Sex-Biased Dispersal: A Result of a Sex Difference in Breeding Site Availability

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ABSTRACT: Sex-biased dispersal is often explained by assuming that the resource-defending sex pays greater costs of moving from a familiar area. We hypothesize that sex-biased dispersal may also be caused by a sex bias in breeding site availability. In avian resource-defense mating systems, site availability is often more constrained for females: males can choose from all vacant sites, whereas females are restricted to sites defended by males. Using data on breeding dispersal of a migratory passerine, we show that average number of available breeding options and availability of the previous year's territory was greater for males than females. The female bias in site unavailability may explain the female bias in probability of breeding dispersal because there was no sex bias in dispersal among birds with their previous year's territory available. We suggest that sex biases in the availability of breeding options may be an important factor contributing to observed variation in sex-biased dispersal patterns.

Keywords: arrival time, breeding dispersal, habitat selection, mating system, site fidelity.

One of the few general patterns of animal dispersal is that one sex is more likely to disperse from the natal or previous breeding site than the other (Greenwood 1980; Greenwood and Harvey 1982; Waser and Jones 1983; Wolff 1994; Clarke et al. 1997). Such sex-biased dispersal is widely accepted to be linked to the type of social mating system (Greenwood 1980). In birds, females are commonly the dispersive sex (Greenwood 1980; Clarke et al. 1997), and birds predominantly have a resource-defense mating system in which males defend resources to attract females (Emlen and Oring 1977; Greenwood 1980). In mammals,

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dispersal is male biased and a mate-defense mating system predominates (Greenwood 1980; Dobson 1982; Waser and Jones 1983). Female mammals generally invest more into reproduction and thus settle in relation to resources, and the distribution of females influences the distribution of males, whose fitness is limited by the number of mates they can defend (Trivers 1972; Clutton-Brock and Harvey 1976; Emlen and Oring 1977; Greenwood 1980). Exceptions to these generalizations (e.g., mate defense or female resource defense in birds, male resource defense in mammals) appear to broadly corroborate Greenwood's view that the sex choosing the resources is less likely to disperse (Wolff 1994; Clarke et al. 1997). Still, these general patterns do not always hold (Waser and Jones 1983; Johnson and Gaines 1990; Wolff 1994; Clarke et al. 1997), suggesting that a single hypothesis is unlikely to explain sex-biased dispersal patterns (Dobson and Jones 1985; Lambin et al. 2001). Similarly, for inbreeding avoidance as a driver of sex-biased dispersal in mammals (see Dobson 1982; Dobson and Jones 1985; Wolff 1994), additional social or ecological factors need to be considered to explain the observed sex bias in dispersal (Pusey 1987; but see Wolff and Plissner 1998).

In the resource-defense mating system of birds, the sex defending the resources and choosing a site first is thought to be less likely to disperse due to the greater costs of moving from a familiar area (Greenwood 1980). In many birds, individuals tend to return to their natal or previous breeding area (Greenwood 1980; Greenwood and Harvey 1982). Philopatry and site fidelity may be advantageous because of the positive effects of local familiarity on, for example, exploitation of food resources and finding safe breeding sites (Greenwood 1980; see also Hinde 1956; Stephens and Krebs 1986; Stamps 1995). These benefits accrue to both sexes, but Greenwood (1980) also suggested a sex difference in the benefits related to resource defense. Males would benefit more from local familiarity if finding and defending a familiar site incurs lower costs compared to an unfamiliar site because of the advantage of prior residency (Krebs 1982), knowledge of potential competitors (Stamps 1987), and knowledge of alternative breeding sites (Pärt 1994).

