



Original Article

Breeding site fidelity is lower in polygamous shorebirds and male-biased in monogamous species

Eunbi Kwon,^{a,*} Mihai Valcu,^{a,*} Margherita Cragolini,^{a,*} Martin Bulla,^{a,b,*} Bruce Lyon,^c and Bart Kempenaers^{a,*}

^aDepartment of Behavioural Ecology & Evolutionary Genetics, Max Planck Institute for Ornithology, Eberhard-Gwinner-Str. 8, D-82319 Seewiesen, Germany, ^bFaculty of Environmental Sciences, Czech University of Life Sciences Prague, Kamýcká 129, 165 00 Prague, Czech Republic, and ^cDepartment of Ecology and Evolutionary Biology, University of California, 130 McAllister Way, Santa Cruz, CA 95060, USA

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Sex-bias in breeding dispersal is considered the norm in many taxa, and the magnitude and direction of such sex-bias is expected to correlate with the social mating system. We used local return rates in shorebirds as an index of breeding site fidelity, and hence as an estimate of the propensity for breeding dispersal, and tested whether variation in site fidelity and in sex-bias in site fidelity relates to the mating system. Among 111 populations of 49 species, annual return rates to a breeding site varied between 0% and 100%. After controlling for body size (linked to survival) and other confounding factors, monogamous species showed higher breeding site fidelity compared with polyandrous and polygynous species. Overall, there was a strong male bias in return rates, but the sex-bias in return rate was independent of the mating system and did not covary with the extent of sexual size dimorphism. Our results bolster earlier findings that the sex-biased dispersal is weakly linked to the mating system in birds. Instead, our results show that return rates are strongly correlated with the mating system in shorebirds regardless of sex. This suggests that breeding site fidelity may be linked to mate fidelity, which is only important in the monogamous, biparentally incubating species, or that the same drivers influence both the mating system and site fidelity. The strong connection between site fidelity and the mating system suggests that variation in site fidelity may have played a role in the coevolution of the mating system, parental care, and migration strategies.

Key words: dispersal, mate fidelity, migration, return rate, sex-bias, site tenacity, shorebird, wader.

INTRODUCTION

In some species, individuals only disperse as maturing juveniles between their location of birth and their first breeding site (“natal dispersal”, Howard 1960), after which they show life-long fidelity to this first breeding location. In other species, however, dispersal can occur throughout life and each adult must decide whether or not to disperse to a new breeding site at the beginning of each breeding season (“breeding dispersal”, Greenwood and Harvey 1982). Individual decisions on whether to stay or disperse, and—if dispersing—on how far to move, determine properties at the population level, such as the probability of site fidelity and the dispersal propensity (Burnham 1993; Kendall and Nichols 2004).

Being faithful to a natal or previous breeding site can be beneficial if it 1) increases the likelihood of finding suitable breeding habitat and mates, 2) increases familiarity with local conditions, 3) increases the chance to mate with locally adapted individuals and hence reduces costs of genetic recombination, 4) increases the chance to remate with a former breeding partner (benefit of pair experience), and 5) avoids potential costs related to movement and to settlement in a new area (Hinde 1956; Waser and Jones 1983; Switzer 1993; Weatherhead and Forbes 1994; Hendry et al. 2003). On the other hand, dispersal might be the more favorable option, because it 1) can buffer against temporal variation and spatial asynchrony in habitat quality, 2) reduces the risk of inbreeding depression, and 3) reduces competition among kin (Howard 1960; Greenwood 1980; Greenwood and Harvey 1982; Clutton-Brock 1989; Dieckmann et al. 1999; Bowler and Benton 2005; Ronce 2007; Clobert et al. 2009; Duputié and Massol 2013).

Address correspondence to E. Kwon. E-mail: eunbi.kwon@gmail.com.

*Present address: Max Planck Institute for Biological Intelligence, in foundation, Seewiesen, Eberhard-Gwinner-Str. 8, 82319 Seewiesen, Germany

Juveniles disperse from the site where they were born to their first breeding site and such natal dispersal typically covers larger distances than breeding dispersal (Greenwood and Harvey 1982; Paradis et al. 1998 and references therein). Thus, theoretical as well as comparative studies on the evolution of dispersal have focused more on natal dispersal (Perrin and Mazalov 1999; Sutherland et al. 2000; Mabry et al. 2013; Henry et al. 2016) or were inexplicit about the distinction (Travis et al. 1999; Bowler and Benton 2005; Ims and Andreassen 2005; Matthysen 2005). Although the distances moved can covary between natal and breeding dispersal (as shown in a study of 69 avian species; Paradis et al. 1998), the causes and consequences of the two are likely different and hence natal and breeding dispersal should be considered separately (Johst and Brandl 1999; Harts et al. 2016). Whilst the evolutionary drivers of natal dispersal (i.e., low natal philopatry) are well understood (avoiding inbreeding depression and kin competition), we still lack insight into the factors driving variation in breeding dispersal or, conversely, the extent of breeding site fidelity.

Breeding dispersal is often strongly sex-dependent (Greenwood 1980; Greenwood and Harvey 1982; Clarke et al. 1997). Multiple hypotheses suggest that this is because the two sexes differ in resource limitation, mating opportunities, competitive ability, morphological capacity to disperse, or even in the genetic basis of dispersal (Mabry et al., 2013; Trochet et al. 2016; Li and Kokko 2019). These sexual asymmetries vary with the social mating system and the intensity of sexual selection, and are linked to the level of sex bias in breeding dispersal (Greenwood 1980; Perrin and Mazalov 1999; Mabry et al. 2013; Brom et al. 2016). For example, in socially monogamous systems, males typically defend resources to gain mating opportunities and are less likely to disperse than females, whereas in polygynous and polyandrous systems, the sex being pursued (i.e., female and male, respectively) is less likely to disperse (Greenwood 1980). In general, the pattern of dispersal is opposite in birds and mammals, presumably due to the difference in the prevalent mating system: in birds, social monogamy, resource defence by males and female-biased dispersal are typical, whereas in mammals, social polygyny, female defence by males and male-biased dispersal are more common (Greenwood 1980).

Sex-biases in breeding dispersal and the underlying potential drivers have been examined across broad taxonomic groups, but the results have been less congruent in birds. For example, a review of 102 bird species from 31 families revealed that 40% of species show no sex-bias in breeding dispersal (while the rest showed female-biased dispersal, as expected; Clarke et al. 1997). Also, female-biased dispersal was linked to male territoriality in mammals, but not in birds (Trochet et al. 2016). Moreover, a recent comparative study on 86 bird species from 41 families showed that the sex-bias in breeding dispersal was not related to the social mating system, nor to other indices of the intensity of sexual selection (e.g., sexual size dimorphism, sex differences in parental care patterns, testis size; Végvári et al. 2018).

The potential reasons for these equivocal findings in birds are manifold. First, other factors that cause individual- or population-level variation in breeding dispersal may override the expected effects of sex at the population level, and previous studies often did not control for confounding factors. For example, dispersal behavior may be condition-dependent (Clobert et al. 2009; Ims and Hjernmann 2001), may vary with population density (Travis et al. 1999; Kokko and Lundberg 2001; Matthysen 2005), or may have co-evolved with other traits under selection (Paradis et al. 1998; Saastamoinen et al. 2018). Second, breeding dispersal and sex

bias in dispersal needs to be carefully defined. Many studies used the median or maximum dispersal distance reported for each species (e.g., Paradis et al. 1998; Sutherland et al. 2000; Serrano et al. 2021). However, one can also define it based on the proportion of individuals that dispersed. Importantly, dispersal distance does not necessarily covary with an individual's propensity to disperse (Hewison et al. 2021). Here, we use site fidelity to a breeding area as an indirect estimate of breeding dispersal propensity and explore variation in site fidelity within and among species of migratory shorebirds. We relate overall site fidelity and sex bias in site fidelity to two variables that reflect the intensity of sexual selection—the social mating system and sexual size dimorphism (Dale et al. 2015), while controlling for confounding factors such as the location of the breeding population.

Shorebirds have evolved one of the most diverse range of mating systems and the mating system is linked to sexual size dimorphism, parental care patterns, and migration strategies (Pitelka et al. 1974; Emlen and Oring 1977; Székely and Reynolds 1995; Borowik and McLennan 1999). Site fidelity varies widely among shorebirds: in some species, most individuals return to the same area, and some even breed in the same nest scrape from the previous year (Herzog et al. 2018), while in other species individuals rarely return to the same site to breed and move across continents even within a single breeding season (Kempnaers and Valcu 2017). An overall higher site fidelity has been reported for monogamous shorebird species regardless of sex (Oring and Lank 1984; $N = 12$ species), or for males regardless of the mating system (Tomkovich and Soloviev 1994; 5–11 species). Both studies drew attention to the apparent link between breeding site fidelity and sex-specific territoriality and parental roles, which vary with the mating system. However, a rigorous test of sex-bias in site fidelity and of the link between site fidelity and the intensity of sexual selection as reflected by the mating system and by sexual size dimorphism is lacking.

Based on previous studies (Oring and Lank 1984; Tomkovich and Soloviev 1994), we expect higher site fidelity for males than for females, and for socially monogamous species compared with non-monogamous species. We hypothesize that the sex-bias in site fidelity is linked to variation in the mating system, that is, to the sex-specific parental roles. Specifically, we predicted that 1) in socially monogamous species, males show higher site fidelity than females, because males defend their nesting territory, and 2) in socially polygamous species, the limiting sex (i.e., the incubating sex) shows higher site fidelity than the opposite sex (i.e., the one competing for mates), because the incubating sex will benefit more from having local experience, whereas the opposite sex will benefit more from freely relocating to find available mates.

MATERIALS AND METHODS

Estimating site fidelity

Site fidelity is defined as the probability that an individual returns to the same breeding site (local population) and does not permanently emigrate, if it survives (Sandercock 2003). True site fidelity of a population can only be estimated when we simultaneously estimate, and thus can disentangle the site fidelity from, the survival rate, breeding propensity, and detection probability (Souchay et al. 2014). Although sophisticated analytical methods are now available and have been used to estimate true site fidelity, such estimates are limited to a handful of species and populations (Sagar et al. 2002; Ledee et al. 2010; Cohen and Gratto-Trevor 2011; Catlin et al. 2015; Murphy et al. 2017; Hunt et al. 2018). Therefore, we

used the most readily available proxy of site fidelity, the local return rate to a breeding population from one year to the next (hereafter, return rate).

We defined “return rate” as the proportion of adult birds marked in one year that was detected in the same study area in the next breeding season. Because the boundary of a study area or a breeding site is typically determined by the researcher, whether a bird returned or not becomes a scale-dependent issue (Barrowclough 1978). Here, we assume that the area of each study site was determined based on the distribution of the species of interest and represents a local breeding population. Nevertheless, we controlled for the effect of study area size in our analysis. Some of the observed variation in return rates is attributable to demographic parameters other than site fidelity, especially the annual survival rate (Payevsky 2016). Because survival rate is most strongly and consistently related to body size (Méndez et al. 2018; Weiser et al. 2018), we also controlled for body size. We only used return rates of adults (previous breeders), and assumed that the risk of not detecting an individual that had actually returned due to temporary emigration was low because most of the data come from comprehensive breeding monitoring studies.

