

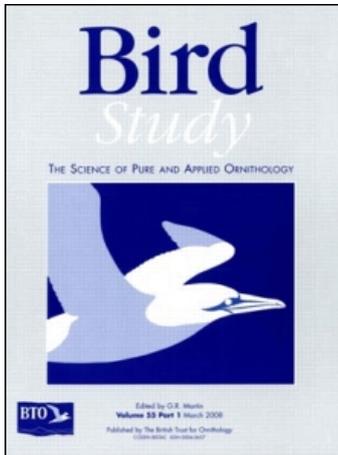
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# Natal and breeding dispersal in a reintroduced population of White-tailed Eagles *Haliaeetus albicilla*

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**Capsule** Natal dispersal distance was significantly shorter in males than in females.

**Aim** To examine the correlates of variation in dispersal in a reintroduced population of White-tailed Eagles *Haliaeetus albicilla* in western Scotland.

**Methods** Observations of natal (or release) sites and subsequent breeding sites of individually marked birds were used to calculate natal dispersal distance (NDD; the distance between natal (or release) site and first breeding site) and breeding dispersal distance, which is the distance moved by adults between sites of reproduction.

**Results** NDD was significantly shorter in males than in females. Male NDD did not change over the 25+-year study as the population expanded. Female NDD appeared to increase over time. Brood size at fledging and fledging date were not associated with NDD in either sex. There was no evidence of an association between parent and offspring NDD. Breeding dispersal was uncommon and involved moves to neighbouring territories when it did occur.

**Conclusions** In White-tailed Eagles, like the vast majority of animals, most movements affecting gene flow and demography result from natal dispersal. Our finding that NDD was lower in males than in females was consistent with the hypothesis that males compete for resources in order to attract females, and hence there is a greater selective advantage for males to stay closer to their natal sites, whereas females choose between the available resources of different males and so can disperse further. The apparent increase in female NDD over time was probably because, when first reintroduced, all birds shared the same 'natal' (release) site and female NDD was initially constrained to follow male NDD (since males settle at breeding sites earlier than females). Later, however, greater female NDD could be expressed in an expanded population with greater range of natal and breeding sites. There was little evidence that NDD of White-tailed Eagles in western Scotland is being affected by increasing population density, suggesting that carrying capacity is far from being realized.

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Dispersal behaviour is increasingly emphasized as an important, but poorly understood influence on animal populations and their conservation (Gadgil 1971, Begon *et al.* 1996, Clobert *et al.* 2001), especially in long-lived species with delayed maturity. For instance, dispersal can affect population persistence through

genetic and demographic linkage within metapopulations (e.g. Brooker *et al.* 1999) and through rapidity or form of geographic spread in establishing and introduced populations (Lensink 1997, South & Kenward 2001, Gammon & Maurer 2002). Greenwood & Harvey (1982) suggested that the movement of an animal between its birth site and the site where it first reproduces be termed 'natal dispersal', to distinguish it from breeding dispersal, which is the subsequent

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movement of adults between sites of reproduction. We follow this terminology here. In the vast majority of animals, most movements affecting gene flow and demography result from natal dispersal, i.e. animals move greater distances between their birth site and first breeding site than between subsequent breeding sites (e.g. Gadgil 1971, Johnson & Gaines 1990). Most research attention has thus focussed on natal dispersal.

Much of the theoretical background to natal dispersal invokes hypotheses relating to selective influences of inbreeding avoidance, or competition avoidance for resources or mates (Greenwood & Harvey 1982, Shields 1983, Liberg & von Schantz 1985, Waser 1985, Pusey 1987, Johnson & Gaines 1990, Gowaty 1993), or combinations of these influences (Dobson & Jones 1985). Discriminating between these alternative hypotheses is difficult, not least because they are not mutually exclusive and may generate identical predictions (Alonso *et al.* 1998) and so consensus on the evolution of natal dispersal has remained elusive (Alonso *et al.* 1998, Clobert *et al.* 2001, Bowler & Benton 2005). These difficulties are confounded by the practical research problems which animal movements bring to their study (Clobert *et al.* 2001, Nathan 2001, Winkler *et al.* 2005). Dispersal theory, therefore, considerably outweighs its empirical basis (MacDonald & Johnson 2001, Cam *et al.* 2004) and this is a serious problem for dispersal research (Bowler & Benton 2005).