We propose an additional mechanism to explain sex-biased dispersal in which a sex bias in breeding site availability causes the sexes to have a different probability of finding their home site available at the time of site establishment. We assume that in male resource-defense mating systems males establish breeding sites and choose from all vacant sites, whereas females are constrained to choose from sites with advertising males (see "Discussion"). As males and females establish sites sequentially, the number of available sites should therefore be greater on average for males than females, especially in socially monogamous species. Furthermore, given an advantage of site fidelity (or philopatry), we expect the probability of acquiring a specific site close to the previous breeding site (or natal site) to be lower for females and, consequently, that females are more likely to disperse than males. A similar mechanism, in which a bird may find its former mate unavailable, has been suggested to explain divorce ("musical chairs hypothesis"; Dhondt and Adriaensen 1994).

We tested our "constrained site availability hypothesis" within the context of breeding dispersal by investigating patterns of breeding site fidelity and territory establishment of northern wheatears (*Oenanthe oenanthe*, hereafter wheatear) in relation to site availability. The wheatear is a small, tropical migrant, establishing territories sequentially in each breeding season. Males generally establish territories a few days before females arrive. In our study population, most males are socially monogamous (<2% are polygynous; D. Arlt and T. Pärt, unpublished data). Between years females shift territory more often than males (72% of 116 females, 54% of 135 males, $P = .004$; Arlt and Pärt 2008). Here, we show (1) that the availability of territory sites was greater for males than females and (2) that the female bias in between-year site shifts was closely linked to a corresponding female bias in the unavailability of the previous territory site, thus suggesting that a sex-biased constraint in site availability may be an important factor for sex-biased dispersal patterns.

Methods

The 40-km^2 study area is situated in southern central Sweden (59°50′N, 17°50′E). Since 1993 all sites potentially suitable for wheatears were monitored throughout the breeding season (for details of methods and breeding parameters collected, see Pärt 2001; Arlt and Pärt 2007). Most males and a large proportion of females were aged as young (1 year old) or old (>1 year old) based on plumage characteristics (see Pärt 2001). We marked adults from on average 56% of all breeding attempts and nestlings from 90% of all successful breeding attempts (i.e., producing ≥1 fledgling) with an aluminum ring and a unique combination of color rings.

During 2002–2005, we recorded arrival dates by visiting sites once a day (2002 and 2003) or once a day to every third day (2004 and 2005) between April 10 (i.e., a few days before the first wheatears arrive) and the end of May. For all years, an individual's arrival date was estimated as the first day this individual was observed. A few territory sites were less frequently monitored, and arrival dates were excluded in these cases. Territories were recorded on detailed maps (scale 1 : 10,000). A territory was determined by territory descriptions based on territory observations of the resident pair or unpaired male (<3%) made during >10 visits, excluding occasional observations of long-distance foraging or exploration movements. Territory sites (i.e., locations of territories) were relatively stable across years irrespective of territory holder because wheatears frequently use landscape features such as prominent stones or fences as territory boundaries. Territory sites were defined as identical between years when individual territories overlapped by more than two-thirds and included nest sites from previous or subsequent years (most cases) or when the distance between nest sites in consecutive years was <50 m (i.e., greater than the average territory radius of 70 m, assuming a circular shape; Arlt and Pärt 2007).

We used marked adults that were observed breeding during 2001–2004 and that returned to breed in the study area in the subsequent year. On average, 50% of males and 41% of females breeding in the 40-km^2 study area returned within a 60-km^2 area monitored annually for breeding wheatears. As indicated by the relatively short dispersal distances of birds shifting to a new territory site (75% moved <790 m) and the high detection probability of adults (98%; i.e., only 2% were recorded in nonconsecutive years and escaped detection in one year), most dispersers were probably detected. We defined all movements to a different territory site in the subsequent year as site shifts.

Availability of Territory Sites

Number of Available Breeding Sites. The total number of available breeding sites was defined as the maximum number of territories occupied in a given year. For each individual establishing a territory, we estimated the number of available breeding sites within the study area on its arrival date as the number of vacant territory sites (for males) or sites with an unpaired male (for females), assuming that females do not settle in the absence of a male (but see below and "Discussion"). We omitted sites with missing data on male arrival dates, leading to a slight overestimation of the actual number of unoccupied sites for males arriving later than the males with missing arrival dates. For females, this omission would instead lead to an

underestimation of the actual number of unpaired males, which, however, was balanced out by missing arrival dates of females in these cases.

