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Northerly dispersal trends in a lowland population of Peregrines *Falco peregrinus* in southwest England

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ABSTRACT

Little is known about the post-natal dispersal of Peregrines *Falco peregrinus* from lowland areas of England. We used the resighting and recovery data from 66 Peregrine nestlings (34 females, 32 males) colour-ringed in the southwest of England to outline their reported dispersal movements. Our results revealed that Peregrines, in particular females, disperse in a north-northeasterly direction, with females being resighted at greater distances than males. Males were resighted a mean of 44 km from their natal site and females significantly further (mean 117 km). Despite more recent local and regional declines in some areas of their UK range, Peregrines have been increasing at a national level in England and extending their breeding range into new areas. Our results indicate that Peregrines have the potential to continue occupying suitable vacant habitats across the UK. Dispersing birds from the southwest of England are potentially helping to increase the breeding population of Peregrines in other areas where they have been absent or scarce for many years.

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raptor; colour-ringing; bird of prey; population recovery; natal dispersal

During the past 40 years, many raptors in England have shown an increase in their populations, as they have been afforded greater protection with the banning of organophosphate pesticides such as DDT and through legislation (Wildlife & Countryside Act 1981). Some, such as the Peregrine *Falco peregrinus*, Goshawk *Accipiter gentilis* and Hobby *Falco subbuteo*, have greater protection through their Schedule 1 status, meaning that they cannot be intentionally disturbed at their nests, and their eggs and young are fully protected. Previously limited to the west of Britain, Buzzards *Buteo buteo*, Peregrines and Red Kites *Milvus milvus* have populated central and eastern counties during the past 30–40 years, with Red Kite supported by reintroductions across parts of England (Carter et al 1999, Balmer et al 2013, Harris et al 2022). These species are now more common in England than when the first atlases of breeding birds in Britain and Ireland were published for 1962–72 and 1988–91 (Sharrock 1976, Gibbons et al 1993, Balmer et al 2013). The population size of Buzzard, for example, increased significantly by 27 454% in the east of England and 8254% in the East Midlands between 1995 and 2020; during the same period, Red Kite increased significantly in England by 25 276% (Harris et al 2022). Despite these positive trends, other raptors, such as Kestrel *Falco tinnunculus* and Sparrowhawk *Accipiter nisus*, have experienced a significant long-term decline across England between 1995 and 2020 (-25% and -23% respectively; Balmer et al 2013, Harris et al 2022).

As raptor populations increase, there is potential for them to be wintering and breeding in greater densities and living in more accessible locations where they offer greater opportunity for observation. Studying the dispersal of now widely distributed species such as the Buzzard, and the success of reintroductions such as for Red Kite, provides insights into how their populations might respond long term, both through increases in their numbers and to changes in their environment (Evans et al 1999, Clements 2000, Arraut et al 2021).

Last century, Peregrines showed the greatest rate of range expansion in Scotland and particularly in Wales...
than they had been previously. However, during
began increasing, young birds were dispersing further
and widened its range of breeding habitats (Wilson et al 2018, Harris et al 2022). Prior to the DDT era, Peregrines bred mainly
along the rocky western seaboard of Britain and
upland moorlands inland (Ratcliffe 1993, Wilson et al 2018). During their population recovery, Peregrines
returned back to these environments and also spread
into inland quarries and urban areas, where they are
now breeding (McGrady et al 2017, Wilson et al 2018).
As Peregrines continue to increase across southern
England, there is an opportunity to study their natal
dispersal in greater detail, particularly in urban
locations where marked individuals can be observed
on web cameras and from easily accessible viewpoints
(Searle et al 2022). Most recent studies of dispersal
have focused on adult Peregrines breeding in rural
parts of northern England and Scotland and do not
allow for an assessment of natal dispersal (Mearns &
Newton 1984, Ratcliffe 1993, Smith & McGrady 2009,
Smith et al 2015, McGrady et al 2017). However,
Morton et al (2018) have studied natal dispersal of
Peregrines at a regional scale in northern England and southern Scotland for the years 1974–82 and 2002–16. They compared their results with the natal dispersal of
Peregrines ringed and recovered anywhere in Britain
during 1964–2016. They found that dispersal patterns
can differ between local and national scales. Sex is
generally the factor determining how far Peregrines disperse, with females travelling further than males
(Mearns & Newton 1984, Ratcliffe 1993, Morton et al 2018). During the period 1974–82 when numbers
began increasing, young birds were dispersing further
than they had been previously. However, during
2002–16, when populations were more stable, both
sexes dispersed over shorter distances. The most
convincing theory proposed by Morton et al (2018) is
that, during early population growth, occupied
territories close to their natal sites encouraged
Peregrines to disperse further afield to find vacant
territories. However, when their population grew,
territories across a wider area became saturated and
post-fledging Peregrines travelled shorter dispersal
distances as they had nowhere to disperse to.