Reintroduction projects are increasingly used as a management tool in raptor conservation (O'Toole *et al.* 2002). The study of reintroduced populations not only allows improved knowledge of processes which may influence the success of other reintroduction projects, but it can also offer important fundamental insights into population ecology (Nicoll *et al.* 2004, Seedon *et al.* 2007), because:

1. reintroductions represent the controlled expansion of a population into an effectively novel environment, initially from a limited number of simulated 'natal' sites;
2. a successfully reintroduced population permits the study of population processes over a wide range of population abundance and competitive influence;
3. all individuals are of known origin;
4. individuals can be more readily marked and therefore followed over their lifespan; and
5. long-term detailed monitoring programmes are often incorporated.

Consequently, the successful reintroduction of White-tailed Eagles *Haliaeetus albicilla* to western Scotland – started in 1975 and where the majority of birds have been individually marked with patagial wing-tags (Love 1983, Bainbridge *et al.* 2003, Evans *et al.* 2003) – presents a unique long-term opportunity for the study of dispersal in a restored population of a large raptor. Like most other large raptors, the dispersal behaviour of White-tailed Eagles is poorly known (e.g. Newton 1979, Paradis *et al.* 1998), although Nygård *et al.* (2003) studied juvenile dispersal (movements in the years prior to settling on a breeding territory) in west Norway using radio telemetry, and other studies have documented natal dispersal distances (NDDs) based on the results of colour-ring resightings and conventional ring recoveries (Helander 2003, Struwe-Juhl & Grünkorn 2007).

In this paper, we use data from the Scottish White-tailed Eagle reintroduction project to address hypotheses concerning the causes of natal dispersal. First, although inbreeding avoidance is thought by many to be the main underlying cause of sex-biased dispersal (Greenwood 1980, Perrin & Mazalov 2000), following Greenwood (1980) (see also Johnson & Gaines 1990, Clarke *et al.* 1997, Wolff & Plissner 1998, Perrin & Mazalov 2000), we assume that in common with most other monogamous birds (and other similar raptors: Newton 1979, Forero *et al.* 2002, Serrano *et al.* 2003), White-tailed Eagles have a breeding system where males compete for resources in order to attract females, and hence there is a greater selective advantage for males to stay closer to their natal sites, whereas without the constraint of establishing a territory, females choose between the available resources of different males. Although female White-tailed Eagles, as well as males, have been observed in territory defence at nest-sites (references in Helander *et al.* 2003), specific evidence in favour of our assumed sex-based difference in prioritization of breeding resource acquisition in White-tailed Eagles involves males first settling on a territory (see Results) and breeding (Bainbridge *et al.* 2003) at a younger age than females. There are also differences in the behaviour of males and females during juvenile dispersal in the years prior to breeding which are consistent with the suggested sex differences in the priority for acquisition of a breeding territory (Whitfield *et al.* in press). Therefore, we hypothesize that NDDs in males should be less than in those of females.

We also examine if NDD has changed as the population has expanded (Matthysen 2005), if NDD is related to fledging date or brood size at fledging (Alonso *et al.*

1998, Pasinelli & Walters 2002, Forero *et al.* 2002) and if there is a genetic influence on NDD by testing for a positive correlation between parental and offspring NDD within-sex (Wheelwright & Mauck 1998). We also present basic descriptive statistics for natal and breeding dispersal distances: this is important for conservation management and planning of further reintroduction projects (e.g. to determine 'search areas' when scoping for the suitability of alternative release sites) (Seedon *et al.* 2007).