Data on return rates

Our study focuses on four families in the order Charadriiformes (Scolopacidae, contains 87 species, Charadriidae with 69, Recurvirostridae with 10, Haematopodidae with 11), which are conventionally categorized as “waders” or “shorebirds”. Return rates were extracted from 1) literature searches through Web of Science with the search phrase “SY = <SPECIES NAME> AND TS = (return OR fidel* OR philo*)”, 2) a general search on Google Scholar and backward citation searches, and 3) a direct estimation from the raw data (either collected ourselves or obtained with permission from others). We only considered return rates of adult birds to a breeding location north of the Equator, because the available data from the Southern Hemisphere was sparse. We only included return rate estimates from studies that marked more than 20 birds, and estimated return rates on a yearly basis. In other words, we excluded return rates that were estimated from all study years pooled (e.g., when reported as the percentage of the population that was resighted at least once during multiple study years). When a publication reported multiple estimates of year-specific return rates, we used the mean value to represent the return rate of the population. We included only individuals that did not carry any type of transmitter. We initially found 462 estimates of adult return rate to a breeding location from 74 species. However, the above-mentioned data filters led to a more restricted dataset (Figure 1; see Data analysis for the final sample size). For populations for which the return rate was reported separately for males and females, we calculated the sex bias in return rate as the return rate of males divided by the sum of return rates for the two sexes. Therefore, a value of 0.5 indicates no sex difference in return rates, a value greater than 0.5 indicates a male bias in return, and a value smaller than 0.5 indicates a female bias in return.

For each study, we extracted the following variables: the total number of birds marked (pooled across years), geographic coordinates of the breeding location, size of the study area, and number of study years during which birds were marked and resighted.

Geographic predictors

Previous studies on shorebirds suggested that site fidelity is lower towards the edge of the breeding range (Ryabitshev and Alekseeva

1998; 12 species), at higher latitudes (Ryabitshev and Alekseeva 1998; Klima and Johnson 2005), or in species that migrate over larger distances (Klima and Johnson 2005; 31 species). We could not address the potential effects of migration distance on site fidelity due to the lack of information on population- and sex-specific migration routes for the species included here. However, to control for the other variables, we obtained the breeding range for each species (Valcu et al. 2012; BirdLife International 2021), and calculated three population-level predictors to include in the model: the breeding range span (in degrees), the relative latitude (in degrees) and the relative distance to the nearest breeding range boundary (in meters). Relative latitude indicates the position of a population in relation to the midpoint of the species’ latitudinal range span, with positive values indicating that the breeding population is further north than the centre of the range. Note that in our dataset this variable is correlated with the species’ latitudinal breeding range span (Pearson’s $r = -0.50$), so we did not include range span in the model. The relative distance to the breeding range boundary indicates how close each breeding population is to its closest range boundary relative to other potential breeding locations. Further details and a visual description of the geographic predictors are provided in the [Supplementary Material A](#).

Life-history predictors

We categorized the social mating system of each species as monogamy, polyandry, polygyny, and mixed, based on the species’ mating strategy as well as parental behavior, described in the Birds of the World (<https://birdsoftheworld.org/bow/home>; Billerman et al. 2020), consultation of species experts, and additional literature. In brief, we considered a species socially monogamous if an exclusive pair bond exists and both members of a pair provide parental care, at least during incubation. Polyandry is defined as females mating with multiple males within a breeding season and not providing any form of parental care. Similarly, polygyny is defined as males mating with multiple females within a season and not providing parental care. We used the term “mixed” to denote systems with various degrees of polyandry and polygyny, but where both males and females can provide parental care (Oring 1986). Therefore, under our classification, serially polygamous species, such as the snowy plover *Charadrius nivosus* and the Kentish plover *C. alexandrinus*, were grouped under “monogamy” because both the male and the female typically incubate their first clutch together. Although a species may be classified as polyandrous or polygynous, the actual rate of polyandry and polygyny varies across years within a population, among populations within a species, or across the species’ geographic range (Pienkowski and Green 1976; Schamel and Tracy 1977; Oring et al. 1983). For example, not all female red phalaropes *Phalaropus fulicarius* are polyandrous, that is, achieve polyandry every breeding season. However, females never invest in parental care (Schamel and Tracy 1977, 1987). The same is true for polygamous species, but with female-only care (e.g., Lanctot et al. 1997). In contrast, in some populations or years all individuals in the “mixed” system might be socially monogamous (e.g., in the sanderling *Calidris alba*; Reneerkens et al. 2014). Because the mating system of the mixed group is highly variable and flexible at the individual level, we excluded this group from statistical analyses, but show the raw (descriptive) data in the figures for comparison. We obtained data on each species’ mean wing length (in mm: Dale et al. 2007; Klima and Jehl 2020; Pakanen, unpublished data), and calculated body size dimorphism as the difference between the \log_{10} -transformed average wing length of males and females.

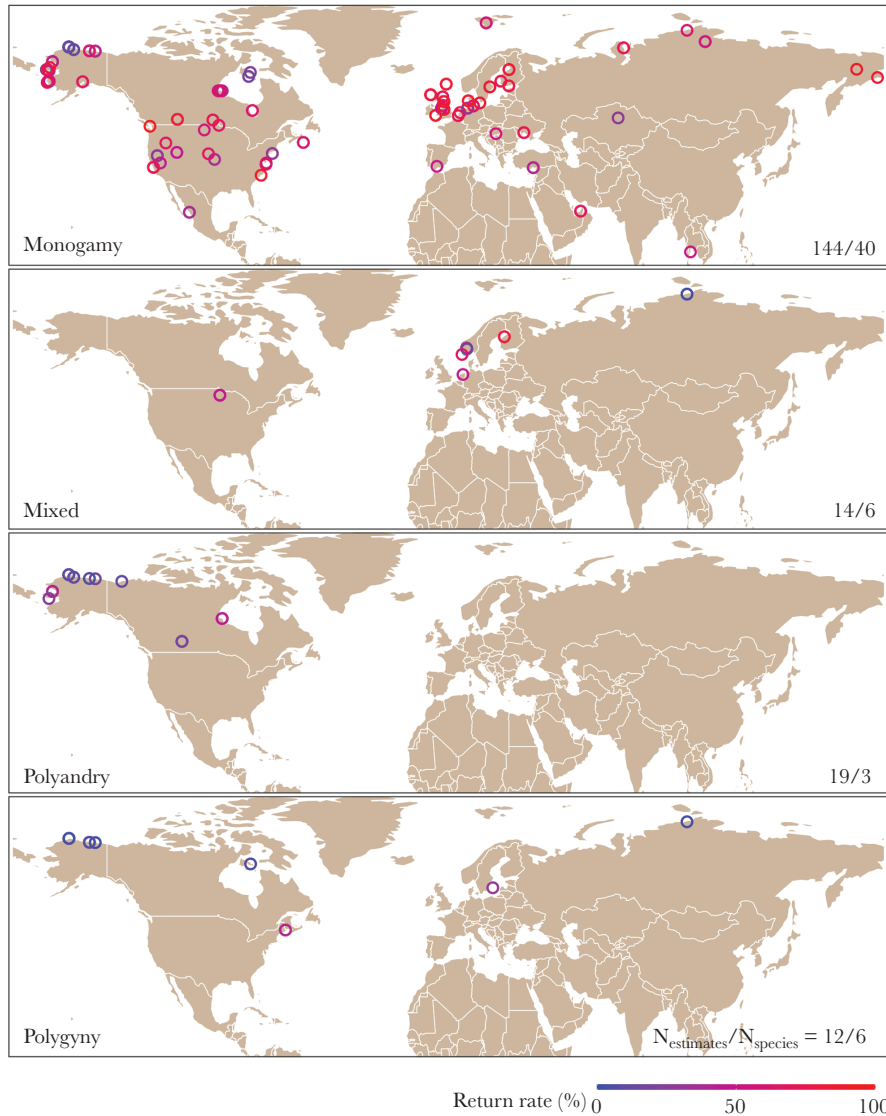


Figure 1

The geographical distribution of shorebird populations for which data on annual adult return rates were included in this study (see Methods for selection criteria). Each panel shows the data for a specific social mating system. “Mixed” denotes species in which both males and females have been reported to mate with more than one social partner within the same breeding season (whereby both partners can provide parental care) and is different from “monogamy” (with biparental incubation), “polyandry” (male-only care) and “polygyny” (female-only care).

Data analyses

We constructed models to investigate variation in two response variables: return rate ($N = 175$ estimates from 111 populations of 49 species) and the sex bias in return rates ($N = 65$ estimates from 65 populations of 33 species). Both response variables vary between 0 and 1 and are beta distributed. Thus, we used a beta logistic regression model with a logit-link function in a Bayesian framework, and replaced values of 0 with 0.00001 and values of 1 with 0.99999 prior to analysis.

To model variation in return rate, we included sex, mating system, and \log_{10} -transformed wing length as fixed effects. We also included the potentially confounding variables relative latitude, relative distance to the range boundary, the year of study initiation, study duration (in years), the total number of marked birds (\log_e -transformed), and study area size (in ha, \log_e -transformed). Finally, we added species or subspecies as random effect. Subspecies

were used for the Red knot (*Calidris canutus roselaari*, *C.c.canutus*), the Dunlin (*Calidris alpina schinzii*, *C.a.pacifica*, *C.a.arctica*), and the Willet (*Tringa semipalmata semipalmata*, *T.s.inornata*), as these may have distinctive migration strategies.

To model variation in sex differences in return rate, we included mating system and sexual size dimorphism (i.e., the difference between the \log_{10} -transformed average wing length of males and females) as fixed effects, and (sub)species as random effect. We did not control for other factors, because the sexes are compared within the same population, and we assumed that geographic factors and study-specific conditions affected males and females similarly. Because sexual dimorphism strongly correlates with the social mating system (Dunn et al. 2001), we ran two additional models that included either the mating system or sexual size dimorphism as a single fixed effect and compared the results with those of the full model. Furthermore, we weighed each observation by the

scaled sample size (i.e., the total number of birds banded for each population).

Prior to modeling, all continuous explanatory variables were standardized by subtracting the mean and dividing by the standard deviation. We examined potential multicollinearity among explanatory variables in two ways. 1) We checked the correlation matrix, which suggested that correlations between variables were relatively small (Fig. S1). 2) We calculated a variance inflation factor (VIF) for each predictor; whereby VIF values > 2 indicate multicollinearity (Zuur et al. 2010). All predictors in our models had a VIF < 1.5 , indicating limited multicollinearity.

Various statistical methods can be used to control for phylogeny in comparative analyses (Rohlf 2001), but it has been argued that the interpretation of these methods has not always been correct (Rohle 2006). Recently, Uyeda et al. (2018) pointed out that the need for phylogenetic control depends on the phylogenetic signal in the residuals of the model and not in the response variable. The authors stated that "...if all of the phylogenetic signal in a data set is present in the predictor trait and the errors are independent and identically distributed, then there is no need for any phylogenetic correction" (Uyeda et al. 2018). After recent recommendations (Hansen 2014; Uyeda et al. 2018), we tested whether the residual variance showed a significant phylogenetic covariance. For each model, we used the residual error from the full model as our new response variable and fitted a Bayesian linear regression model with an intercept only and with species and their phylogenetic relatedness as random effects (see Supplementary Material B for details) to reveal whether phylogeny explains any left-over variation in the data. Additionally, we ran a Bayesian hypothesis test comparing the above-described model against the same model without the random effect of phylogeny (Wagenmakers et al. 2010). We compared the model with and without phylogeny using the Bayes factor, which indicates strong evidence favoring the alternative hypothesis when > 10 (Lee and Wagenmakers 2014). We found that 1) phylogeny explained little variation in the residuals for both models (for return rate: 0.08, 95% CI: 0.00–0.24; for sex difference in return rates: 0.13, 0.01–0.40), and 2) the Bayes factor equaled 31.1 (return rate) and 17.4 (sex difference in return rates), respectively, in favor of a non-phylogenetic model (see Supplementary Material B for details). Thus, we did not use a phylogenetic comparative method for the main analyses.