While Morton et al (2018) analyse natal dispersal
data from across Britain, they give no information
specific to southern and central England, where there
have been large increases in population (Wilson et al 2018). In this paper, we present a detailed study of the
natal dispersal of Peregrines from nests across the lowlands of southwest England. This addresses a gap
in the wider literature and contributes towards our
understanding of how this species might increase and
establish itself in areas where they are currently absent or present in low densities.

### Material and methods

Peregrine nests chosen for study had relatively easy
access, such as those on nest platforms fixed to
buildings, or natural cliff sites that could be accessed
safely by experienced climbers. Nests were visited in
the counties or unitary authorities of Bristol, Bath
and North East Somerset, North Somerset,
Gloucestershire, Wiltshire, Dorset and Devon.
Cornwall was excluded as this had a separate ringing
project. For the purpose of this study, these counties
were defined as the southwest region of England. This
region, excluding Cornwall, is 20 292 km² (8% of the
UK, 16% of England; Office for National Statistics
2013, 2021). In 2014, when the last national Peregrine
survey was conducted, there were at least 212 pairs in
this region, excluding Cornwall. This is the largest
population in the English regions and 11% of the UK’s
population (Mitchell & Taylor 2015, Wilson et al 2018).

During the breeding seasons 2007–21, 316 Peregrine
nestlings were ringed in the study area by licensed
ringers. Nestlings were ringed when aged between 17
and 23 days, when their tarsi are large enough to
secure a colour ring and when they are less likely to
wander from the nest. A standard British Trust for
Ornithology (BTO) metal identification ring, carrying
a unique number, was fitted to the right tarsus, and a
plastic colour ring was fitted to the left tarsus. The
colour rings were pale blue or orange, engraved with a
black two-letter or three-character alphanumeric code.
Biometrics, including tarsus width, minimum tarsus
length, total head length, bill to cere length and mass
were taken to determine each bird’s sex and to
contribute to a wider biometric database for the species.

Between 2007 and 2021, the locations of 66 of the
ringed birds were reported. Live, dead or injured birds
were recorded directly by the authors or via local
Peregrine Watch groups, members of the public,
veterinary surgeons and the Royal Society for the
Prevention of Cruelty to Animals (RSPCA). These
were communicated directly to us from the observers,
through the BTO, or via Euring’s online ring-
reporting system (www.ring.ac). Colour-ringing
activities were promoted on social media and people
were encouraged to report sightings of ringed birds. The colour-ring letters on live birds were observed and read at ground level through binoculars, telescopes or digital cameras. Resightings by photographers were usually posted online, particularly on Twitter or Facebook, or emailed directly. Nest cameras streaming online provided seven resightings of individuals either breeding at nest sites or individuals in their second calendar year remaining at their natal location with their parents.

For multiple resightings that involved different locations, we used the last known resighting location. This would be more likely to be close to where the bird chooses to breed, if not the actual breeding location, and provide more detail on dispersal distance and direction from their natal location.