## METHODS

From 1975 to 1985, 82 young White-tailed Eagles, collected from Norway when aged between 6 and 8 weeks, were subsequently released by 'hacking' on the island of Rum in the Inner Hebrides of western Scotland. Between 1975 and 1981 each bird was fitted with colour-rings as well as a standard metal ring. From 1982, all eagles were fitted with patagial wing-tags so as to allow easier identification after release, by cohort and by individual. The first breeding attempts by two pairs were recorded in 1983. Wild-bred birds, initially offspring of the first release eagles, first attempted to breed in 1995. A second phase of releases, of 58 Norwegian birds, was undertaken between 1993 and 1998 in Wester Ross, on the north-west mainland of Scotland. All second-release birds were fitted with individually and cohort-unique patagial wing-tags. The majority of wild-bred birds (155 of 221, up to 2006) were also fitted with such patagial wing-tags as nestlings. More detailed descriptions of the reintroduction methods are given by Love (1983), Green *et al.* (1996), Bainbridge *et al.* (2003) and Evans *et al.* (2003). We recognized three 'stages' of the reintroduction analytically: first release, second release and wild-bred, and analyzed results up to 2006 when there were 36 occupied territories, 33 breeding attempts and mean nearest neighbour distance between occupied territories was 9.9 km (range 1.1–35.4 km).

Birds were assigned to a sex based on biometrics (Helander 1981, Helander *et al.* 2007) and, from 1993 onwards, molecular sexing (Fridolfsson & Ellegren 1999) of nestlings (or birds held prior to release) and, once adult, on behavioural and within-pair size differences. Brood size at fledging was recorded at all successful nests. Fledging dates were also recorded when possible as a result of nest-monitoring efforts: the mid-point between the dates of two nest visits was calculated in those cases when it was known that fledging had occurred between the two visits but an exact date was unknown. Dates were converted to numbers by assuming 1 July = 1. Small

sample sizes in several years did not allow us to control for any annual differences in population fledging dates by taking individuals' fledging dates as residuals of annual cohort averages, and so we had to use raw values. Released birds were held in captivity for legal quarantine requirements beyond the dates when wild birds fledged, and so analyses involving fledging dates only considered wild-bred birds. This required that we could not include all potential variables and test all hypotheses using multivariate analyses; hence, reported sample sizes also varied between statistical tests.

Studies of avian dispersal are often confounded by study area effects (Baker *et al.* 1995, Winkler *et al.* 2005) when dispersal distances are greater than study site limits. This problem was not relevant in the present study because of the conspicuous nature of the species and its comparative rarity in the context of nationwide and intensive surveillance efforts to identify breeding locations (Bainbridge *et al.* 2003, Evans *et al.* 2003). Natal site (or release site for first- and second-release birds) and breeding site grid references were recorded to the nearest 100 m using 1:25 000 topographic maps according to individual colour-ring or patagial wing-tag identification and entered into a geographical information system (GIS). Using the GIS we calculated two metrics: Full NDD (the straight-line distance between a bird's natal site and first breeding site) and Terrestrial NDD (Full NDD subtracting those parts of the distance overlying the sea). We calculated Terrestrial NDD primarily to allow comparison between our results and those when White-tailed Eagles do not inhabit coastal habitats (Helander *et al.* 2003). Year of recruitment to the breeding population, when a bird first showed evidence of territory occupation (settlement and nest-building at a site), was also recorded for each bird.

NDD was not normally distributed and so we used non-parametric statistical tests on untransformed data, and a square-root transformation to normalize NDD when a parametric test was employed. We preferred presenting median values in descriptive statistics due to non-normality, but also present mean values for comparison with other studies which use this statistic. Analyses were undertaken using SPSS 15.0 and R 2.4.1 via BRODGAR 2.5.3.