We ran the Bayesian models with the probabilistic programming language STAN (Stan Development Team 2020) through the R package "brms" v. 2.14.4 (Bürkner 2017) in R v. 4.0.2 (R Core Team 2020). We sampled from 5 chains of 50 000 iterations each and used the first 25 000 iterations as burn-in. We then saved the output from every fifth iteration to avoid autocorrelation, resulting in 25 000 estimates to generate posterior distributions of parameters. We increased the target average proposal acceptance probability from 0.95 to 0.99 so that our sampling is more conservative to posterior distributions with high curvature (Bürkner 2017). We generated priors using the "get_prior" function in "brms", which sets non-informative priors for all slope coefficients and uses a Student's *t* distribution for the intercept and standard deviation, and a gamma distribution for phi (Bürkner 2017). For each model, we checked the convergence by visually checking the trace plot (Fig. S2 & S3) and using the Gelman-Rubin convergence diagnostics, which was < 1.1 for all estimates of model parameters (values approaching 1 indicate that the estimated between- and within-chain variances for model parameters are similar and hence indicate model convergence; Brooks and Gelman 1998).

RESULTS

Return rates varied widely among species, from zero (female long-billed dowitcher *Limnodromus scolopaceus*, $N = 63$ marked individuals, Utqiagvik) to 1 (male and female marbled godwit *Limosa fedoa*, $N = 57$ individuals, South Alberta; Figure 2). Mating system was the strongest predictor of variation in return rate: on average 51.5% of all individuals returned in monogamous species, compared with only 11.7% in polyandrous species and 12.5% in polygynous species (Figures 2 and 3, Table S1). In general, return rates were higher for males (on average 64.6%) than for females (51.5%; Figures 2 and 3). As expected, return rates were higher for larger species, but the effect size was relatively small (Figure 3, Table S1). Return rates were lower for populations further north within the breeding range (Figure 3, Table S1). A sensitivity analysis showed that the estimated effect sizes were robust to varying cutoffs for the minimum number of individuals in a population (Fig. S4).

Sex differences in return rate within each population also varied considerably, from a 28.5% higher return rate in females (American woodcock *Scolopax minor*) to a 46.1% higher return rate in males (Pacific golden plover *Pluvialis fulva*; Figure 4). Sexual dimorphism in wing length was strongly correlated with the mating system (one-way ANOVA: $F_{2,61} = 11.14$, $P < 0.001$), such that females were larger than males in polyandrous species and vice versa in polygynous species. However, neither mating system nor sexual dimorphism in wing length predicted sex differences in return rate (Figure 5, Table S2). The lack of a relationship between mating system and the sex-bias in return rates remained when we treated the latter as a binary response variable (i.e., 0 if females return more than males and 1 if males return more than females; Table S2).

DISCUSSION

Our data show that return rates and the sex bias in return rates vary widely between shorebird species and populations. Part of this variation might be due to differences in survival, as indicated by a significant positive effect of body size (our study, also see Méndez et al. 2018; Weiser et al. 2018). However, even after controlling for this effect, return rates of both sexes depended on the social mating system and, as predicted, were strongly male-biased in monogamous species.

Based on data from 111 populations of 49 shorebird species, return rates were significantly lower for polyandrous and polygynous species compared with monogamous species (Figure 3). Hypotheses on the evolution of sex-biased dispersal can explain why the competing sex of polygamous mating systems would benefit from dispersing more, but they do not explain why the return rates of the limiting sex (i.e., males of polyandrous and females of polygynous species) are lower than those of monogamous birds. The low return rate of the limiting sex (i.e., incubating sex) in polygamous systems can be explained by three evolutionary scenarios. 1) The benefits of dispersal may be higher for both sexes. In polygamous shorebirds, the number of breeders at a given site often fluctuates greatly between years (Pitelka et al. 1974; Troy 1996). This may have arisen because the incubating sex benefits from dispersal, for example, because of yearly variation in local habitat quality. Heterogeneity in the spatiotemporal distribution of the dispersing sex could then have increased the benefit of dispersal for the opposite sex as well in pursuit of finding a mate. This could have led to a positive feedback loop leading to increased dispersal propensity for both sexes. 2) The benefit of being site faithful might be lower in polygamous

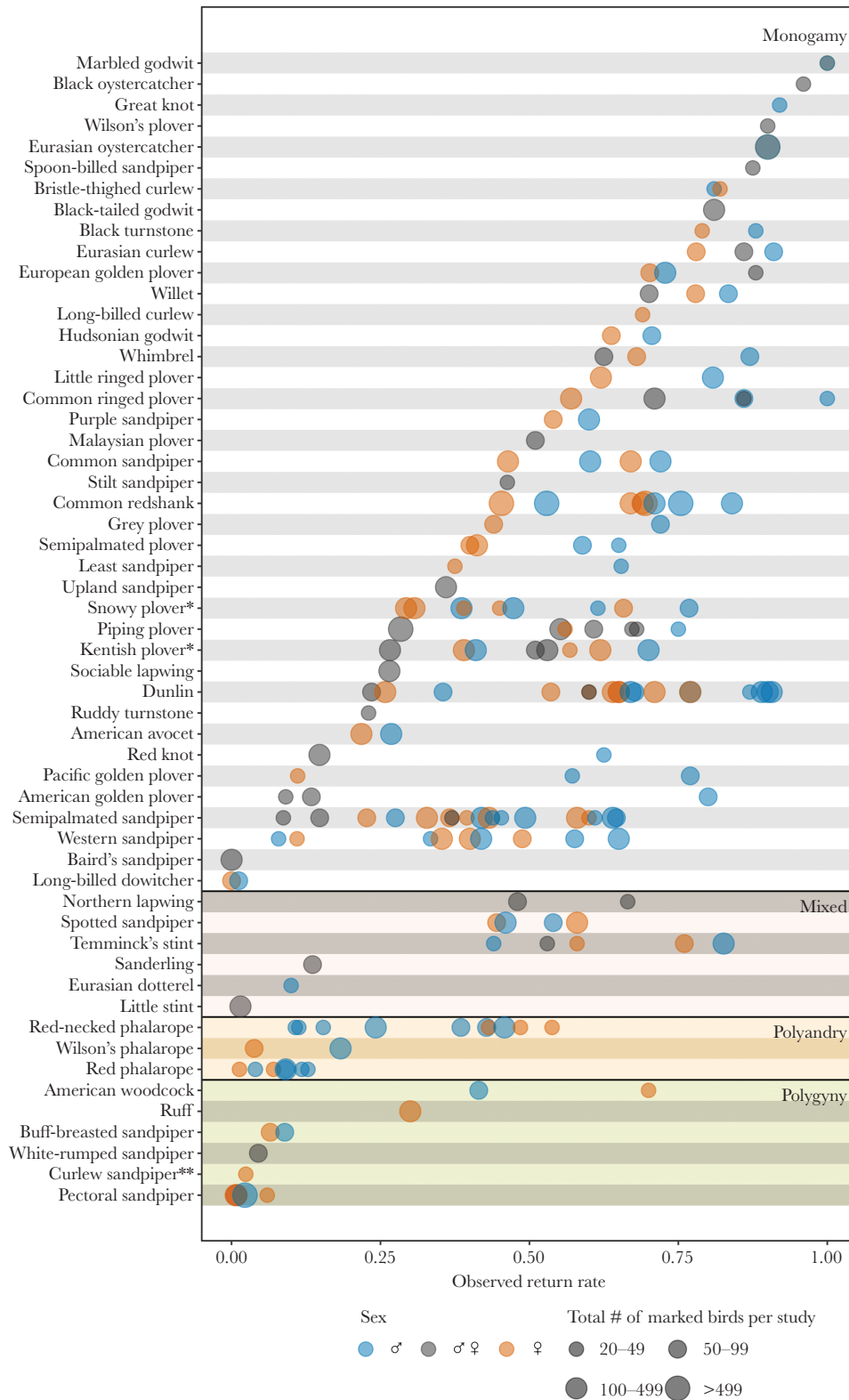


Figure 2

Observed return rates for 55 species of shorebirds with different social mating system. Each dot indicates an observed return rate for a given population (N = 120 populations), whereby dot size indicates the total number of marked individuals in the study, and color refers to sex (gray = sex unknown or sexes combined). Species are listed in descending order of average return rates within each mating system category. *Snowy plovers and Kentish plovers are typically classified as serially polygamous, but considered monogamous in this study because they normally maintain a pair bond for the first clutch and both pair members incubate the eggs. **The mating system of the curlew sandpiper is unknown, but suspected to be polygyny from observations of female-only incubation and early departure of males from the breeding grounds (Holmes and Pitelka 1964).

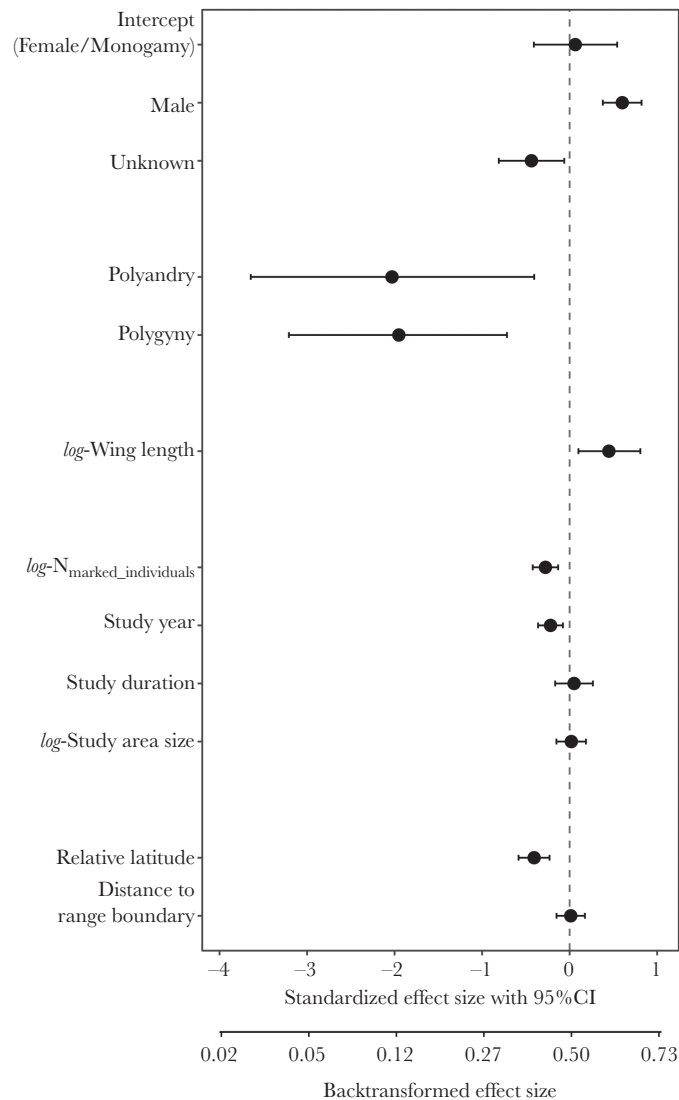


Figure 3

Standardized effect sizes (posterior means) of predictors explaining variation in annual return rates of 49 species of shorebirds ($N = 175$ estimates from 111 populations; sample sizes are different from Figure 1 because the “Mixed” group is excluded from the analysis). Error bars indicate 95% Bayesian credible intervals. A predictor has a significant effect if the 95% CI does not overlap zero. “Female” and “social monogamy” are the reference group.

species. This seems counterintuitive, because in uniparental species, a direct benefit of breeding in a familiar environment with local knowledge, for example, about suitable foraging areas should be higher for the caring sex (Widemo 1997). On the other hand, a key benefit of returning to the same site, namely the opportunity to reunite with a social mate from the previous year, is irrelevant for uniparental species (see below). 3) The high dispersal tendency of one sex may constrain the evolution of high site fidelity in the other sex. Given that dispersal propensity presumably has a genetic basis (Doligez et al. 2009; Saastamoinen et al. 2018), the low return rates of one sex may be a by-product of strong selection favoring dispersal in the competing sex. However, this is true independent of the mating system, and would lead to no or reduced sex bias in dispersal.