Natal dispersal of birds is typically defined as the movement that they make from their hatching site to their breeding territory (Greenwood & Harvey 1982). At least 12 individuals (18% of our total) were resighted at confirmed breeding locations which they used for nesting during the summer months, and a further 13 were over two years of age and likely to be at unconfirmed breeding locations. The remaining 41 were two years old or younger and still in their pre-dispersal or dispersal phase (Cramp & Simmons 1980, Bondi et al 2018, Morton et al 2018). Peregrines are capable of breeding from their second calendar year onwards, when they are sexually mature. However, they generally spend their first two years dispersing, although some may be on a territory with a partner in their second calendar year and even breed (Cramp & Simmons 1980, Zuberogoitia et al 2009, Wegner & Thomas 2012). Therefore, our study involved examining both natal dispersal to where Peregrines were found to be nesting as adults and the general movement of individuals up to two years of age. We also assessed the duration between ringing and resighting, to analyse whether there were any differences or changes in their detection over time. The complete data set included Peregrines found ‘0 km’ from their ringing location (n = 3) and one bird that had been found away from its natal site only 36 days after ringing; this was still within the six-week period in which juveniles remain dependent on their parents, and the two- to three-month period in which they are often still in the natal area but have yet to reach full independence (Cramp & Simmons 1980).

However, to analyse the direction of travel, only individuals (n = 58) that had travelled more than 1 km from the ringing location after 90 days were included. After 90 days it is highly likely a juvenile Peregrine has begun its wandering phase and moved away from its natal area; using 1 km excludes those individuals that had not moved any significant distance from where they had hatched (Cramp & Simmons 1980, Ratcliffe 1993, Bondi et al 2018).

**Data handling and analysis**

The location details, such as GPS coordinates and habitat, and the dates for when the bird was ringed at the nest and their subsequent resightings or recovery, were tabulated and subjected to analysis using R v3.5.1 (R Development Core Team 2018). Maps to compare the distance travelled between male and female Peregrines were produced using the R packages maps (Minka & Deckmyn 2018) and mapdata (Brownrigg 2018); kernels were produced using the adehabitatHR package (Calenge 2006). Rose charts to illustrate bearings and coordinates were produced using the packages geosphere (Hijmans 2019a), circular (Agostinelli & Lund 2017), raster (Hijmans 2019b) and rasterVis (Lamigueiro & Hijmans 2019). Geographic boundary data were developed using rgeos (Bivand & Rundel 2019).

Given that ringing locations were in the southwest, with the English Channel and Irish Sea to the south and west, a uniform distribution of dispersal bearings is not a realistic null hypothesis. Although Peregrines certainly do cross the sea, and did so in our study, some birds may have turned back at the coast, and others may have been lost at sea. We therefore took a randomisation approach to generate a suitable null hypothesis for dispersal bearings, conditional upon the ringing locations and recorded dispersal distances. This can be thought of as a randomised version of the Rayleigh test that accounts for the availability of land. For each of the 58 birds that met our criterion for dispersal (see earlier), we calculated the destination it would have reached if it had dispersed the same distance as observed, but in a random direction, subject to the constraint that the end point has to be on land (Figure 1b). The latter was determined with the function map.where from the maps package. The mean bearing and vector length (rho) for the 58 random samples was then calculated. This process was repeated 10 000 times to create the null distribution of mean bearings and rho for 58 birds flying the distance they did fly, but in random directions and subject to the constraint of ending on land. By calculating the proportion of the random mean bearings and rho values that are equal to or greater than the observed rho, we obtained a $P$ value for the probability of obtaining a test statistic as large as that observed, or greater, under the null hypothesis. For the probability
of the observed rho under the null hypothesis we used a one-tailed test. This is because the left-hand tail of the simulated distribution represents values that are unusually small, corresponding to a very regular uniform distribution of bearings. We consider this part of the null hypothesis as it is the opposite of directionality in dispersal.