## RESULTS

### Natal dispersal

Males first recruited at a median age of 4.0 years ( $n = 30$ ) and females at a median age of 5.0 years ( $n = 33$ ):

**Table 1.** Median (range in brackets) values (km) of natal dispersal distance (NDD) for male and female White-tailed Eagles according to stage of the reintroduction programme.

|                         | All        | Release 1  | Release 2  | Wild       |
|-------------------------|------------|------------|------------|------------|
| Male; Full NDD          | 28 (2–152) | 45 (7–125) | 33 (2–152) | 21 (4–97)  |
| Male; Terrestrial NDD   | 14 (2–95)  | 11 (5–48)  | 18 (2–95)  | 11 (0–48)  |
| Female; Full NDD        | 57 (2–154) | 47 (7–125) | 54 (2–128) | 58 (5–154) |
| Female; Terrestrial NDD | 26 (2–143) | 11 (5–48)  | 34 (2–112) | 26 (5–143) |

Full NDD, full straight-line distance; Terrestrial NDD, straight-line distance subtracting distance over the sea; All, all birds (37 males, 39 females); Release 1, first release birds (11 males, 13 females); Release 2, second release birds (6 males, 9 females); Wild, wild-bred birds (20 males, 17 females).

the frequency distributions of first recruitment age were significantly different by sex (Kolmogorov–Smirnov Test,  $Z = 2.56$ ,  $P < 0.001$ ).

Median values for Full NDD were 21–45 km in males and 47–58 km in females, depending on reintroduction programme phase. Median values for Terrestrial NDD were lower, because the distances excluded sections which overlaid the sea, at 11–18 km for males and 11–34 km for females (Table 1). For all birds, mean Full NDD was 42 km and 59 km for males and females respectively, and mean Terrestrial NDD was 21 km and 33 km for males and females respectively.

Considering all birds, the tendency towards greater NDD in females than males was significant only for Terrestrial NDD (Table 2). However, first-release birds which established the initial breeding sites of the reintroduction probably biased this result because both males and females were constrained to have identical NDD, since all shared a common ‘natal’ site (the release site) and each male and female of a pair shared

**Table 2.** Results of Mann–Whitney  $U$ -tests for differences between male (M) and female (F) White-tailed Eagle natal dispersal distance (NDD).

| M versus F | Full NDD |                       |           | Terrestrial NDD |                       |           |
|------------|----------|-----------------------|-----------|-----------------|-----------------------|-----------|
|            | All      | Exclude first release | Wild only | All             | Exclude first release | Wild only |
| $U$        | 538.5    | 223.5                 | 94        | 515.5           | 201                   | 86        |
| $P$        | 0.057    | 0.036                 | 0.020     | 0.032           | 0.012                 | 0.010     |

Full NDD, full straight-line distance; Terrestrial NDD, straight-line distance subtracting distance over the sea; All, all birds (37 males, 39 females); Exclude first release, wild bred and second release birds only (26 males, 26 females); Wild only, wild-bred birds only (20 males, 17 females); female NDD was greater than male NDD in each case.

a novel breeding site. Any sex difference in NDD could thus only be expressed once the population had expanded beyond the initial breeding sites established by first-release birds. Examination of temporal changes in NDD confirmed that, initially, NDD was identical for males and females for the first breeding birds after reintroduction; but as the population expanded, sex differences became more apparent (Fig. 1). Hence, ignoring first release birds, sex differences in NDD were significant for both Full and Terrestrial metrics, with females dispersing further than males (Table 2, Fig. 2): median NDDs were approximately two times greater in females than in males (Table 1). This result was consistent with our hypothesis that male NDD should be lower than female NDD, and all subsequent analyses, therefore, considered males and females separately.