Availability of the Previous Year's Territory Site. The previous year's breeding territory site of a male was defined as available when it was vacant at arrival. For females a site was defined as available when it was defended by an unpaired male. For females a territory site was thus unavailable either because it was unoccupied or because of the presence of an already-paired female. In a few cases, a male was able to establish a territory at its previous year's site despite the presence of another already-established male (i.e., by territory compression or insertion; Getty 1981; Ridley et al. 2004; two cases of 119). We also observed females that apparently had settled at a territory site before a male (two cases of 78). According to our general definition, these exceptions were still defined to have unavailable territory sites. Availability of the previous year's territory site could be determined for 119 males and 78 females.

Statistical Analyses

Arrival dates were standardized for annual variation within sex (annual residuals from an ANOVA unless stated otherwise). For differences between proportions, lower/upper confidence limits are reported for 95% confidence intervals according to Newcombe and Altman (2000). All other estimates of variation are ordinary 95% confidence intervals unless stated otherwise. Sample sizes may vary because of missing values (e.g., age classification). Analyses were performed in JMP 6.0 (SAS Institute).

Results

Females arrived on average 3.6 ± 0.6 days (mean $\pm$ SE) later than males (*t*-test: $t = 5.97$, df $= 607$, $P < .0001$). The median number of available sites per day was about three times higher for males (median $= 30$, 10%/90% quantile $= 12/90$, $N = 184$) than for females (median $= 9$, 10%/90% quantile $= 4/22$, $N = 184$; Wilcoxon test: $Z = -13.1$, $P < .0001$; fig. 1). The number of available sites declined continuously with time for males; for females there was a peak at intermediate arrival dates (fig. 1).

Males were more likely to find their previous year's territory site available (83.2% of 119) than females (48.7% of 74; difference $= 34.5\%$ [21.1/46.6], $\chi^2 = 26.34$, df $= 1$, $P < .0001$). Fewer than 20% of the wheatears found their previous territory to be occupied by another individual of the same sex (males: 16.8%, females: 18.0%; difference $= -1.1\%$ [−12.6/9.3], $\chi^2 = 0.04$, df $= 1$,
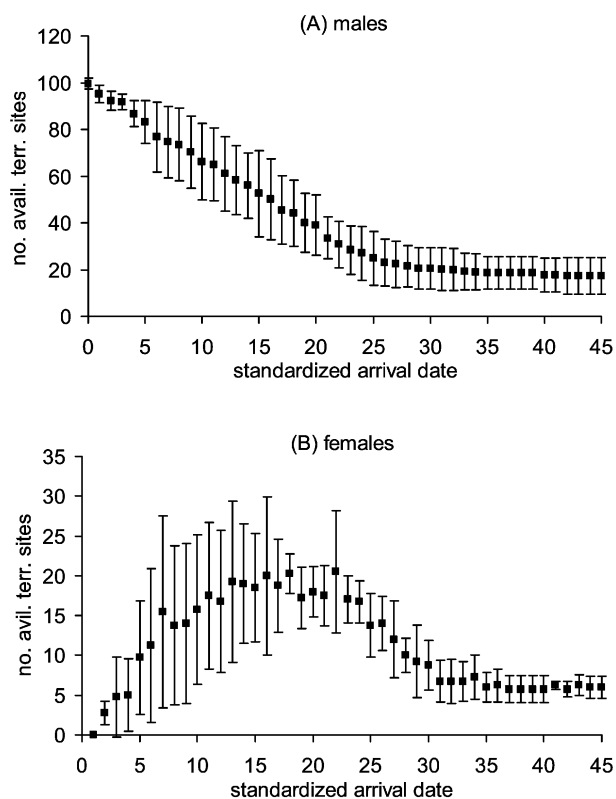

Figure 1: Number of available territory sites for arriving (*A*) male and (*B*) female wheatears in relation to arrival date (standardized for annual variation, day 1 = arrival of first male) in 2002–2005. Error bars refer to standard deviations.