To understand the evolution of low site fidelity in polygamous species, we can also consider the selection pressures favoring high site fidelity in monogamous species and examine whether those selection pressures are missing in polygamous species. Several studies

on monogamous shorebirds suggest a strong correlation between site fidelity and reproductive success based on observations that 1) successful breeders are more likely to return (long-billed curlew *Numenius americanus*; Redmond & Jenni 1982, common redshank *Tringa totanus*; Thompson & Hale 1989, black turnstone *Arenaria melanocephala*; Handel & Gill 2000), and that 2) males with prior site experience have higher fitness (western sandpiper *Calidris mauri*; Johnson & Walters 2008). However, evidence for a causal relationship between site fidelity and reproductive success is largely missing, and requires showing decreased reproductive success of dispersers at the new breeding sites (piping plover *Charadrius melodus*; Saunders et al. 2012). Fitness benefits of high site fidelity may arise from accumulated experience with the local environment or with the mate, or it may simply reflect an age-related improvement in performance. Two studies that aimed to discern between these effects found that the fitness benefit of prior site experience arose from breeding earlier in the season (Johnson and Walters 2008) or from taking a shorter time to reneest after failure (van Leeuwen and Jamieson

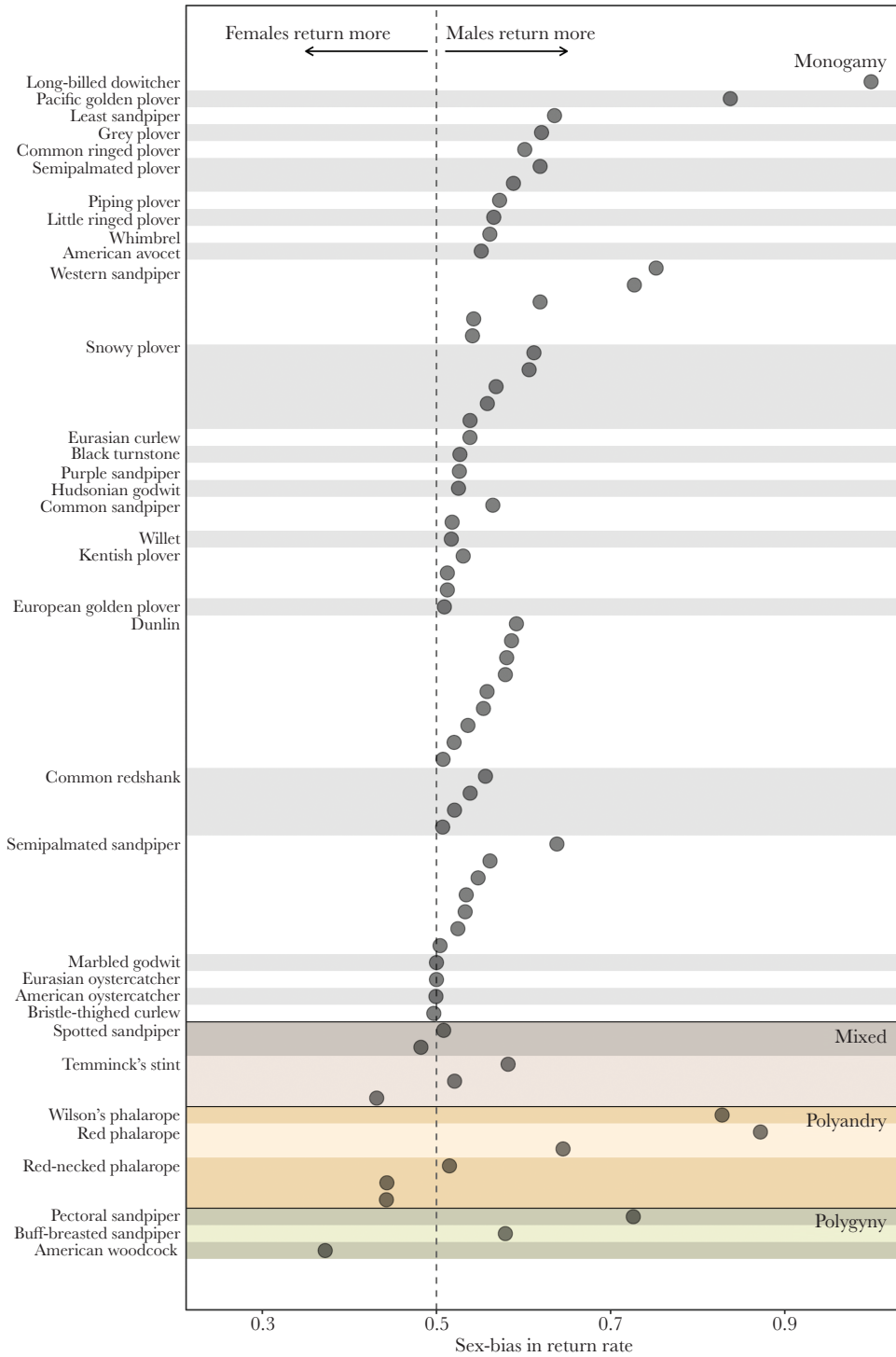


Figure 4

Observed sex bias in annual return rate of 35 species of shorebirds with different social mating system. Estimates for each population are shown separately ($N_{total} = 70$ populations). Species are listed in descending order of observed mean sex bias in return rates within each mating system category.

2018). In both studies, the advantage of breeding site fidelity came from the time saved by mating with the previous partner rather than from the site experience per se. This so-called “fast-track hypothesis” may also be the driver of long-term monogamy in other systems (e.g., in wild zebra finches *Taeniopygia guttata*; Adkins-Regan & Tomaszyccki 2007).

The fast-track hypothesis states that the benefit of returning to the same site lies in mate reunion allowing early breeding, and

predicts low site fidelity for both sexes of polygamous species, because 1) no or only short-term pair bonds are formed in these species and 2) selection favoring high dispersal of one sex implies that there will no longer be a reason to return to the same site for the opposite sex. It is interesting to note that polygamous species generally breed later in the season than monogamous species at the same site (Whitfield and Tomkovich 1996; Saalfeld and Lanctot 2017). One hypothesis to explain this observation is that

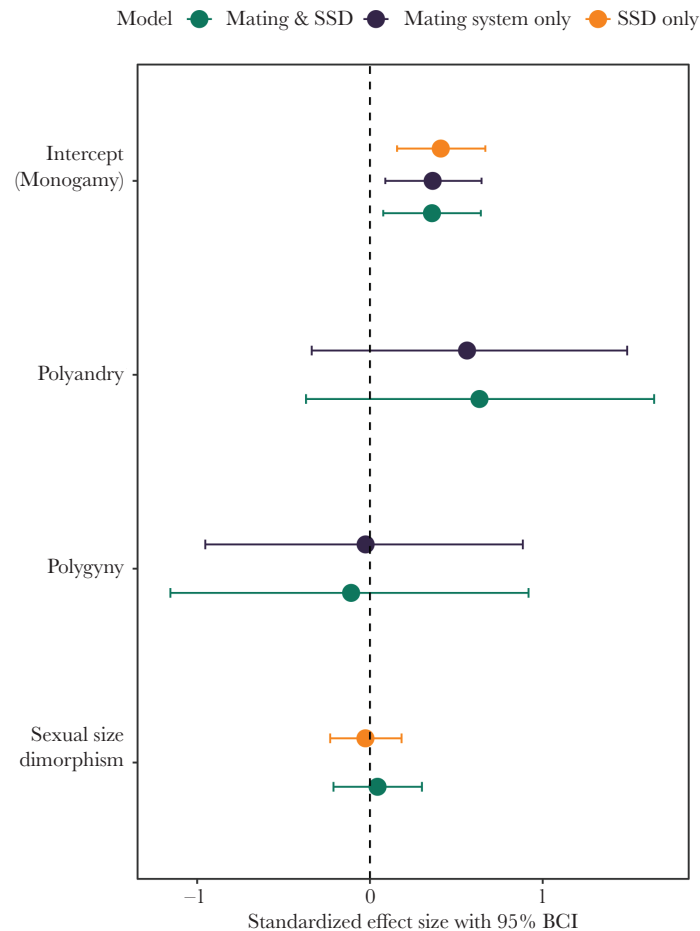


Figure 5

Standardized effect sizes (posterior means) of predictors on the sex bias in annual return rates of 33 species of shorebirds ($N = 65$ estimates from 65 populations; sample sizes are different from Figure 4 because the “Mixed” group is excluded from the analysis). We assessed the effect of the mating system and of sexual size dimorphism (SSD) by adding them as fixed effects in combination or separately (three models, as indicated by color). Error bars indicate 95% Bayesian credible intervals. A predictor has a significant effect when the 95% CI does not overlap zero. “Social monogamy” is the reference group.

polygamous species are “forced” to breed later, because polygamous males provide less or no care to females (Yom-Tov 1992). However, this hypothesis is based on observations of passerine species in which monogamous males provide food to their mate, which does not apply to shorebirds. For the incubating sex of polygamous shorebirds, the energetic need for self-maintenance directly trades off against incubation. Therefore, a more likely hypothesis is that uniparental incubation may be harder under harsher environmental conditions earlier in the season, especially in the Arctic where many shorebirds breed. Yet another alternative hypothesis is that polygamous species are not as constrained by the timing of breeding (for reasons that remain unknown), and hence, individuals do not need to “race” back to the previous breeding site. Although these hypotheses still need empirical testing, the general pattern of delayed breeding in polygamous shorebirds suggests that the lack of site fidelity might be linked to relaxed selection on the initiation of breeding in these species.

If the fast-track hypothesis is true and high site fidelity evolved as a means to reunite with the previous breeding partner, we would expect a strong connection between mate and site fidelity. Cézilly et al. (2000) reported a significant relationship between site fidelity and divorce rate in 42 species of Ciconiiforms (11 of which were also included in our study). Cézilly et al. (2000)

suggested that the likely evolutionary pathway was first gaining site fidelity and subsequently mate fidelity. Note that in their study birds were considered “site faithful” only when returning to within 11 meters from the previous nest. Their results favor the idea that mate fidelity initially evolved as a by-product of site fidelity (rather than site fidelity being the strategy to maintain pair bonds). However, as the authors underscored in their paper, this transition only corresponds to the initial evolution of site fidelity, and they suggest that site and mate fidelity have been frequently lost and regained in recent times (Cézilly et al. 2000). The large variation in return rates seen in our data also suggests that migration or breeding site sampling processes can shift rapidly and reversibly over evolutionary time (Zink 2011). For example, the ruff *Calidris pugnax*, the pectoral sandpiper *Calidris melanotos*, and the great knot *Calidris tenuirostris* are closely related species with similar body size, and breed at similar latitudes. However, male return rates are vastly different, with 92% of great knots ($N = 26$) returning versus 33% of ruffs ($N = 12$) and only 1.5% of pectoral sandpipers ($N = 891$) (Scheufler and Stiefel 1985; Tomkovich 1996; Kempnaers, unpublished data). The most obvious difference between the three species is that the great knot breeds monogamously, whereas the ruff and pectoral sandpiper are polygynous with female-only care.