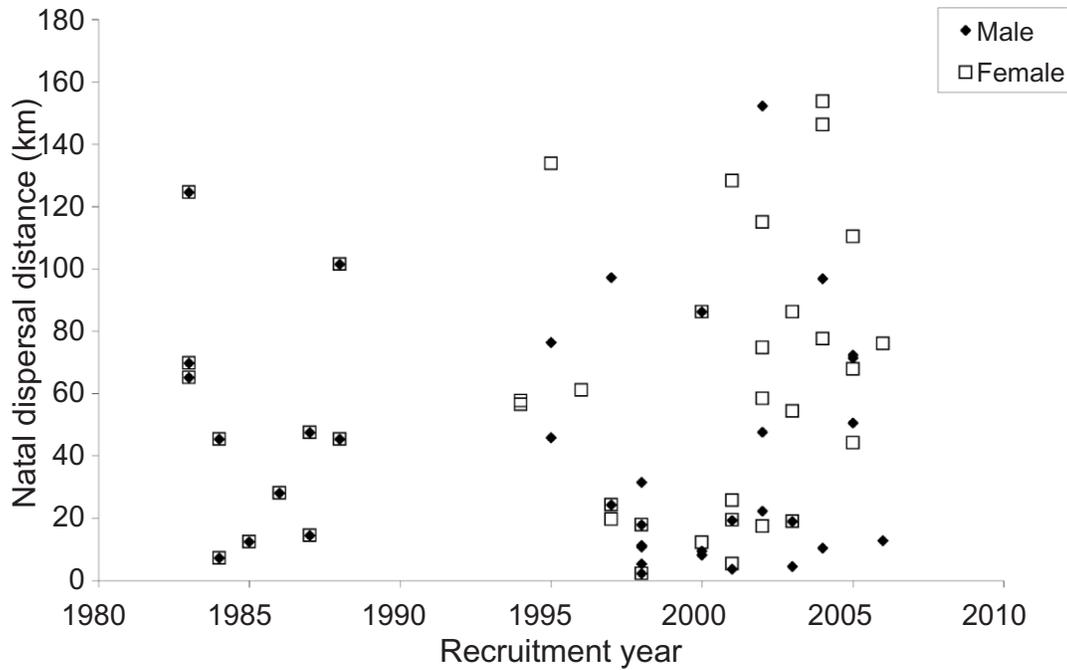
Male NDD ( $n = 37$ ) showed no relationship with recruitment year for either Full (Spearman's  $r_s = -0.103$ ,  $P = 0.541$ ) or Terrestrial metrics (Spearman's  $r_s = 0.001$ ,  $P = 0.994$ ). Females ( $n = 39$ ) also showed no relationship with recruitment year for Full NDD (Spearman's  $r_s = 0.254$ ,  $P = 0.119$ ) but there was a positive correlation for Terrestrial NDD (Spearman's  $r_s = 0.387$ ,  $P = 0.015$ ).

In Gaussian general linear models (GLMs) with Full NDD (square-root transformed) of females or males as response variable, and fledging date and brood size at fledging as factorial explanatory variables, no significant associations were found (Table 3).

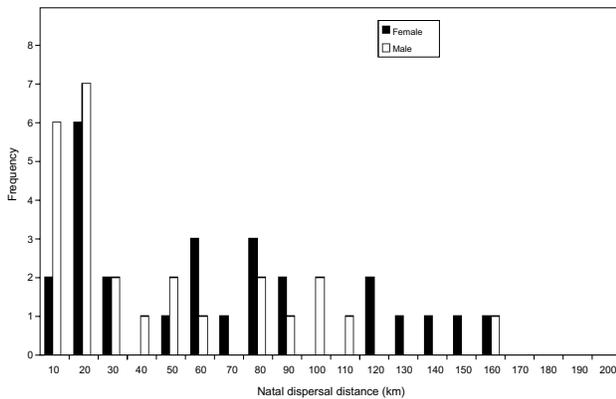
In Gaussian GLMs with offspring Full NDD (square-root transformed) as response variable and parent Full NDD (square-root transformed) as a fixed explanatory variable, and fitting parent identity as a random factor (e.g. Brambilla *et al.* 2006), offspring and parent NDD (within-sex) were not related in males ( $F_{7,10} = 1.261$ ,  $P = 0.357$ ) or females ( $F_{6,7} = 2.136$ ,  $P = 0.172$ ).

Stage of reintroduction programme (first release, second release or wild: Table 1 gives sample sizes) had no apparent association with Full NDD for males (Kruskal–Wallis test,  $\chi^2 = 1.723$ ,  $df = 2$ ,  $P = 0.422$ ) or females (Kruskal–Wallis test,  $\chi^2 = 0.708$ ,  $df = 2$ ,  $P = 0.702$ ). Stage of reintroduction also showed no association with Terrestrial NDD, both for males (Kruskal–Wallis test,  $\chi^2 = 1.755$ ,  $df = 2$ ,  $P = 0.418$ ) and females (Kruskal–Wallis test,  $\chi^2 = 3.203$ ,  $df = 2$ ,  $P = 0.202$ ).