$P = .34$). For many females, the previous site was unavailable because it was not yet occupied by a male (65.0% of 40). Females were overall more constrained to choose their previous breeding site than males, and except for two males and two females (see "Methods"), all wheatears for which their previous year's site was defined to be unavailable at the time of site selection moved to a new territory site. Among birds included in this study, females tended to be more likely to shift breeding sites between years (64.1% of 78) than males (51.3% of 119; difference $= 12.8\%$ [−1.3/26.0], $\chi^2 = 3.19$, df $= 1$, $P = .074$). In comparison, when the previous year's territory site was available at the time of establishment, this sex difference was reversed (females: 34.2% of 38, males: 44.4% of 99; difference $= -10.2\%$ [−28.7/6.1], $\chi^2 = 1.20$, df $= 1$, $P = .27$).

Also, among old and successful breeders (≥ 1 young fledged), that is, birds expected to be less likely to shift sites voluntarily and display a strong degree of site fidelity (see Greenwood and Harvey 1982; Arlt and Pärt 2008), males were more likely to have their previous site available

(81.2% of 69 vs. 60.9% of 46 females; difference = 20.3% [3.6/36.5], $\chi^2 = 5.69$, df = 1, $P = .017$) and shifted sites significantly less frequently (35.7% of 70 vs. 58.3% of 48 females; difference = −22.6% [−39.0/−4.3], $\chi^2 = 5.91$, df = 1, $P = .015$). When the previous site was available, this sex difference in breeding dispersal was greatly reduced (25.0% of 56 for males vs. 32.1% of 28 for females; difference = −7.1% [−28.0/11.9], $\chi^2 = 0.47$, df = 1, $P = .49$).

Thus, whereas the overall probability of between-year site shifts was greater for females, our results show that this sex difference was linked to a female bias in the unavailability of the previous year's breeding site (fig. 2). Most site shifts among females were linked to the unavailability of the previous year's breeding site, whereas this was not true for males (combining the two causes of unavailability for females; see "Methods"; χ^2 test of sex difference in frequency of site unavailability for birds that shifted sites; all birds: difference = −46.1% [−60.1/−27.8], $\chi^2 = 24.3$, df = 1, $P < .0001$; old successful: difference = −21.4% [−44.4/5.6], $\chi^2 = 2.37$, df = 1, $P = .12$; fig. 2).

Discussion

We found that a female bias in the probability of breeding dispersal in wheatears was linked to a female bias in breeding site unavailability at the time of site selection. Most female between-year site shifts were actually linked to the unavailability of their previous year's territory site. In contrast, females were not more likely to shift sites than males when their previous year's site was available (fig. 2). Our data therefore support the hypothesis that a female-biased constraint in site availability may be a proximate cause of sex-biased dispersal patterns. According to Greenwood's (1980) hypothesis of a male-biased dispersal constraint due to resource-defense costs, females would also be expected to shift sites more frequently when the previous year's site was available, but this was not supported by our data. However, we cannot reject Greenwood's idea as this would require sex-specific estimates of actual costs and benefits linked to settlement at familiar and unfamiliar sites, and such costs and benefits may differ between individuals because of various other factors, for example, the quality of the previous breeding site if individuals attempt to improve breeding conditions (e.g., failed breeding increases the likelihood of a site shift; Arlt and Pärt 2008). Below we discuss important assumptions of the constrained site availability hypothesis and the hypothesis's general applicability.