The validity of the assumptions behind our parametric statistics was assessed following Thomas et al. (2017), by graphical examination of the normality of residuals, homoscedasticity and leverage. As a result of the significant skew in the distance data, we used the Mann–Whitney–Wilcoxon tests to compare the distance data both between sexes and between those breeding and not apparently breeding (at over two years of age). Spearman rank correlation was used to test whether distance increases with time. Dispersal bearings were analysed using circular statistics (Pewsey et al. 2013) as implemented in the circular package (Agostinelli & Lund 2017). We used a Watson test (function watson.test) to assess the goodness-of-fit of dispersal bearings to a von Mises distribution (a normal distribution wrapped around 360°). This forms the alternative hypothesis for the Rayleigh test (function rayleigh.test) which assesses departures from a uniform distribution. A difference in dispersal bearings between the sexes was investigated with a Watson two-sample test of

Figure 1. (a) Individual dispersals of 58 marked Peregrines originating in south and southwest England. Arrows join locations of ringing with locations of resighting or recovery: black, location where Peregrines were ringed as nestlings; red, location where females were resighted or recovered; blue, location where males were resighted or recovered. (b) Simulations of random dispersals from ringing locations (black) with observed dispersal distances: green, destinations on land; blue, destinations in sea; clear circles, actual resighting or recovery locations. (c) Rose diagram of dispersal bearings for females and (d) equivalent diagram for males: grey dots on the perimeter of the circle are individual data points; yellow segments represent the frequency of simulated random dispersal bearings that end on land; blue segments are the frequencies of observed dispersal bearings; black arrow is the mean dispersal bearing, of length equivalent to the mean vector length.
homogeneity (function `watson.two.test`). Descriptive statistics for mean bearings, with 95% confidence intervals, are provided as maximum likelihood estimates, calculated using bootstrap methods (functions `mle.vonmises` and `mle.vonmises.bootstrap.ci`).

**International dispersal**

One male Peregrine in the study, not included in the analyses, was recovered dead in Tiznit, Morocco, in November 2019, having been ringed as a nestling six months earlier in Taunton, Somerset. It had travelled a minimum distance of 2435 km from its ringing location (Drewitt & Sutton 2021).

**Results**

We analysed the data for 66 Peregrines, of which 34 were female and 32 were male. Of these, 39 (59%) were seen alive, 13 (20%) were found dead and 14 (21%) were found injured or sick (Table 1).

**Age of Peregrines when resighted**

Overall, 62% of Peregrines resighted were two years old or younger (n = 41) and 33% were under one year old (n = 22). For females, 59% (n = 20) were two years old or younger and 29% (n = 10) were one year old or younger. For males, 66% (n = 21) were two years or younger; 38% (n = 12) were one year or younger. Six Peregrines (three of each sex) had recently left their nest and were recovered within three months after ringing. The age of resighted Peregrines over two years of age (n = 25, 38%) ranged from 740 days (just over two years) to 13 years of age (median 1445 days, interquartile range 1034–1799 days).

**Multiple resightings**

Eight Peregrines were resighted on multiple occasions in different locations. For example, three dispersed to breeding locations and were subsequently resighted multiple times thereafter. One moved to the Malvern Hills, 73 km from its natal site and then moved a further 68 km away (141 km from the natal site). Another moved 66 km from Bristol to Tewkesbury and then headed into the county of Shropshire to breed, 134 km from its natal site.