The direction of natal dispersal appeared to be primarily on a north–south axis in both females and males (Fig. 3). These tendencies were not formally tested because available coastal habitat in western Scotland is primarily distributed on a north–south axis and so this result probably did not indicate any inherent bias in dispersal direction.



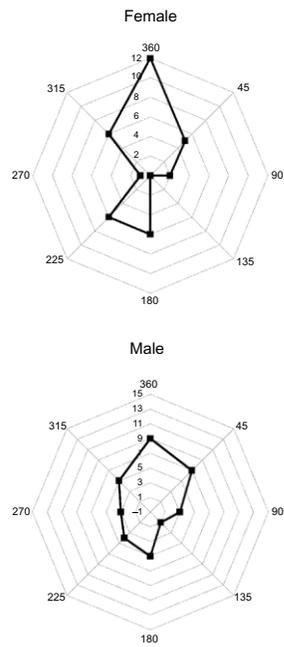
**Figure 1.** Plot of Full natal dispersal distance (NDD) (km) for male (solid diamond) and female (open square) White-tailed Eagles according to the year in which the bird recruited to the breeding population.



**Figure 2.** Frequency histogram for male (white bars) and female (black bars) Full natal dispersal distance (NDD), excluding birds from the first release programme

**Table 3.** Results of Gaussian GLMs examining potential relationships between (square root) Full natal dispersal distance (NDD) and fledge date and brood size in female ( $n = 8$ ) and male ( $n = 14$ ) White-tailed Eagles.

| Explanatory | Response    | Estimate | se     | <i>t</i> | <i>P</i> |
|-------------|-------------|----------|--------|----------|----------|
| Female NDD  | Fledge date | 0.04     | ± 0.08 | 0.47     | 0.694    |
|             | Brood size  | -0.50    | ± 2.76 | -0.18    | 0.863    |
| Male NDD    | Fledge date | -0.03    | ± 0.05 | -0.57    | 0.581    |
|             | Brood size  | -0.49    | ± 1.53 | -0.32    | 0.755    |



**Figure 3.** Frequency of natal dispersal direction by 45° compass point categories for female (top) and male (bottom) White-tailed Eagles in western Scotland.

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## Breeding dispersal

There were 607 bird-years of opportunities for breeding dispersal to occur. Excluding movements of tertiary birds originally in trios (see Bainbridge *et al.* (2003) for the occurrence of two-female-one-male trios at territories during the earlier years of the reintroduction programme), six incidents of breeding dispersal were recorded, involving four males and two females, dispersing a median of 12.3 km (mean 19.9 km, range 5–63 km) (Table 4). In all cases, birds shifted to a neighbouring territory and in only one case was the territory to which dispersal occurred newly established by the dispersing bird. In at least four of these six cases, the dispersing bird did not retain the same partner (probably through death of the partner). In two cases, the identity of the dispersing bird's initial partner was unclear due to a lack of wing-tags.

These records did not include movements of birds considered to have shifted to an alternative nest-site as part of the same territory. Breeding birds typically either stayed at the same nest-site or moved a short distance to an alternative site between years, although there were odd exceptions. For example, in 18 territories involving 148 pair-years of potential movements (average per territory = 8.2 potential movements), taking the median distance between sites in consecutive years for each territory as a datum, the median was 0.1 km (range = 0.0–4.5 km), and taking the maximum distance moved between years for each territory as a datum, the median was 2.0 km (range = 0.0–15.5 km).

