in Europe, to the extent that by the 1970s they were nearly eradicated (Heinrich et al. 1995). Similar to the British population, dispersing Peregrines in the United States exhibited a directional bias (Dennhardt and Wakamiya 2013) and females dispersed generally further than males (Kauffman et al. 2004, Katzner et al. 2012, Dennhardt and Wakamiya 2013). Although explicit tests of the relationship between natal population density and distance from breeding locations have yet to be conducted in North American Peregrines, asymmetric dispersal patterns suggest density-driven emigration from low quality sites (Kauffman et al. 2004). These results highlight the need for characterizing density-dispersal relationships at appropriate scales, while also accounting for heterogeneity in the quality of breeding sites.

Most dispersal studies are based on capture-mark-recapture and VHF (very high frequency) radio-tracking data. However, depending on the species, population, and individual, dispersal distances can vary considerably (<0.1 to >1,000 km; Greenwood and Harvey 1982). Dispersal distances could be underestimated if the study area is small relative to the maximum dispersal distance; this alone or in combination with spatial heterogeneity in habitat quality can lead to a biased interpretation of the relationship between population density and dispersal distance. For many species, population density is heterogeneous across the landscape and dispersal patterns can be influenced by density not only at natal sites, but also at potential breeding sites and areas in between (Bitume et al. 2013). In this study, physical geography of the area could have also influenced the patterns observed. For example, patchiness of suitable breeding habitat, the fact that Britain is an island, and that it is elongated north to south, may all have affected dispersal direction and distance without undermining comparisons between the sexes.

Understanding the causes and consequences of animal movement patterns is essential for effective conservation of species. Range-wide studies of dispersal of birds that can travel long distances across a range of landscapes are logistically challenging. Nonetheless, we emphasize the need to exercise caution while interpreting results of dispersal studies conducted at limited spatial and temporal scales, and while formulating or implementing conservation plans for wide-ranging species.

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