**How far were Peregrines found from their natal site?**

Figure 1a shows the ringing and subsequent resighting or recovery locations of individual Peregrines ringed in southwest England (n = 58). For all Peregrines (n = 66), the mean distance travelled from their natal site to where they were resighted was 82 km (median 49 km, interquartile range 15–133 km). Males (n = 32) travelled a mean of 44 km (median 25 km, range 0–272 km, interquartile range 11–50 km). Females (n = 34) travelled significantly further (mean 117 km, median 120 km, range 7–355 km, interquartile range 42–162 km) (W = 247.5, n1 = 32, n2 = 34, P < 0.0001; Figure 2). Ten (15%) of the male Peregrines had been resighted or recovered within 10 km of where they had hatched. Three Peregrines were resighted at their natal site (0 km): one remained and bred for over a period of 13 years, one remained with its parents as a helper over winter and into the following breeding season before disappearing, and one was found injured 42 days after fledging.

**Table 1.** The age at which male and female Peregrines were found dead or injured/ill.

| State | Sex | Two years old or younger (frequency) | More than two years old (frequency) |
|-------|-----|-------------------------------------|-------------------------------------|
| Alive | Male | 9                                   | 9                                   |
| Alive | Female | 9                                   | 12                                  |
| Dead  | Male | 6                                   | 1                                   |
| Dead  | Female | 6                                   | 0                                   |
| Injured or ill | Male | 6                                   | 1                                   |
| Injured or ill | Female | 5                                   | 2                                   |

**Figure 2.** Comparison of distances travelled by female (F, n = 34) and male (M, n = 32) Peregrines. The plot shows the median (horizontal bar), first and third quartiles (box limits), the last points within 1.5 interquartile ranges of the nearest quartile (bars at the end of the dotted ‘whiskers’) and outliers (open symbols).
Natal dispersal

Of the 25 Peregrines resighted or recovered at more than two years of age, 12 were confirmed to be breeding. Breeding females (n = 9) travelled a mean of 123 km (median 117 km, range 41–287 km, interquartile range 66–161 km) and non-breeders (n = 5) a mean of 97 km (median 101 km, range 56–134 km, interquartile range 62–131 km); breeding males (n = 3) travelled a mean of 37 km (median 40 km, range 25–47 km) and non-breeders (n = 8) a mean of 18 km (median 11 km, range 0–55 km, interquartile range 9–19 km). There are too few data to analyse differences between breeders and non-breeders for each sex separately, but the pooled data suggest that breeders had dispersed a greater distance those apparently not breeding (W = 116.5, n1 = 12, n2 = 13, P < 0.05).

Four resightings or recoveries (6% of individuals) were found over 200 km from their natal site. All were female and less than two years old. For the remaining Peregrines, 19 (29%) were found 100–199 km from their natal ringing site. For distances of less than 100 km from their natal site, nine (14%) were found 51–99 km away, 12 (18%) were found 25–50 km away, 11 (17%) were found 11–24 km away and another 11 (17%) were found up to 10 km away.

Does distance of resighting or recovery increase with time since ringing?

The mean duration between being ringed and being resighted or recovered was 819 days (n = 66, median 614 days, interquartile range 305–1095 days). For 34 females, the mean duration was 865 days (median 657 days, interquartile range 353–1264 days); for 32 males, the mean duration was 770 days (median 514 days, interquartile range 275–838 days). Forty-one (62%) Peregrines were resighted or recovered at less than two years of age (mean 352 days, median 359 days, interquartile range 144–506 days). There is no compelling evidence that distance increases with the duration since ringing (females: rs = 0.31, n = 34, P = 0.075; males: rs = -0.11, n = 32, P = 0.55; Figure 3).

What directions do dispersing Peregrines take?