The early observations of Greenwood (1980), and both theoretical and empirical studies that followed (Mabry et al. 2013; Trochet et al. 2016; Li and Kokko 2019), predict male-biased breeding site fidelity under monogamy and polyandry and female-biased breeding site fidelity under social polygyny. The idea behind this is that the sex that defends resources would show higher site fidelity. Our results only partly support these predictions (Figure 5). As predicted, return rates were strongly male-biased in monogamous species. All 56 populations of 27 monogamous species showed a male-biased return (i.e., female-biased dispersal), except for one case of a weak female-bias in return (in the bristle-thighed curlew *Numenius tahitiensis*, 81% of the males returned and 82% of the females, Marks et al. 2020; Figure 4). These findings support the original idea that monogamous males that acquire mates by defending territories show higher fidelity to a breeding location. However, we found no support for a male-biased return rate in polyandrous species or a female-bias in polygynous species. Although the data are limited, the sex-bias in return rates in the non-monogamous systems was highly variable (Figures 4 and 5). The fact that non-monogamous species generally have low return rates suggests that benefits related to local experience or former residency are not the only reason why males and females of monogamous species return. The main difference is that individuals from polygamous species would not benefit from reuniting with a previous partner.

An important assumption of our study is that the survival rate is independent of the mating system, and therefore that variation in return rates and in sex bias in return rates reflect dispersal rather than survival. A recent review using mark-recapture and dead-recovery data showed significantly lower survival rates for females across 37 shorebird species (Mendez et al. 2018), despite the general trend that females are larger than males. This result fits the general idea that females have higher mortality because they are the heterogametic sex (ZW) in birds (Maklakov and Lummaa 2013). However, most survival estimates are confounded with female-biased dispersal. In fact, after accounting for sex-specific dispersal distances, the estimated true survival rates did not differ between the sexes in American golden plover *Pluvialis dominica*, dunlin *Calidris alpina*, semipalmated sandpiper *Calidris pusilla*, red phalarope *Phalaropus fulicarius*, and red-necked phalarope *Phalaropus lobatus* (Weiser et al. 2018). Similarly, no sex difference in survival was found in other groups in which females are larger than males, such as raptors (Newton et al. 2016). Therefore, we interpret the sex bias in return rates shown in our study as a true sex bias in site fidelity rather than differential survival. However, the observed return rates may still be lower than the true site fidelity (Martin et al. 1995), because of variation in the probability of detection, which depends on the sex and sex-specific behaviors (Sandercock 2003 and references therein). However, we note that none of the four confounding variables related to data quality (observation intensity) showed a strong effect on return rate (see Figure 3). Moreover, in polygamous shorebirds, individuals of the caring sex are often found through intense nest searching, while individuals of the competing sex are often highly detectable because of their conspicuous courtship behavior (Lancot et al. 1998; Lesku et al. 2012), which might reduce a sex bias in detection.

This study shows the full spectrum of variation in return rates to previous breeding locations among 49 species of shorebirds. Local return rates varied by sex, with body size, and with relative breeding latitude, but it is most strongly related to the mating system. Our study indicates a strong connection between species-specific site

fidelity and the social mating system, with monogamous species generally having higher return rates. The available evidence suggests that the benefit of breeding site fidelity might be linked to mate fidelity, allowing earlier breeding in a given season. Variation in the degree of site fidelity may have played a role in the coevolution of the mating system, the pattern of parental care, and migration strategies in shorebirds.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at *Behavioral Ecology* online.

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REFERENCES

- Adkins-Regan E, Tomaszycki M. 2007. Monogamy on the fast track. *Biol Lett.* 3:617–619. doi: 10.1098/rsbl.2007.0388.
- Barrowclough GF. 1978. Sampling bias in dispersal studies based on finite area. *Bird Banding.* 49:333–341.
- Billerman SM, Keeney BK, Rodewald PG, Schulenberg TS. 2020. *Birds of the world.* Ithaca, NY, USA: Cornell Laboratory of Ornithology. <https://birdsoftheworld.org/bow/home>.
- BirdLife International. 2021. <http://Datazone.Birdlife.Org>.
- Borowik OA, McLennan DA. 1999. Phylogenetic patterns of parental care in Calidridine Sandpipers. *Auk.* 116:1107–1117. doi: 10.2307/4089689.
- Bowler DE, Benton TG. 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biol Rev.* 80:205–225. doi: 10.1017/S1464793104006645.
- Brom T, Massot M, Legendre S, Laloï D. 2016. Kin competition drives the evolution of sex-biased dispersal under monandry and polyandry, not under monogamy. *Anim Behav.* 113:157–166. doi: 10.1016/j.anbehav.2016.01.003.
- Brooks SP, Gelman A. 1998. General methods for monitoring convergence of iterative simulations. *J Comput Graph Stat.* 7:434–455. doi: 10.1080/10618600.1998.10474787.
- Bürkner P-C. 2017. Brms: an R package for Bayesian multilevel models using Stan. *J Stat Softw.* 80:1–28. doi: 10.18637/jss.v080.i01.
- Burnham, KP. 1993. A theory for combined analysis of ring recovery and recapture data. In: Lebreton J.-D., North P. M., editors. *Marked individuals in the study of bird population.* Basel, Boston, Berlin: Birkhäuser Verlag. p. 199–213.
- Catlin DH, Fraser JD, Felio JH. 2015. Demographic responses of Piping Plovers to habitat creation on the Missouri river. *Wildl Monogr.* 192:1–42. doi: 10.1002/wmon.1016.
- Cézilly F, Dubois F, Pagel M. 2000. Is mate fidelity related to site fidelity? A comparative analysis in Ciconiiforms. *Anim Behav.* 59:1143–1152. doi: 10.1006/anbe.2000.1422.
- Clarke AL, Sæther B-E, Roskaft E. 1997. Sex biases in avian dispersal: a reappraisal. *Oikos.* 79:429–438. doi: 10.2307/3546885.
- Clobert J, Le Galliard J-F, Cote J, Meylan S, Massot M. 2009. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecology Lett.* 12:197–209. doi: 10.1111/j.1461-0248.2008.01267.x.

- Clutton-Brock TH. 1989. Female transfer and inbreeding avoidance in social mammals. *Nature*. 337:70–72. doi: 10.1038/337070a0.
- Cohen JB, Gratto-Trevor C. 2011. Survival, site fidelity, and the population dynamics of Piping Plovers in Saskatchewan. *J Field Ornithol*. 82:379–394.
- Dale J, Dey CJ, Delhey K, Kempnaers B, Valcu M. 2015. The effects of life history and sexual selection on male and female plumage colouration. *Nature*. 527:367–370. doi: 10.1038/nature15509.
- Dale J, Dunn PO, Figuerola J, Lislevand T, Székely T, Whittingham LA. 2007. Sexual selection explains Rensch's rule of allometry for sexual size dimorphism. *Proc R Soc B Biol Sci*. 274:2971–2979. doi:10.1098/rspb.2007.1043.
- Dieckmann U, O'Hara B, Weisser W. 1999. The evolutionary ecology of dispersal. *Trends Ecol Evol*. 14(3):88–90. doi: 10.1016/S0169-5347(98)01571-7.
- Doligez B, Gustafsson L, Pärt T. 2009. Heritability of dispersal propensity in a patchy population. *Proc R Soc B Biol Sci*. 276:2829–2836. doi: 10.1098/rspb.2009.0454.
- Dunn PO, Whittingham LA, Pitcher TE. 2001. Mating systems, sperm competition, and the evolution of sexual dimorphism in birds. *Evolution*. 55:161–175. doi: 10.1111/j.0014-3820.2001.tb01281.x.
- Duputié A, Massol F. 2013. An empiricist's guide to theoretical predictions on the evolution of dispersal. *Interface Focus*. 3:20130028. doi: 10.1098/rsfs.2013.0028.
- Emlen ST, Oring LW. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science*. 197:215–223. doi: 10.1126/science.327542.
- Greenwood PJ, Harvey PH. 1982. The natal and breeding dispersal of birds. *Annu Rev Ecol Syst* 13:1–21. doi: 10.1146/annurev.es.13.110182.000245.
- Greenwood PJ. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Anim Behav* 28:1140–1162. doi: 10.1016/S0003-3472(80)80103-5.
- Handel CM, Gill RE. 2000. Mate fidelity and breeding site tenacity in a monogamous sandpiper, the Black Turnstone. *Anim Behav*. 60:471–481. doi: 10.1006/anbe.2000.1505.
- Hansen T. 2014. Use and misuse of comparative methods in the study of adaptation. In: Garamszegi L, editor. *Modern phylogenetic comparative methods and their application in evolutionary biology*. Springer, Berlin: Heidelberg. doi: 10.1007/978-3-662-43550-2_14.
- Harts AMF, Jaatinen K, Kokko H. 2016. Evolution of natal and breeding dispersal: when is a territory an asset worth protecting? *Behav Ecol*. 27:287–294. doi: 10.1093/beheco/arv148.
- Hendry AP, Castric V, Kinnison MT, Quim TP. 2003. The evolution of philopatry and dispersal: homing versus straying in Salmonids. In: Hendry AP, Stearns SC, editors. *Evolution illuminated: salmon and their relatives*. New York, NY: Oxford University Press.
- Henry RC, Coulon A, Travis JMJ. 2016. The evolution of male-biased dispersal under the joint selective forces of inbreeding load and demographic and environmental stochasticity. *Am Nat*. 188:423–433. doi: 10.1086/688170.
- Herzog P, Saalfeld ST, Kaatz H-H, Lanctot RB. 2018. Nest reuse in arctic-breeding shorebirds: an analysis of potential benefits and factors affecting the occurrence of this rare behavior. *J Avian Biol*. 49:e01737. doi: 10.1111/jav.01737.
- Hewison AJM, Gaillard J-M, Morellet N, Cagnacci E, Debeffe L, Cargnelutti B, Gehr B, Kröschel M, Heurich M, Coulon A, et al. 2021. Sex differences in condition dependence of natal dispersal in a large herbivore: dispersal propensity and distance are decoupled. *Proc R Soc B Biol Sci*. 288:20202947. doi: 10.1098/rspb.2020.2947.
- Hinde A. 1956. The biological significance of the territories of birds. *Ibis*. 98:340–369. doi: 10.1111/j.1474-919X.1956.tb01419.x.
- Holmes RT, Pitelka FA. 1964. Breeding behaviour and taxonomic relationships of the Curlew Sandpiper. *Auk*. 81:362–379.
- Howard WE. 1960. Innate and environmental dispersal of individual vertebrates. *Am Midl Nat*. 63:152–161. doi: 10.2307/2422936.
- Hunt KL, Fraser JD, Friedrich MJ, Karpanty SM, Catlin DH. 2018. Demographic response of Piping Plovers suggests that engineered habitat restoration is no match for natural riverine processes. *Condor*. 120:149–165. doi: 10.1650/CONDOR-17-93.1.
- Ims RA, Hjermandt DØ. 2001. Condition-dependent dispersal. In: Clobert J, Danchin E, Dhondt AA, Nichols JD, editors. *Dispersal*. Oxford: Oxford University Press. p. 203–216. <https://ci.nii.ac.jp/naid/10021024304/>.
- Ims RA, Andreassen HP. 2005. Density-dependent dispersal and spatial population dynamics. *Proc R Soc B Biol Sci*. 272:913–918. doi: 10.1098/rspb.2004.3025.
- Johnson M, Walters JR. 2008. Effects of mate and site fidelity on nest survival of Western Sandpipers (*Calidris mauri*). *Auk*. 125:76–86. doi: 10.1525/auk.2008.125.1.76.
- Johst K, Brandl R. 1999. Natal versus breeding dispersal: evolution in a model system. *Evol Ecol Res*. 1:911–921.
- Kempnaers B, Valcu M. 2017. Breeding site sampling across the arctic by individual males of a polygynous shorebird. *Nature*. 541:528–531. doi: 10.1038/nature20813.
- Kendall WL, Nichols JD. 2004. On the estimation of dispersal and movement of birds. *Condor*. 106:720–731. doi: 10.1093/condor/106.4.720.
- Klima J, Jehl JR Jr. 2020. Stilt Sandpiper (*Calidris himantopus*), version 1.0. In: Poole AF, editor. *Birds of the World*. Ithaca, NY, USA: Cornell Lab of Ornithology. doi: 10.2173/bow.stisan.01.
- Klima J, Johnson OW. 2005. Return rates of male and female monogamous shorebirds to their breeding grounds. *Wader Study Group Bull*. 106:42–46.
- Kokko H, Lundberg P. 2001. Dispersal, migration, and offspring retention in saturated habitats. *Am Nat*. 157:188–202. doi: 10.1086/318632.
- Kwon E, Valcu M, Cragnolini M, Bulla M, Lyon B, Kempnaers B. 2022. Data from: Breeding site fidelity is lower in polygamous shorebirds and male-biased in monogamous species. *Behav Ecol*. doi:10.5061/dryad.1vhhmgqvd.
- Lanctot RB, Scribner KT, Kempnaers B, Weatherhead PJ. 1997. Lekking without a paradox in the Buff-breasted Sandpiper. *Am Nat*. 149:1051–1070.
- Lanctot RB, Weatherhead PJ, Kempnaers B, Scribner KT. 1998. Male traits, mating tactics and reproductive success in the *Buff-Breasted Sandpiper*, *Tryngites subruficollis*. *Anim Behav*. 56:419–432. doi: 10.1006/anbe.1998.0841.
- Ledee OE, Arnold TW, Roche EA, Cuthbert FJ. 2010. Use of breeding and nonbreeding encounters to estimate survival and breeding-site fidelity of the Piping Plover at the Great Lakes. *Condor*. 112:637–643.
- Lee MD, Wagenmakers E-J. 2014. *Bayesian cognitive modeling: a practical course*. Cambridge, UK: Cambridge University Press.
- van Leeuwen CHA, Jamieson SE. 2018. Strong pair bonds and high site fidelity in a subarctic-breeding migratory shorebird. *Wilson J Ornithol*. 130:140–151. doi: 10.1676/16-116.1.
- Lesku JA, Rattenborg NC, Valcu M, Vyssotski AL, Kuhn S, Kuemmeth F, Heidrich W, Kempnaers B. 2012. Adaptive sleep loss in polygynous Pectoral Sandpipers. *Science*. 337:1654–1658. doi: 10.1126/science.1220939.
- Li X-Y, Kokko H. 2019. Sex-biased dispersal: a review of the theory. *Biol Rev*. 94:721–736. doi: 10.1111/brv.12475.
- Mabry KE, Shelley EL, Davis KE, Blumstein DT, Van Vuren DH. 2013. Social mating system and sex-biased dispersal in mammals and birds: a phylogenetic analysis. *PLoS One*. 8:e57980. doi: 10.1371/journal.pone.0057980.
- Maklakov AA, Lummaa V. 2013. Evolution of sex differences in lifespan and aging: causes and constraints. *BioEssays*. 35:717–724. doi: 10.1002/bies.201300021.
- Marks JS, Tibbitts L, Gill RE, McCaffery BJ. 2020. Bristle-Thighed Curlew (*Numenius tahitiensis*). *Birds of the World*, March. <https://birdsoftheworld.org/bow/species/btrcur/cur/introduction>
- Martin TE, Clobert J, Anderson DR. 1995. Return rates in studies of life history evolution: are biases large? *J Appl Stat*. 22:863–876. doi: 10.1080/02664769524676.
- Mathysen E. 2005. Density-dependent dispersal in birds and mammals. *Ecography*. 28:403–416. doi: 10.1111/j.0906-7590.2005.04073.x.
- Méndez V, Alves JA, Gill JA, Gunnarsson TG. 2018. Patterns and processes in shorebird survival rates: a global review. *Ibis*. 160:723–741. doi: 10.1111/ibi.12586.
- Murphy SP, Virzi T, Sanders F. 2017. Exploring differences in adult survival and site fidelity of migratory and non-migratory American Oystercatcher (*Haematopus palliatus*) Populations. *Waterbirds*. 40:32–43. doi: 10.1675/063.040.sp105.
- Pienkowski MW, Green GH. 1976. Breeding biology of Sanderlings in North-East Greenland. *Br Birds*. 69:165–177.
- Newton I, McGrady MJ, Oli MK. 2016. A review of survival estimates for raptors and owls. *Ibis*. 158:227–248. doi: 10.1111/ibi.12355.
- Oring LW. 1986. Avian polyandry. In: Johnston RF, editor. *Current ornithology*, Vol. 3. New York: Plenum. p. 309–351.

