Article:

van Dijk, R.E., Covas, R., Doutrelant, C. et al. (2 more authors) (2015) Fine-scale genetic structure reflects sex-specific dispersal strategies in a population of sociable weavers (Philetairus socius). Molecular Ecology. ISSN 0962-1083

https://doi.org/10.1111/mec.13308

Received Date : 14-Oct-2014
Revised Date : 29-Jun-2015
Accepted Date : 06-Jul-2015
Article type : Original Article

Fine-scale genetic structure reflects sex-specific dispersal strategies in a population of sociable weavers (*Philetairus socius*)

René E. van Dijk[1,*], Rita Covas[2,3,4], Claire Doutrelant[4,5], Claire N. Spottiswoode[4,6] & Ben J. Hatchwell[1]

[1]Department of Animal and Plant Sciences, University of Sheffield, Western Bank, Sheffield S10 2TN, United Kingdom

[2]CIBIO, Research Centre in Biodiversity and Genetic Resources, Vairão, Portugal

[3]Biology Department, Science Faculty, University of Porto, Porto, Portugal

[4]Percy FitzPatrick Institute of African Ornithology, DST-NRF Centre of Excellence, University of Cape Town, Rondebosch 7701, South Africa

[5]CEFE-CNRS, 1919 Route de Mende, F 34293, Cedex 5, Montpellier, France

[6]Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, United Kingdom

*corresponding author

E-mail: r.van.dijk@sheffield.ac.uk; Fax: +44 (0)114 2220002

Keywords: dispersal, fine-scale population genetics, kin selection, cooperation, sociable weaver

Running title: Dispersal and fine-scale genetic structure

Abstract

Dispersal is a critical driver of gene flow, with important consequences for population genetic structure, social interactions and other biological processes. Limited dispersal may result in kin-structured populations in which kin selection may operate, but it may also increase the risk of kin competition and inbreeding. Here, we use a combination of long-term field data and molecular genetics to examine dispersal patterns and their consequences for the population genetics of a highly social bird, the sociable weaver (*Philetairus socius*), which exhibits cooperation at various levels of sociality from nuclear family groups to its unique communal nests. Using 20 years of data, involving capture of 6508 birds and 3151 recaptures at 48 colonies, we found that both sexes exhibit philopatry and that any dispersal occurs over relatively short distances. Dispersal is female-biased, with females dispersing earlier, further, and to less closely related destination colonies than males. Genotyping data from 30 colonies showed that this pattern of dispersal is reflected by fine-scale genetic structure for both sexes, revealed by isolation by distance in terms of genetic relatedness and significant genetic variance among colonies. Both relationships were stronger among males than females. Crucially, significant relatedness extended beyond the level of the colony for both sexes. Such fine-scale population genetic structure may have played an important role in the evolution of cooperative behaviour in this species, but it may also result in a significant inbreeding risk, against which female-biased dispersal alone is unlikely to be an effective strategy.

Introduction

The genetic structure of populations (i.e. the frequency and distribution of alleles and genotypes) is a fundamental demographic characteristic that influences many biological processes, including local adaptation (Winker *et al.* 2013; Papadopulos *et al.* 2014), life-history decisions (Postma & van Noordwijk 2005), inbreeding risk (Keller & Waller 2002), and the evolution of sociality via kin selection (Hamilton 1964; Hewitt & Butlin 1997; Bourke 2014). The genetic structure of a population describes patterns of isolation that may emerge through the existence of physical barriers (Watts *et al.* 2007; Frantz *et al.* 2010; Edelaar *et al.* 2012), and/or of behavioural traits, such as natal philopatry or territoriality (Sugg *et al.* 1996; Woxvold *et al.* 2006; Lee *et al.* 2010; Leslie *et al.* 2015) that limit gene flow between groups of organisms. In highly mobile animals, such as birds, gene flow within populations is generally expected to be high, with genetic structure most likely to be observed at a landscape scale, i.e. between populations (Avise 1996; Van Treuren *et al.* 1999). However, demographic patterns associated with certain social systems, for instance coloniality or cooperative breeding in social vertebrates, may lead to or result from genetic structure at a much finer spatial scale, which is apparent at the level of discrete social groups or across territories (Emlen 1997; Hatchwell 2009).

Many social animals live in kin-based groups, and such fine-scale spatial genetic structure has far-reaching consequences in terms of its effect on the behaviour and fitness of individuals (Cornwallis *et al.* 2009; Hatchwell 2010). Although a number of hypotheses have been proposed to explain the evolution of cooperative breeding that do not require cooperation among kin, including pay-to-stay (Gaston 1978) and group augmentation (Kokko *et al.* 2001), high relatedness among individuals is likely to be a critical factor in the evolution of cooperative breeding, because kin-selected helping can evolve only when individuals have the opportunity to interact with kin. Indeed, population viscosity leading to the emergence of kin-structured populations is usually a precursor to the evolution of cooperation via kin selection (Hamilton 1964; Dickinson & Hatchwell 2004).