## DISCUSSION

We found that male White-tailed Eagles had shorter NDDs than females. This is consistent with our assumed sex-differences in selection for priority of access to breeding resources. We conclude, therefore,

**Table 4.** Sex, establishment year (year in which bird was recorded as settled on first territory), dispersal year (year in which bird was recorded as settled on second territory) and distance between nest-sites of first and second territory for six incidents of breeding dispersal.

| Sex | Establishment year | Dispersal year | Distance (km) |
|-----|--------------------|----------------|---------------|
| M   | 1985               | 1989           | 5.1           |
| M   | 1998               | 2001           | 7.6           |
| M   | 1998               | 2002           | 13.0          |
| M   | 2003               | 2005           | 63.3          |
| F*  | 1990               | 1994           | 18.5          |
| F   | 1991               | 2005           | 11.6          |

\*Second territory did not exist prior to bird dispersing to it.

that competitive differences between the sexes affected NDD. In most other birds (Greenwood 1980, Greenwood & Harvey 1982, Clarke *et al.* 1997), female NDD is greater than male NDD, and this holds in most raptor species too (e.g. Newton 1979, Newton & Marquiss 1983, Forero *et al.* 2002, Serrano *et al.* 2003; although see Newton *et al.* 1989, Miller & Smallwood 1997, Negro *et al.* 1997).

Nygård *et al.* (2003) found that in west Norway during juvenile dispersal (i.e. movements in the years preceding settlement at a breeding site), female White-tailed Eagles moved further from their natal site than did males. Intriguingly, given that this was the donor area for birds used in the western Scotland reintroduction, maximum juvenile dispersal distances in Norway were similar to maximum NDDs in western Scotland. With means of 90 km and 114 km for males and females respectively, however, White-tailed Eagle NDDs in south Sweden (Helander 2003) were higher than documented for western Scotland by the present study. An explanation for the difference may lie in the greater breeding density of the longer-established Swedish population forcing longer dispersal to find vacant breeding sites. Struwe-Juhl & Grünkorn (2007), in an analysis of colour-ring sightings of White-tailed Eagles from Schleswig-Holstein, northern Germany, described median NDD as 89 km (range 16–450 km) and remarked that NDD increased with population density. There was no indication that male White-tailed Eagle NDD increased over the study period in western Scotland. Within the geographical range currently occupied by the White-tailed Eagle population in western Scotland it seems unlikely that carrying capacity has been reached because, for example, several islands originally occupied by first-release birds continue to support new breeding sites annually (see also Bainbridge *et al.* 2003, Evans *et al.* 2009). This may suggest that competition for breeding sites is still low, even 25 years after the first sites were occupied.

We found no effect of fledging date or brood size on NDD. Other studies of birds have found a positive effect of fledging date on NDD (Miller & Smallwood 1997) or failed to find an effect (Dhondt 1979, Verhulst *et al.* 1997, Wheelwright & Mauck 1998). Similarly, a positive effect of brood size on NDD has been found in some studies (e.g. Tinbergen 2005) but not others (e.g. Kenward *et al.* 2001). Contradictory results pervade much of the field-based literature on influences on avian NDD: further examples would include body condition or body mass (e.g. Alonso *et al.* 1998, Wheelwright & Mauck 1998, Pasinelli & Walters 2002, Altwegg *et al.* 2000),

although unfortunately we could not investigate if body condition was influential in Scottish White-tailed Eagles. Such contradictions illustrate the complexity of, and interaction between, factors affecting NDD (Weatherhead & Forbes 1994, Verhulst *et al.* 1997, Snoeijs *et al.* 2004) and the difficulty in teasing these apart in the absence of experiments (Massot & Clobert 2000).

Our finding that female Terrestrial NDD increased over the study period could be interpreted as evidence of competition, and implicitly that we were incorrect in our assumption that males should be more likely to be subject to competition for breeding resources than should females. Female defence of breeding territories immediately around the nest-site (see references in Helander *et al.* 2003) could also indicate that our assumption was wrong. We suggest, however, that an alternative explanation is more likely. As we have noted, male and female first-release birds were constrained by their shared natal site to have identical NDD, but subsequently as more breeding birds originating from more natal sites entered the population this constraint was increasingly relaxed. Choice of breeding site is primarily by the male (males settle and breed when younger than females: this study, Bainbridge *et al.* 2003, Evans *et al.* 2009) and so we suggest that first-release female NDD was constrained to follow male NDD, rather than *vice versa*. Other females entering the population later were less constrained, however, and this allowed females to have a greater expression in choice of breeding sites regarding distance from natal sites and, as we have illustrated, have greater NDD than males; hence, female NDD increased over the study period (see Fig. 1). Any sex difference in NDD could thus only be expressed once the population had expanded beyond the initial breeding sites established by first-release birds.