Our definition of site availability assumes a priority principle with no between-year site dominance effects. Between-year site dominance, where previous year's site
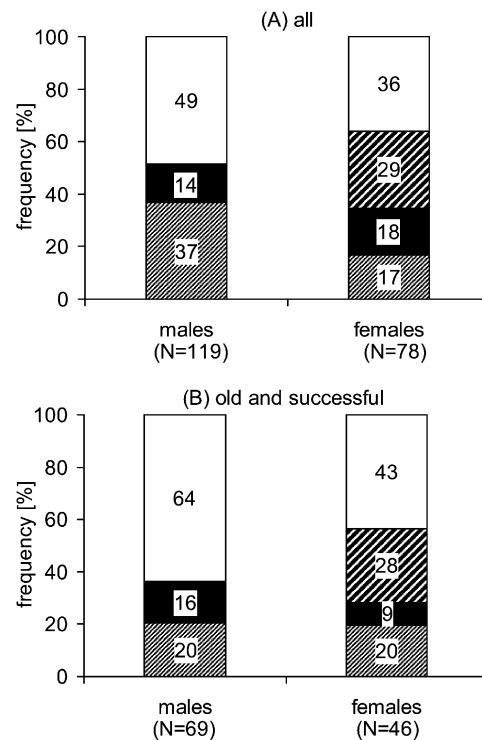

Figure 2: Percentage of males and females that shifted sites between years when their previous year's site was available (*narrow hatched*), unavailable due to the earlier arrival of another individual of the same sex (*solid*), or unavailable because it was not defended by an unpaired male (*broad hatched*; only for females) at the time of establishment or that remained site faithful (*open*), shown for (*A*) all birds and (*B*) only old and successfully breeding wheatears. Numbers in bars refer to percentages.

owners may evict an earlier-arrived new owner, has been reported for some migratory species (Nolan 1978; Lanyon and Thompson 1986; Jakobsson 1988; Piper et al. 2000). In our case, males did not seem to develop between-year site dominance: none of the 24 males arriving at their previous year's territory site after (1–25 days, median = 5.5, 10%/90% quantile = 3/21.5) another male had already established a territory evicted the new owner. Similarly, no female replaced another female. Males also rarely established a territory by territory compression at a site where another male had already settled. Whereas the effects of site dominance on site availability are difficult to predict (effects may depend on individual dominance status and/or site attractiveness; i.e., an attractive vacant site may not be available if the probability of being evicted is high), including territory compression would only increase availability of sites for males.

For female site availability, we also assume that males arrive earlier (i.e., protandry) and establish territories and that females settle only on sites with a displaying male.

Protandry is widely found among migratory bird species (Lack 1940; Morbey and Ydenberg 2001), and asymmetric roles in territory establishment where males defend territories and females choose between males and their territories seem to be a general pattern in avian resource-defense mating systems (Lack 1940; Andersson 1994). Alternatively, females may decide to settle in the absence of a male. Such a strategy may be advantageous for certain individuals, for example, those settling on attractive or high-quality sites where risk of remaining unpaired is low and the delay in the timing of breeding due to waiting is negligible. The two wheatear females that settled in the absence of a male were site faithful, early arriving, and old females returning to highly attractive territory sites (i.e., territory sites occupied during all of the 12 study years; cf. Arlt and Pärt 2007). The overall success of such a strategy, however, may be restricted to situations when limitation of mating opportunities is more severe for females (Kokko et al. 2006; see also Myers 1981). Kokko et al.'s (2006) models suggest that competition for mating opportunities determines which sex arrives first. When mating opportunities become a rare resource for females, that is, with female-biased sex ratios, no or low extrapair paternity (sperm competition), and/or fewer males than territories, competition for mating opportunities is stronger among females, which then may benefit from arriving earlier than males (Kokko et al. 2006). The above arguments should apply equally to sex-role-reversed species that have male-biased dispersal, where females arrive first and defend resources (Oring and Lank 1982) and males instead are more constrained in terms of site availability. In socially polygynous mating systems, females and males may have a more equal number of options because females can settle with paired males. But even in such systems, only a fraction of females mate polygynously in most species (see, e.g., Møller 1986; Hasselquist and Sherman 2001), hence only reducing the sex difference in site availability. In summary, the present evidence suggests that earlier arrival of one sex and asymmetric roles in establishment are a common phenomenon among birds and, therefore, the later-arriving sex should be more constrained in terms of selecting a specific breeding site, such as the home site.