- Oring LW, Lank DB. 1984. Breeding area fidelity, natal philopatry, and the social systems of sandpipers. In: Burger J, Olla BL, editors. Shorebirds: breeding behavior and populations. Boston, MA: Springer. p. 125–147. doi: 10.1007/978-1-4684-4691-3_4.
- Oring LW, Lank DB, Maxson SJ. 1983. Population studies of the polyandrous Spotted Sandpiper. *Auk*. 100:272–285.
- Paradis E, Baillie SR, Sutherland WJ, Gregory RD. 1998. Patterns of natal and breeding dispersal in birds. *J Anim Ecol*. 67:518–536. doi: 10.1046/j.1365-2656.1998.00215.x.
- Payevsky VA. 2016. Sex-biased survival and philopatry in birds: do they interact? *Biol Bull*. 43:804–818. doi: 10.1134/S1062359016080136.
- Perrin N, Mazalov V. 1999. Dispersal and inbreeding avoidance. *Am Nat*. 154:282–292.
- Pitelka FA, Holmes RT, MacLean SE. 1974. Ecology and evolution of social organization in arctic sandpipers. *Am Zool*. 14:185–204.
- R Core Team. 2020. R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. URL <https://www.R-project.org/>.
- Redmond RL, Jenni DA. 1982. Natal philopatry and breeding area fidelity of Long-Billed Curlews (*Numenius americanus*): patterns and evolutionary consequences. *Behav Ecol Sociobiol*. 10:277–279. doi: 10.1007/BF00302817.
- Reneerkens J, van Veelen P, van der Velde M, Luttikhuisen P, Piersma T. 2014. Within-population variation in mating system and parental care patterns in the Sanderling (*Calidris alba*) in Northeast Greenland. *Auk*. 131:235–247. doi: 10.1642/AUK-13-247.1.
- Rohlf FJ. 2001. Comparative methods for the analysis of continuous variables: geometric interpretations. *Evolution*. 55:2143–2160. doi: 10.1111/j.0014-3820.2001.tb00731.x.
- Rohlf FJ. 2006. A comment on phylogenetic correction. *Evolution*. 60:1509–1515. doi: 10.1111/j.0014-3820.2006.tb01229.x.
- Ronce O. 2007. How does it feel to be like a rolling stone? Ten questions about dispersal evolution. *Annu Rev Ecol Syst*. 38:231–253. doi: 10.1146/annurev.ecolsys.38.091206.095611.
- Ryabitshev VK, Alekseeva NS. 1998. Nesting density dynamics and site fidelity of waders on the middle and northern Yamal. *Int Wader Stud*. 10:195–200.
- Saalfeld ST, Lancot RB. 2017. Multispecies comparisons of adaptability to climate change: a role for life-history characteristics? *Ecol Evol*. 7:10492–10502. doi: 10.1002/ece3.3517.
- Saastamoinen M, Bocedi G, Cote J, Legrand D, Guillaume F, Wheat CW, Fronhofer EA, Garcia C, Henry R, Husby A, et al. 2018. Genetics of dispersal. *Biol Rev Camb Philos Soc*. 93:574–599. doi: 10.1111/brv.12356.
- Sagar P, Barker RJ, Geddes D. 2002. Survival of breeding Finsch's Oystercatchers (*Haematopus finschi*) on farmland in Canterbury. *New Zealand. Notornis*. 49:233–240.
- Sandercock BK. 2003. Estimation of survival rates for wader populations: a review of mark-recapture methods. *Wader Study Group Bull*. 100:163–174.
- Saunders SP, Roche EA, Arnold TW, Cuthbert FJ. 2012. Female site familiarity increases fledging success in Piping Plovers (*Charadrius melodus*). *Auk*. 129:329–337. doi: 10.1525/auk.2012.11125.
- Schamel D, Tracy D. 1977. Polyandry, replacement clutches, and site tenacity in the Red Phalarope (*Phalaropus fulicarius*) at Barrow, Alaska. *Bird Banding*. 48:314–324.
- Schamel D, Tracy DM. 1987. Latitudinal trends in breeding Red Phalaropes. *J Field Ornithol*. 58:126–134.
- von Scheuffler H, Stiefel A. 1985. Der Kampfäufer: *Philomachus pugnax*/1. Ziemsen: Aufl. – Wittenberg Lutherstadt.
- Serrano D, Cortés-Avizanda A, Zuberogoitia I, Blanco G, Benitez JR, Poncho C, Grande JM, Ceballos O, Morant J, Arrondo E, et al. 2021. Phenotypic and environmental correlates of natal dispersal in a long-lived territorial vulture. *Sci Rep*. 11:5424. doi: 10.1038/s41598-021-84811-8.
- Souchay G, Gauthier G, Pradel R. 2014. To breed or not: a novel approach to estimate breeding propensity and potential trade-offs in an arctic-nesting species. *Ecology*. 95:2745–2756. doi: 10.1890/13-1277.1.
- Stan Development Team. 2020. RStan: the R interface to Stan. R Package Version 2.21.2, <http://Mc-Stan.Org/>.
- Sutherland G, Harestad A, Price K, Lertzman K. 2000. Scaling of natal dispersal distances in terrestrial birds and mammals. *Conserv Ecol*. 4:16. doi: 10.5751/ES-00184-040116.
- Switzer PV. 1993. Site fidelity in predictable and unpredictable habitats. *Evol Ecol*. 7:533–555. doi: 10.1007/BF01237820.
- Székely T, Reynolds JD. 1995. Evolutionary transitions in parental care in shorebirds. *Proc R Soc Lond B Biol Sci*. 262:57–64.
- Thompson PS, Hale WG. 1989. Breeding site fidelity and natal philopatry in the Redshank *Tringa totanus*. *Ibis*. 131:214–224. doi: 10.1111/j.1474-919X.1989.tb02764.x.
- Tomkovich PS, Soloviev MY. 1994. Site fidelity in high arctic breeding waders. *Ostrich*. 65:174–180. doi: 10.1080/00306525.1994.9639680.
- Tomkovich PS. 1996. A third report on the biology of the Great Knot, *Calidris tenuirostris*, on the breeding grounds. *Stilt*. 28:43–45.
- Travis MJJ, Murrell DJ, Dytham C. 1999. The evolution of density-dependent dispersal. *Proc R Soc Lond B Biol Sci*. 266:1837–1842. doi: 10.1098/rspb.1999.0854.
- Trochet A, Courtois EA, Stevens VM, Baguette M, Chaine A, Schmeller DS, Clobert J, Wiens JJ. 2016. Evolution of sex-biased dispersal. *Q Rev Biol*. 91:297–320. doi: 10.1086/688097.
- Troy DM. 1996. Population dynamics of breeding shorebirds in arctic Alaska. *Int Wader Stud*. 8:15–27.
- Uyeda JC, Zenil-Ferguson R, Pennell MW. 2018. Rethinking phylogenetic comparative methods. *Syst Biol*. 67:1091–1109. doi: 10.1093/sysbio/syy031.
- Valcu M, Dale J, Kempnaers B. 2012. RangeMapper: a platform for the study of macroecology of life-history traits. *Glob Ecol Biogeogr*. 21:945–951. doi: 10.1111/j.1466-8238.2011.00739.x.
- Végvári Z, Katona G, Vági B, Freckleton RP, Gaillard J-M, Székely T, Liker A. 2018. Sex-biased breeding dispersal is predicted by social environment in birds. *Ecol Evol*. 8:6483–6491. doi: 10.1002/ece3.4095.
- Wagenmakers E-J, Lodewyckx T, Kuriyal H, Grasman R. 2010. Bayesian hypothesis testing for psychologists: a tutorial on the savage-dickey method. *Cogn Psychol*. 60:158–189. doi: 10.1016/j.cogpsych.2009.12.001.
- Waser PM, Jones WT. 1983. Natal philopatry among solitary mammals. *Q Rev Biol*. 58:355–390. doi: 10.1086/413385.
- Weatherhead PJ, Forbes MRL. 1994. Natal philopatry in passerine birds: genetic or ecological influences? *Behav Ecol*. 5:426–433. doi: 10.1093/beheco/5.4.426.
- Weiser EL, Lancot RB, Brown SC, Gates HR, Bentzen RL, Bety J, Boldenow ML, English WB, Franks SE, Koloski L, et al. 2018. Environmental and ecological conditions at arctic breeding sites have limited effects on true survival rates of adult shorebirds. *Auk*. 135:29–43.
- Whitfield DP, Tomkovich PS. 1996. Mating system and timing of breeding in holarctic waders. *Biol J Linn Soc*. 57:277–290. doi: 10.1111/j.1095-8312.1996.tb00313.x.
- Widemo F. 1997. The social implications of traditional use of lek sites in the ruff *Philomachus pugnax*. *Behav Ecol*. 8:211–217. doi: 10.1093/beheco/8.2.211.
- Yom-Tov Y. 1992. Mating system and laying date in birds. *Ibis*. 133:52–55.
- Zink RM. 2011. The evolution of avian migration. *Biol J Linn Soc*. 104:237–250. doi: 10.1111/j.1095-8312.2011.01752.x.
- Zuur AF, Ieno EN, Elphick CS. 2010. A protocol for data exploration to avoid common statistical problems. *Methods Ecol Evol*. 1:3–14. doi: 10.1111/j.2041-210X.2009.00001.x.