Peregrines (n = 58) were generally found at a north-northeasterly bearing from their natal site. This direction of dispersal was significantly different from a uniform distribution (mean bearing 13.1°, 95% c.i. -16.2–37.3°; Rayleigh Test of Uniformity, test statistic = 0.361, n = 58, P < 0.0005), with the assumption that the alternative hypothesis is a von Mises distribution being satisfied (Watson Goodness-of-Fit Test statistic = 0.075, P = 0.079). The mean female bearing was 27.8° (n = 31, c.i. -3.6–55.8°; Figure 1c) and male -13.0° (n = 27, c.i. -87.4–26.0°; Figure 1d), and there was no significant difference in these bearings between the sexes (Watson’s Two-sample Test of Homogeneity, test statistic = 0.062, P > 0.10). While the direction of dispersal is non-random, so too is the available land where birds might stop or be resighted or recovered: the North Sea and English Channel lie to the west and south of the ringing locations. Taking this into account, the observed mean bearing of all 58 birds of 13.1° falls well within the distribution of random bearings, subject to the constraint of ending on land: the mean of that distribution is -0.7° (north), and the observed value falls at the 67th percentile. However, the observed bearings are significantly more concentrated (P = 0.027) than expected by chance: the observed rho, 0.36, falls in the 2.7th percentile of the distribution of the simulated random values (Figure 1b).

Discussion

Our study is the first to focus on the specific movements of Peregrines fledging from nests in lowland southwest England (excluding Cornwall). It provides insights into where Peregrines are found, both during their first two years of life and after two years of age when they are likely to begin breeding. The southwest region of England holds the largest regional population of Peregrines in the UK, with a recent estimate – when Cornwall’s population is excluded – of 212 pairs (Wilson et al 2018, Mitchell & Taylor 2015). Our analysis reveals that Peregrines appear to disperse significantly in a north-northeasterly direction, either as part of their ongoing juvenile dispersal within their first two years of life, or while choosing a breeding location. While this is in part
because more land is available to the north and east of the ringing locations in southwest England, the directionality is stronger than can be explained by this alone.

We recognise observations of marked Peregrines also coincide with high densities of the human population and may be subject to observer bias; more people are likely to be looking for and recording Peregrines in these areas and there is a greater chance therefore of finding a ringed bird, whether healthy, injured or dead (Balmer et al 2013, O’Brien & Cheshire 2016). Undetected Peregrines may have dispersed to remote areas or places that are difficult to access or where there are lower densities of people. Those that fly overseas could be going to countries where reporting rates of colour-ringed birds are lower or where the geography or the environment makes resightings and ring recoveries challenging.

Our results differ from most other studies in the UK, which found that Peregrines did not show a preferred dispersal direction. These studies used data from breeding birds that had already dispersed from their natal site when ringed or tagged, rather than birds that were ringed as pulli and still had natal dispersal ahead of them (Mearns & Newton 1984, Smith & McGrady 2009). However, like our study, that by Morton et al (2018) did analyse data that included subsequent locations of breeding or potential breeding adult Peregrines that had been ringed as nestlings, and juvenile birds that had been found after 60 days of being ringed and where their dispersal period appeared to have ended. They found that Peregrines hatched in southern Scotland and northern England showed a northerly bias in dispersal direction, primarily driven by male birds. In our study we found no evidence for a sex difference in dispersal bearing.

With at least one colour-ringed Peregrine with letters unidentified seen at a rural location in South Wales and two others identified to individual level in Pembrokeshire – one on Skokholm Island (192 km from natal site) and another near Haverfordwest (166 km from natal site) – it is apparent that Peregrines from southwest England are also dispersing northwest into Wales. Probably due to the remote upland landscape and lower human population density, however, colour-ringed Peregrines are not being resighted or recovered in Wales as regularly as elsewhere. Using nest cameras at remote rural nest sites may help to overcome this problem in the future, by detecting more colour-ringed birds. In addition, the use of Passive Integrated Transponder (PIT) tags, such as those deployed in central Scotland (Smith & McGrady 2009), may reveal how Peregrines are utilising a landscape and interacting with each other and their nest locations.