In general, we suggest that variations in site availability may be linked to both intra- and interspecific variation in dispersal patterns. For example, in some resident bird species, males and females have symmetrical roles in territory establishment (i.e., both sexes can choose a vacant site) and dispersal is not sex biased (see, e.g., Matthysen and Schmidt 1987; Arcese 1989). In comparison to all-year resident populations, we may expect migratory birds reestablishing territories annually to find their previous territory unavailable more frequently and thus display less

site fidelity. Although this idea still has to be formally tested at a local scale of territory sites, in terms of dispersal distances at larger spatial scales (i.e., several kilometers) migratory species appear to have more extensive breeding and natal dispersal than resident species (Paradis et al. 1998). Furthermore, differential site availability may also explain age differences in dispersal (i.e., natal dispersal is more extensive than breeding dispersal; Greenwood and Harvey 1982; Paradis et al. 1998), which have been explained by the earlier establishment of old breeders, constraining the settlement of first-time breeders (Greenwood and Harvey 1982). In species in which pair formation is not linked to a resource and takes place before arrival at the breeding grounds (e.g., migratory geese and ducks; Greenwood 1980; Greenwood and Harvey 1982; Anderson et al. 1992), observed sex biases in dispersal cannot be linked to site availability. Instead, the frequently male-biased dispersal of geese and ducks is thought to be a consequence of their mate-defense mating system (Greenwood 1980; Lindenberg et al. 1998).

As for avian mating systems, Greenwood (1980) used a similar logic to suggest that female mammals stay site faithful as a result of the greater benefits of local familiarity with resources, whereas males disperse to maximize mating opportunities or to avoid inbreeding (see also Dobson 1982; Dobson and Jones 1985). According to our constrained site availability hypothesis, it is also possible that males of some mammalian species disperse more frequently because they are restricted to settle at sites with established females. Our hypothesis may look superficially similar to Wolff and Plissner's (1998) "first choice hypothesis" of male-biased dispersal in mammals, but their hypothesis neglects a possible sex difference in site availability and instead focuses on inbreeding avoidance as the driving selective force for male dispersal.

There has been a long debate about the causes of sex-biased dispersal and especially about the relative importance of inbreeding avoidance and intrasexual competition (reviewed in Johnson and Gaines 1990). Dispersal patterns and the magnitude of sex-biased dispersal are likely affected by a number of factors, including costs of establishing a territory or home range (Greenwood 1980), intraspecific competition for resources (Lambin et al. 2001), inbreeding avoidance (Pusey 1987), and availability of breeding sites (this study). The relative effects of these factors are likely to vary according to the biology of species and environmental conditions. Our study suggests that, besides other factors, a possible sex difference in the availability of breeding sites needs to be taken into account when investigating the causes of sex-biased dispersal. The greater constraint to settle at a specific site for females may be an important cause for female-biased dispersal in birds, especially territorial species. This does not mean, however,

that females also have a more constrained choice, as the ability to choose among fewer and well-advertised breeding options may be more beneficial in terms of fitness than when confronted with many options. A key issue of our constrained site availability hypothesis is which sex chooses a breeding site first. The underlying question that should be addressed by future work is which factors allow one sex to choose first (see Kokko et al. 2006) since this will constrain the choice of the other. Nevertheless, because site availability in relation to a home site adds a stochastic component that is likely to vary depending on, for example, the breeding system, adult survival rates, and spatial selective range, our hypothesis gives an additional explanation of why we observe such intra- and interspecific variation in the degree of sex-biased dispersal and why there is often a great overlap in male and female dispersal propensity.

Acknowledgments

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Female northern wheatear color-ringed for individual identification (photograph by Debora Arlt).