The constraint on female NDD in first-release birds may have influenced other results, and so an absence of any apparent effect of parent NDD on offspring NDD in females will also have been affected by the constraint on first-release females and so this should not be seen as reliable evidence for an absence of genetic influence on female NDD. On the other hand, if we assume that male NDD was not restricted by the initial reintroduction method, the lack of a relationship in father–son NDD is probably a more reliable indicator of minimal genetic influence on within-sex NDD.

Long-term studies of dispersal are rare (Belichon *et al.* 1996), but even in the absence of comparable research, the similarity in White-tailed Eagle NDD across our lengthy study period was perhaps surprising in light of

no corroborative evidence for genetic influence on NDD, because it suggested that NDD was ‘fixed’. It also highlighted that first-release birds, despite being reintroduced to an environment with an unconstrained choice of breeding sites, did not settle at some breeding sites which were much closer to the release location than those occupied, despite being apparently suitable for successful breeding, judging by the performance of birds which used them later (Bainbridge *et al.* 2003, Evans *et al.* 2003). As we noted earlier, the influences on NDD are liable to be complex (Dobson & Jones 1985, Johnson & Gaines 1990, Verhulst *et al.* 1997, Perrin & Mazalov 2000) and genetic variation in dispersal may be difficult to detect in the field (Waser & Jones 1989, Massot & Clobert 2000). Moreover, our analyses investigating genetic influence had low power due to small sample size and were conceivably overly simplistic (Arcese 1989, Waser & Jones 1989, Massot & Clobert 2000, Kruuk & Hadfield 2007, Postma & Charmantier 2007; although see Wheelwright & Mauck 1998, Pasinelli & Walters 2002). The unique research opportunities provided by reintroductions could be better exploited in this regard by the future inclusion of genetic profiling of birds from the outset: survival and recruitment can also be monitored by this method (Rudnick *et al.* 2005), as can dispersal (Berry *et al.* 2004).

Breeding dispersal was rare in White-tailed Eagles in western Scotland, and relatively localized when it did occur, indicating that natal dispersal was the main mechanism by which gene flow and population expansion occurred, in common with another White-tailed Eagle population (Struwe-Juhl & Grünkorn 2007), with most or all other raptors (Newton 1979, Lensink 1997) and most other birds (Greenwood & Harvey 1982, Johnson & Gaines 1990; but see Dale *et al.* 2005). It is interesting, given a relative lack of constraint in choice of alternative sites for a newly established population, that it was uncommon for eagles to shift to alternative breeding locations once settled. This strongly indicates that breeding dispersal is not a common trait of White-tailed Eagles and emphasizes the importance of birds’ initial decisions in breeding-site choice.

Our study provides several pointers for conservation management of White-tailed Eagles, especially regarding reintroduction projects, of which there are several currently in operation or in planning (Dennis 2003). Food dumps in the western Scotland reintroduction were provided close to release sites to provide newly released birds with an easy food source (Love 1983, Bainbridge *et al.* 2003, Evans *et al.* 2003) and as we

found no difference in NDD according to stage of the reintroduction, the implication is thus that the provisioning did not apparently serve to 'tie' released birds close to the point of release long enough to affect subsequent dispersal (cf. Kennedy & Ward 2003). This may suggest that food dumps may influence the survival/condition of released birds but do not affect natal dispersal, if a subsidiary objective of dumps is to retain juveniles' presence close to the release site to keep them in a known 'safe' location. Finally, although it should be acknowledged that both the prevailing release environment and the genetic origin of the western Scottish released birds could have affected their dispersal (Weatherhead & Forbes 1994, Pasinelli *et al.* 2004), our results would suggest that when future reintroduction programmes consider the suitability of potential release sites it would be reasonable to assume that, initially, most birds will select breeding sites within 50 km of the release site and that all birds will probably breed within 150 km of the release site.

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