Many parts of England have seen an increase in Peregrine numbers: between 2002 and 2012, Peregrine populations increased by 38% in the southwest of England, 116% in the southeast of England, 822% in central eastern England (including London), 142% in the West Midlands, Merseyside and lowland Lancashire, 35% in the Pennines and 340% in the northeast of England (Wilson et al 2018). They declined by 16% in the northwest of England. Our results suggest many Peregrines have dispersed to regions experiencing growth in Peregrine populations; if they breed successfully they are potentially helping the population to grow and disperse further into new unoccupied territories. This replicates similar population expansions by other species such as Buzzard and Raven {Corvus corax (Ratcliffe 1993, Balmer et al 2013, Wilson et al 2018)}.

Dispersing north and east also makes sense from the point of view of competition, allowing the Peregrines to make an easy transition into areas that have fewer Peregrines and more vacant territories waiting to be occupied. Moving south and west into Devon and Cornwall takes Peregrines into areas of higher Peregrine population densities and, while they may be more likely to move overland rather than cross the sea, the English Channel is no barrier to them. Peregrines originating from nests in Cornwall have occasionally appeared further south in Europe, while birds from the Low Countries, including Belgium, may appear in the UK (Wernham et al 2002, Walker et al 2016, Walker et al 2020, Spina et al 2022). Likewise, the record of a juvenile hatched in Taunton, Somerset, in 2019 and recovered dead in Morocco six months later, is considered to be exceptional for a UK-ringed Peregrine (Drewitt & Sutton 2021). Only one other UK-ringed Peregrine has made such a long journey, travelling slightly further south to Lanzarote in the Canary Islands, and two other Peregrines have been recovered along the west coast of Portugal (Robinson et al 2019). Therefore, it is possible that Peregrines disperse at random. Some may reach the coastline and travel back inland while those that continue out to sea either die or arrive in locations such as France or the Republic of Ireland, where they are not resighted or where there is lower reporting of colour-ringed birds.

In our study, just under two-thirds of the Peregrines were two years old or under (n = 41). Therefore, it is likely many or most of these individuals were still in their phase of pre-breeding movement and natal dispersal. While we do not know exactly what they are
doing during this period, these non-breeding or non-territorial Peregrines are probably honing their hunting skills, familiarising themselves with potential nest sites and associated hunting grounds, and searching for potential partners and available breeding territories (Kauffman et al. 2004, Morton et al. 2018).

The increasing use of remote cameras on urban nests across England has revealed regular and repeated occurrences of both adults and younger birds of both sexes, still identifiable in their first or second calendar years, investigating occupied nest sites (EJAD pers. obs.). At some locations, such as Norwich and Leicester, new female Peregrines have taken over a nest site, already with nestlings or eggs, respectively, and the original females have disappeared (Norwich Cathedral 2016, Leicester Peregrines 2020). While some young birds may begin to breed in their second calendar year, most do so in their third calendar year or older (Ratcliffe 1993, Zabala & Zuberogoitia 2015).

In western Germany, female Peregrines have often attempted to nest in their first spring, although these birds often laid later in the season and had lower breeding success than more experienced females. In stable, fully occupied areas, only 3% of females in their second calendar year may attempt to breed, whereas in areas where the Peregrine population is still recovering this may increase to 20% (Wegner & Thomas 2012). Meanwhile, male Peregrines in their second calendar year rarely attempt to breed; when there are fewer territories available it is likely they may become helpers or simply wander (Wegner 2017).

The short dispersal distance for male Peregrines in our study aligns with the findings of Mearns & Newton (1984) and Morton et al. (2018); the proportion of male Peregrines with shorter dispersal distances has increased as the population has grown and stabilised. Morton et al. (2018) also found that, as the Peregrine population increased, the proportion of females dispersing over 100 km fell from 56% to 49%; for males, the proportion reduced by almost half (30% to 16% travelling >100 km).