DATA SOURCES FOR ANNUAL RETURN RATES

Any source for a particular data point can be indexed within the supplementary data (Kwon et al. 2022).

- Amat JA, Fraga RM, Arroyo GM. 1999. Brood desertion and polygamous breeding in the Kentish Plover *Charadrius alexandrinus*. *Ibis*. 141:596–607. doi: 10.1111/j.1474-919X.1999.tb07367.x.
- Berg Å. 1994. Maintenance of populations and causes of population changes of curlews *Numenius arquata* breeding on farmland. *Biological Conservation*. 67:233–238. doi: 10.1016/0006-3207(94)90614-9.
- Colwell MA, Burrell NS, Hardy MA, Kayano K, Muir JJ, Pearson WJ, Peterson SA, Sesser KA. 2010. Arrival times, laying dates, and reproductive success of Snowy Plovers in two habitats in coastal northern California. *Journal of Field Ornithology*. 81:349–360. doi: 10.1111/j.1557-9263.2010.00291.x.
- Colwell MA, Gratto CL, Oring LW, Fivizzani AJ. 1988. Effects of blood sampling on shorebirds: Injuries, return rates, and clutch desertions. *The Condor*. 90:942–945. doi: 10.2307/1368855.
- Dougall TW, Holland PK, Yalden DW. 2010. The population biology of Common Sandpipers in Britain. *British Birds*. 103:100–114.
- Dwyer TJ, Sepik GF, Derleth EL, McAuley DG. 1988. Demographic characteristics of a Maine woodcock population and effects of habitat management. *Fish and Wildlife Research 4*. U.S. Fish and Wildlife Service, Patuxent Wildlife Research Center, Laurel, Maryland, USA. <https://pubs.er.usgs.gov/publication/5230097>.
- Eberhart-Phillips LJ, Cruz-López M, Lozano-Angulo L, del Ángel SG, Rojas-Abreu W, Bucio-Pacheco M, Küpper C. 2020a. CeutaOPEN, individual-based field observations of breeding Snowy Plovers *Charadrius nivosus*. *Scientific Data*. 7:149. doi: 10.1038/s41597-020-0490-y.
- Eberhart-Phillips LJ, Cruz-López M, Lozano-Angulo L, del Ángel SG, Rojas-Abreu W, Bucio-Pacheco M, Küpper C. 2020b. CeutaOPEN v1.5. Open Science Framework. doi: 10.17605/OSF.IO/3K4FHI.
- Eichhorn G, Bil W, Fox JW. 2017. Individuality in Northern Lapwing migration and its link to timing of breeding. *Journal of Avian Biology*. 48:1132–1138. doi: 10.1111/jav.01374.
- English W, Norman B, Smith P. 2020. Data on White-rumped Sandpiper contributed via personal communication.
- Flynn L, Nol E, Zharikov Y. 1999. Philopatry, nest-site tenacity, and mate fidelity of Semipalmated Plovers. *Journal of Avian Biology*. 30:47–55. doi: 10.2307/3677242.
- Foppen RPB, Majoor FA, Willems FJ, Meininger PL, van Houwelingen GC, Wolf PA. 2006. Survival and emigration rates in Kentish *Charadrius alexandrinus* and Ringed Plovers *Ch. Hiaticula* in the Delta area, SW-Netherlands. *Ardea*. 94:159–173.
- Grant MC. 1991. Nesting densities, productivity and survival of breeding Whimbrel *Numenius phaeopus* in Shetland. *Bird Study*. 38:160–169. doi: 10.1080/00063659109477085.
- Gratto-Trevor C. 2020. Marbled Godwit (*Limosa fedoa*), version 1.0. In *Birds of the World* (A. F. Poole and F. B. Gill, Editors). Cornell Lab of Ornithology, Ithaca, NY, USA. doi: 10.2173/bow.margod.01.
- Gratto-Trevor C. 2020. Data on Willet contributed via personal communication.
- Groen NM, Hemerik L. 2002. Reproductive success and survival of Black-tailed Godwits *Limosa limosa* in a declining local population in The Netherlands. *Ardea*. 90:239–248.
- Haig SM, Oring LW. 1988. Mate, site, and territory fidelity in Piping Plovers. *The Auk*. 105:268–277. doi: 10.2307/4087489.
- Handel CM, Gill RE. 2000. Mate fidelity and breeding site tenacity in a monogamous sandpiper, the Black Turnstone. *Animal Behaviour*. 60:471–481. doi: 10.1006/anbe.2000.1505.
- Hazlitt SL, Butler RW. 2001. Site fidelity and reproductive success of Black Oystercatchers in British Columbia. *Waterbirds*. 24:203–207. doi: 10.2307/1522031.
- Heldt VR. 1966. Zur Brutbiologie des Alpenstrandläufers, *Calidris alpina schinzii*. *Corax*. 1:173–188.
- Hildén O, Hilden O. 1978. Population dynamics in Temminck's Stint *Calidris temminckii*. *Oikos*. 30:17–28. doi: 10.2307/3543520.
- Hoefs C. 2020. Data on Eurasian Dotterel contributed via personal communication.
- Holland PK, Yalden DW. 1991. Population dynamics of Common Sandpipers *Actitis hypoleucos* breeding along an upland river system. *Bird Study*. 38:151–159. doi: 10.1080/00063659109477084.
- Holmes RT. 1971. Density, habitat, and the mating system of the Western Sandpiper (*Calidris mauri*). *Oecologia*. 7:191–208. doi: 10.1007/BF00346361.
- Howe MA. 1982. Social organization in a nesting population of Eastern Willets (*Catoptrophorus semipalmatus*). *The Auk*. 99:88–102. doi: 10.2307/4086024.
- Jackson DB. 1994. Breeding dispersal and site-fidelity in three monogamous wader species in the Western Isles, U.K. *Ibis*. 136:463–473. doi: 10.1111/j.1474-919X.1994.tb01123.x.
- Jehl JR. 1973. Breeding biology and systematic relationships of the Stilt Sandpiper. *The Wilson Bulletin*. 85:115–147.
- Jehl JR. 2007. Disappearance of breeding Semipalmated Sandpipers from Churchill, Manitoba: more than a local phenomenon. *The Condor*. 109:351–360.
- Johnson J. 2020. Data on Red Knot contributed via personal communication.
- Johnson M, Ruthrauff DR, McCaffery BJ, Haig SM, Walters JR. 2010. Apparent survival of breeding Western Sandpipers on the Yukon-Kuskokwim river delta, Alaska. *The Wilson Journal of Ornithology*. 122:15–22. doi: 10.1676/09-089.1.
- Johnson OW, Bruner PL, Bruner AE, Johnson PM, Kienholz RJ, Brusseau PA. 2001. Features of breeding biology in Pacific and American Golden-Plovers nesting on the Seward Peninsula, Alaska. *Wader Study Group Bulletin*. 95:59–65.
- Jonsson PE. 1991. Reproduction and survival in a declining population of the Southern Dunlin *Calidris alpina schinzii*. *Wader Study Group Bulletin*. 61:56–68.
- Kålås JA, Byrkjedal I. 1984. Breeding chronology and mating system of the Eurasian Dotterel (*Charadrius morinellus*). *The Auk*. 101:838–847. doi: 10.2307/4086911.
- Klima J, Johnson OW. 2005. Return rates of male and female monogamous shorebirds to their breeding grounds. *Wader Study Group Bulletin*. 106:42–46.
- Kosztolányi A, Javed S, Küpper C, Cuthill IC, Shamsi AA, Székely T. 2009. Breeding ecology of Kentish Plover *Charadrius alexandrinus* in an extremely hot environment. *Bird Study*. 56:244–252. doi: 10.1080/00063650902792106.
- Lancot RB, Brown SC, Sandercock BK. 2016. Arctic Shorebird Demographics Network. NSF Arctic Data Center. doi: 10.18739/A2222R68W.
- Lancot RB, Scribner KT, Lancot RB, Weatherhead PJ, Kempnaers B. 1997. Lekking without a paradox in the Buff-breasted Sandpiper. *The American Naturalist*. 149:1051–1070. doi: 10.1086/286038.
- Lancot RB, Weatherhead PJ, Kempnaers B, Scribner KT. 1998. Male traits, mating tactics and reproductive success in the Buff-breasted Sandpiper, *Tryngites subruficollis*. *Animal Behaviour*. 56:419–432. doi: 10.1006/anbe.1998.0841.
- Lishman C, Nol E, Abraham KF, Nguyen LP. 2010. Behavioral responses to higher predation risk in a subarctic population of the Semipalmated Plover. *The Condor*. 112:499–506. doi: 10.1525/cond.2010.090059.
- Lislev T, Byrkjedal I, Grønstøl GB. 2008. Dispersal and age at first breeding in Norwegian Northern Lapwings (*Vanellus vanellus*). *Ornis Fennica*. 86:11–17.
- Lislevand T, Hahn S. 2013. Effects of geolocator deployment by using flexible leg-loop harnesses in a small wader. *Wader Study Group Bulletin*. 120:108–113.
- Loefering JP. 1992. Piping Plover breeding biology, foraging ecology and behavior on Assateague Island National Seashore, Maryland. M.S. thesis, Virginia Polytechnic and State University, Blacksburg, VA, USA.
- Lowther PE, Douglas HD, Gratto-Trevor C. 2020. Willet (*Tringa semipalmata*), version 1.0. In *Birds of the World* (A. F. Poole and F. B. Gill, Editors). Cornell Lab of Ornithology, Ithaca, NY, USA. doi: 10.2173/bow.willet.01.
- Marks JS, Tibbitts TL, Gill RE, McCaffery BJ. 2020. Bristle-thighed Curlew (*Numenius tahitiensis*), version 1.0. In *Birds of the World* (A. F. Poole and F. B. Gill, Editors). Cornell Lab of Ornithology, Ithaca, NY, USA. doi: 10.2173/bow.brteur.01.
- Mayer PM, Ryan MR. 1986. Population ecology of the Piping Plover in the northern Great Plains. Progress Report to U.S. Fish and Wildlife Service. <https://www.fws.gov/northeast/pipingplover/pdf/I.pdf>
- Miller EH. 1983. Habitat and breeding cycle of the Least Sandpiper (*Calidris minutilla*) on Sable Island, Nova Scotia. *Canadian Journal of Zoology*. 61:2880–2898. doi: 10.1139/z83-376.