While sex is the overall determining factor that influences the dispersal distances of Peregrines (Smith & McGrady 2009, Smith et al. 2015, Morton et al. 2018), population density also has some effect on Peregrine dispersal, although to varying degrees under different situations. This is supported by the reduced dispersal observed in the Netherlands and Germany after Peregrine populations had increased (Rockenbauch 2002, van Geneijgen 2014, Wegner 2017). Our study supports this pattern of change for male Peregrines, but finds opposite results for females. Female Peregrines in our study dispersed over greater distances than in all three previous studies (Mearns & Newton 1984, Smith & McGrady 2009, Morton et al. 2018) (Table 2). This may be due to a combination of the females’ tendency to disperse further when seeking a territory in which to breed, and the result of increasing population density closer to their natal site causing them to seek places further afield with less competition for food and nest sites (Morton et al. 2018). Even for young females that may still be dispersing, long dispersal distances may be explained by the presence of territorial pairs across the landscape (and at favourable nesting locations) challenging them and moving them out of their territories. There is evidence that, as population density increases, first-year Peregrines may disperse further than adults (Smith et al. 2015).

For male Peregrines in a high-density population, dispersing longer distances to find a vacant territory may be riskier than staying close to their natal site. Also, there may be greater male mortality and turnover nearby, meaning they do not need to travel far to find a vacant breeding location (Smith et al. 2015, Morton et al. 2018). As part of this, some young Peregrines – often males – in their first to second calendar years may show fidelity to where they were hatched. They remain as ‘helpers’, assisting their parents with rearing the nestlings, through cooperative breeding. Staying with their parents provides them with the opportunity to hone their hunting skills, to

| Area | Mean Distance (km) | Sample size | Range (km) | Reference |
|------|--------------------|-------------|------------|-----------|
| Scotland | 68 | 15 | 3–185 | Mearns & Newton 1984 |
| Scotland and northeast England (ringed as nestlings and captured as breeders) | 80 | 12 | 11 - 104 | Smith & McGrady 2009 |
| Scotland and northeast England (ringed as nestlings elsewhere or in the study area and subsequently recovered dead in the study area) | 98 | 9 | 9 - 211 | Smith & McGrady 2009 |

| Area | Median Distance (km) | Sample n | Range (km) | Reference |
|------|----------------------|----------|------------|-----------|
| South Scotland and northern England | 85 | 47 | 31–125 (IQR) | Morton et al 2018 |
| Across Britain (1964–2016) | 76 | 299 | 35–143 (IQR) | Morton et al 2018 |
obtain ‘free’ food by begging like recently fledged nestlings, and to become more familiar with their local area (Opdam et al. 2003). This behaviour, while still uncommon, has been reported in the UK, for example in Brighton in 2005, London in 2018, South Gloucestershire and Cumbria, and often involves identifiable colour-ringed birds whose natal origins are known (EJAD pers. obs.). In Bath, single colour-ringed male individuals, ringed as chicks as part of our study, were still on site with the known breeding pair in their second calendar years in 2008 and 2012 respectively. They were involved with incubating eggs and feeding young. In 2008, the breeding male disappeared and the immature bird continued to rear the young with the breeding female. He subsequently became the breeding male at this location. Further afield, such behaviour has been documented in Germany, France, Italy, Australia, Canada and Japan (Kurosawa & Kurosawa 2003, Wegner & Thomas 2012, Drewitt 2014, Wegner 2017).

In conclusion, our results provide an indication of where new Peregrines may appear from to recolonise vacant territories across the UK in the future. There are many urban Peregrines breeding north of the English Midlands, for example in Rochdale, Sheffield, Leeds and Wakefield (Rochdale Borough Council 2022, University of Sheffield 2022, University of Leeds 2022, Wakefield Peregrines 2022), which may contribute to this process of recolonisation; some of these breeding birds may themselves have originated in southwest England. Southern birds heading northwards may also encounter Peregrines dispersing southwards from southern Scotland and northern England, resulting in a mixing of regional populations and an increase in genetic diversity. Therefore, Peregrines dispersing from the southwest of England appear to play an important role towards establishing new populations in areas where they have been absent, or present in low densities, according to the most recent national Peregrine surveys (Wilson et al. 2018).

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