- Moitoret CS, Walker TR, Martin PD. 1996. Predevelopment surveys of nesting birds at two sites in the Kuparuk oilfield, Alaska, 1988–1992. Fish and Wildlife Service Technical Report NAES-TR-96-02. Pp. 104. U.S. Fish and Wildlife Service, Anchorage, USA.
- Mong TW, Sandercock BK. 2007. Optimizing radio retention and minimizing radio impacts in a field study of Upland Sandpipers. *Journal of Wildlife Management*. 71:971–980. doi: 10.2193/2005-775.
- Moskoff W, Montgomerie R. 2020. Baird's Sandpiper (*Calidris bairdii*), version 1.0. In *Birds of the World* (A. F. Poole and F. B. Gill, Editors). Cornell Lab of Ornithology, Ithaca, NY, USA. doi: 10.2173/bow.baisan.01.
- Nol E. 1985. Sex roles in the American Oystercatcher. *Behaviour*. 95:232–260. doi: 10.1163/156853985X00145.
- Oring LW, Lank DB. 1982. Sexual selection, arrival times, philopatry and site fidelity in the polyandrous Spotted Sandpiper. *Behavioral Ecology and Sociobiology*. 10:185–191. doi: 10.1007/BF00299684.
- Oring LW, Lank DB, Maxson SJ. 1983. Population studies of the polyandrous Spotted Sandpiper. *The Auk*. 100:272–285.
- Page GW, Stenzel LE, Winkler DW, Swarth CW. 1983. Spacing out at Mono Lake: Breeding success, nest density, and predation in the Snowy Plover. *The Auk*. 100:13–24. doi: 10.1093/auk/100.1.13.
- Pakanen V-M, Hildén O, Rönkä A, Belda EJ, Luukkonen A, Kvist L, Koivula K. 2011. Breeding dispersal strategies following reproductive failure explain low apparent survival of immigrant Temminck's Stints. *Oikos*. 120:615–622. doi: 10.1111/j.1600-0706.2010.18953.x.
- Pakanen V-M, Lampila S, Arppe H, Valkama J. 2015. Estimating sex specific apparent survival and dispersal of Little Ringed Plovers (*Charadrius dubius*). *Ornis Fennica*. 92:172–186.
- Pakanen V-M, Rönkä N, Thomson RL, Koivula K. 2015. No strong effects of leg-flagged geolocators on return rates or reproduction of a small long-distance migratory shorebird. *Ornis Fennica*. 92:101–111.
- Parr R. 1992. The decline to extinction of a population of Golden Plover in North-East Scotland. *Ornis Scandinavica* (Scandinavian Journal of Ornithology). 23:152–158. doi: 10.2307/3676443.
- Paton P, Edwards T. 1996. Factors affecting interannual movements of Snowy Plovers. *The Auk*. 113:534–543. doi: 10.2307/4088973.
- Pearce-Higgins JW, Yalden DW. 2003. Golden Plover *Pluvialis apricaria* breeding success on a moor managed for shooting Red Grouse *Lagopus lagopus*. *Bird Study*. 50:170–177. doi: 10.1080/00063650309461309.
- Perkins DE, Smith PA, Gilchrist HG. 2007. The breeding ecology of Ruddy Turnstones (*Arenaria interpres*) in the eastern Canadian Arctic. *Polar Record*. 43:135–142. doi: 10.1017/S0032247407006092.
- Pienkowski MW. 1984. Behaviour of young Ringed Plovers *Charadrius hiaticula* and its relationship to growth and survival to reproductive age. *Ibis*. 126:133–155. doi: 10.1111/j.1474-919X.1984.tb07994.x.
- Ray KL. 2010. Factors affecting Wilson's Plover (*Charadrius wilsonia*) demography and habitat use at Onslow Beach, Marine Corps Base Camp Lejeune, North Carolina. M.S. thesis, Virginia Polytechnic and State University, Blacksburg, VA, USA.
- Redmond RL, Jenni DA. 1982. Natal philopatry and breeding area fidelity of Long-billed Curlews (*Numenius americanus*): Patterns and evolutionary consequences. *Behavioral Ecology and Sociobiology*. 10:277–279. doi: 10.1007/BF00302817.
- Reed JM, Oring LW. 1993. Philopatry, site fidelity, dispersal, and survival of Spotted Sandpipers. *The Auk*. 110:541–551. doi: 10.2307/4088418.
- Reynolds JD, Cooke F. 1988. The influence of mating systems on philopatry: A test with polyandrous Red-necked Phalaropes. *Animal Behaviour*. 36:1788–1795. doi: 10.1016/S0003-3472(88)80118-0.
- Rittinghaus H. 1956. Untersuchungen am Seeregenpfeifer (*Charadrius alexandrinus* L.) auf der Insel Oldeog. *Journal für Ornithologie*. 97:117–155. doi: 10.1007/BF01671028.
- Robinson JA, Oring LW. 1997. Natal and breeding dispersal in American Avocets. *The Auk*. 114:416–430. doi: 10.2307/4089243.
- Roche EA, Sherfy MH, Ring MM, Shaffer TL, Anteau MJ, Stucker JH. 2016. Demographics and movements of Least Terns and Piping Plovers in the Central Platte River Valley, Nebraska: U.S. Geological Survey Open-File Report 2016–1061, 27 p., <http://dx.doi.org/10.3133/ofr20161061>.
- Rodrigues TMG. 2020. Data on Common Snipe contributed via personal communication.
- Ryabitshev VK. 2000. On the population ecology of the Gray Plover in the northern Yamal Peninsula. *Russian Journal of Ecology*. 31:108–112. doi: 10.1007/BF02828364.
- Safriel UN, Harris MP, Brooke MDL, Britton CK. 1984. Survival of breeding Oystercatchers *Haematopus ostralegus*. *Journal of Animal Ecology*. 53:867–877. doi: 10.2307/4664.
- Sandercock BK, Gratto-Trevor CL. 1997. Local survival in Semipalmated Sandpipers *Calidris pusilla* breeding at La Pérouse Bay, Canada. *Ibis*. 139:305–312. doi: 10.1111/j.1474-919X.1997.tb04629.x.
- Sandercock BK, Székely T, Kosztolányi A. 2005. The effects of age and sex on the apparent survival of Kentish Plovers breeding in Southern Turkey. *The Condor*. 107:583–596.
- Schamel D, Tracy DM. 1991. Breeding site fidelity and natal philopatry in the sex role-reversed Red and Red-necked Phalaropes (Fidelidad al Área de Reproducción y Filopatría Natal en *Phalaropus fulicaria* y *P. lobatus*). *Journal of Field Ornithology*. 62:390–398.
- Senner NR, Hochachka WM, Fox JW, Afanasyev V. 2014. An exception to the rule: Carry-over effects do not accumulate in a long-distance migratory bird. *PLOS ONE*, 9:e86588. doi: 10.1371/journal.pone.0086588.
- Senner NR, Swift R. 2020. Data on Hudsonian Godwit contributed via personal communication.
- Sheldon RD, Kamp J, Koshkin MA, Urazaliev RS, Isakov TK, Field RH, Salemgareev AR, Khrokov VV, Zhuly VA, Sklyarenko SL, Donald PF. 2013. Breeding ecology of the globally threatened Sociable Lapwing *Vanellus gregarius* and the demographic drivers of recent declines. *Journal of Ornithology*. 154:501–516. doi: 10.1007/s10336-012-0921-4.
- Skeel MA. 1983. Nesting success, density, philopatry, and nest-site selection of the Whimbrel (*Numenius phaeopus*) in different habitats. *Canadian Journal of Zoology*. 61:218–225. doi: 10.1139/z83-027.
- Sviridova T. 2000. Site fidelity and territory establishment in breeding Pacific Golden-Plovers and Grey Plovers at Taimyr, Siberia. In: Ebbinge BS, Editor. *Heritage of the Russian Arctic: Research, Conservation, and International Co-operation*. Moscow: Ecopros Publishers, Moscow, Russia.
- Székely T, Williams TD. 1995. Costs and benefits of brood desertion in female Kentish Plovers, *Charadrius alexandrinus*. *Behavioral Ecology and Sociobiology*. 37:155–161. doi: 10.1007/BF00176712.
- Thompson PS, Hale WG. 1993. Adult survival and numbers in a coastal breeding population of Redshank *Tringa totanus* in northwest England. *Ibis*. 135:61–69. doi: 10.1111/j.1474-919X.1993.tb02810.x.
- Thorup O. 1999. Breeding dispersal and site-fidelity in Dunlin *Calidris alpina* at Tipperne, Denmark. *Journal of the Danish Ornithological Society*. 93:255–265.
- Thuman K. 2003. Female Reproductive Strategies in the Ruff (*Philomachus pugnax*). PhD dissertation. University of Uppsala, Uppsala, Sweden.
- Tomkovich PS, Soloviev MY. 1994. Site fidelity in high Arctic breeding waders. *Ostrich*. 65:174–180. doi: 10.1080/00306525.1994.9639680.
- Tomkovich PS. 1996. A third report on the biology of the Great Knot, *Calidris tenuirostris*, on the breeding grounds. *Stilt*. 28:43–45.
- van Leeuwen CHA, Jamieson SE. 2018. Strong pair bonds and high site fidelity in a subarctic-breeding migratory shorebird. *The Wilson Journal of Ornithology*. 130:140–151. doi: 10.1676/16-116.1.
- Warriner JS, Warriner JC, Page GW, Stenzel LE. 1986. Mating system and reproductive success of a small population of polygamous Snowy Plovers. *Wilson Bulletin*. 98:15–37.
- Weiser EL, Lancot RB, Brown SC, Gates HR, Bentzen RL, Bety J, Boldenow ML, English WB, Franks SE, Koloski L, Kwon E, Lamarre J-F, Lank DB, Liebezeit JR, McKinnon L, Nol E, Rausch J, Saalfeld ST, Senner NR, ... Sandercock BK. 2018. Environmental and ecological conditions at Arctic breeding sites have limited effects on true survival rates of adult shorebirds. *Auk*. 135:29–43. doi: 10.1642/AUK-17-107.1.
- Wiens TP. 1986. Nest-site tenacity and mate retention in the Piping Plover. M.S. Thesis, University of Minnesota at Duluth, Duluth, MN, USA.
- Wilcox LR. 1959. A twenty year banding study of the Piping Plover. *The Auk*. 76:129–152. doi: 10.2307/4081772.
- Yasué M, Dearden P. 2008. Replacement nesting and double-brooding in Malaysian Plovers *Charadrius peronii*: Effects of season and food availability. *Ardea*. 96:59–72. doi: 10.5253/078.096.0107.
- Ye ZM. 1992. Territorial relations and population structure of the Redshank *Tringa totanus* during the nesting period in the south of Ukraine. *Wader Study Group*. 64:45–46.
- Yezerinac S, Lancot RB, Sage GK, Talbot SL. 2013. Social and genetic mating system of the American Golden-Plover. *Condor*. 115:808–815.
- Zöckler C, Syroechkovskiy EE, Atkinson PW. 2010. Rapid and continued population decline in the Spoon-billed Sandpiper *Eurynorhynchus pygmaeus* indicates imminent extinction unless conservation action is taken. *Bird Conservation International*. 20:95–111. doi: 10.1017/S0959270910000316.