The demographic and behavioural processes that operate at a range of spatial scales to generate the genetic structure observed in diverse social systems are, however, still not fully understood (Hatchwell 2009; García-Navas *et al.* 2014). For example, although kin-selected cooperation has often evolved within discrete family groups that form through delayed dispersal, kin-directed cooperation has also evolved within 'kin neighbourhoods' (Dickinson & Hatchwell 2004), where natal dispersal over a limited distance precedes cooperative interactions among kin (e.g. Dickinson *et al.* 1996; Painter *et al.* 2000; Woxvold *et al.* 2006). Moreover, even when dispersal outside the natal area does occur, kin associations may be retained via the coordinated dispersal of family members to the same destination (Heinsohn *et al.* 2000; Sharp *et al.* 2008; Wang & Lu 2014). Finally, other demographic processes, such as strongly skewed reproductive success, may influence the kin structure of populations by reducing effective population size (Lehmann & Balloux 2007; Lehmann & Rousset 2010). Another example of such demographic processes is predation acting on entire broods, rather than on individuals, which may increase the kin structure of adult populations, potentially influencing kin-selected cooperation (Beckerman *et al.* 2011).

Genetically structured populations that result in long-term associations with kin are clearly important in the evolution of cooperative breeding systems, but such structure is more widespread than cooperative breeding alone, at least among birds (Covas & Griesser 2007). Indeed, there are several potential benefits of interacting with kin in contexts other than cooperative breeding, including cooperative investment in public goods, communal defence, and mate attraction (Krams *et al*. 2008; Díaz-Muñoz *et al*. 2014; van Dijk *et al.* 2014), that have received little attention in vertebrates (Hatchwell 2010). On the other hand, interactions among kin may be costly if they result in kin competition for resources or mates (Taylor 1992; West *et al.* 2002; Lehmann & Rousset 2010) or increase the likelihood of inbreeding (Keller & Waller 2002; Koenig & Haydock 2004). These costs may be mitigated by sex-biased dispersal strategies that reduce the chance of competing or mating with relatives (Greenwood 1980; Johnson & Gaines 1990) or by kin recognition mechanisms that reduce the risk of kin competition or inbreeding (Komdeur & Hatchwell 1999). However, the relationship between sex-biased dispersal and social behaviours is not clear (Mabry *et al*. 2013), partly as a consequence of the difficulty of studying the dispersal of marked individuals in finite natural populations (Koenig *et al*. 1996).

Here, we use a combination of molecular genetics and field observations to investigate dispersal behaviour and population genetic structure in a long-term study of sociable weavers (*Philetairus socius*). Sociable weavers have a social organisation that is unique among birds. They construct massive communal nests that may house hundreds of birds and last for decades (Maclean 1973a). Nests are occupied throughout the year, buffering environmental extremes and providing support for the nest chambers of breeding groups (van Dijk *et al.* 2013). Previous studies have shown that sociable weavers are cooperative breeders, with some pairs being assisted by non-breeding helpers that are usually male relatives of the breeders they help and that may gain indirect fitness benefits by assisting kin (Doutrelant *et al*. 2011; Covas *et al*. 2006). Furthermore, cooperative investment in the communal structure of a colony is kin-directed (van Dijk *et al.* 2014). These kin-directed cooperative behaviours are expected to be related to genetic structure, and it was previously found that there is fine-scale kin structure among males within colonies (Covas *et al*. 2006) and limited dispersal of individuals between colonies (Altwegg *et al*. 2014). However, little is known about the demographic processes that maintain this structure or the consequences of dispersal for genetic patterns at different spatial scales.

First, we describe the pattern of dispersal in relation to the age and sex of birds, expecting delayed, female-biased dispersal as typically found in cooperatively breeding species (Doutrelant *et al*. 2004; Ekman *et al.* 2004). Second, we address the hypothesis that the function of dispersal is to reduce the risk of inbreeding. We therefore investigate whether dispersing females were less related to members of their destination colony than they were to their original colony. In contrast, males are predicted to benefit more than females from being among kin, because their access to breeding and roosting chambers, their social interactions and their contribution to communal nest construction appear to be driven by kin-associations (van Dijk *et al.* 2014), and helpers of parents are usually male relatives (Doutrelant *et al.* 2004; Covas *et al.* 2006). Males were thus expected to be less likely to disperse and to disperse over a shorter distance than females. Third, we investigate whether these patterns of dispersal were reflected in population genetic structure, predicting that limited dispersal by either sex would be associated with patterns of isolation by distance and genetic differentiation among colonies. Such patterns were expected to be stronger for males than for females if dispersal is female-biased. Finally, we discuss how the dispersal behaviour of males and females and patterns of relatedness within and between colonies are related to cooperative behaviour and inbreeding risk.

Materials and Methods

Study area and field methods

The sociable weaver is a colonial, cooperatively breeding passerine endemic to the semi-arid Acacia savannahs of southern Africa that are associated with the Kalahari ecosystem (Maclean 1973a; Spottiswoode 2005). These socially and genetically monogamous weavers live in huge, colonial nests varying in size from five to over 300 individuals that are built communally by the colony members (Covas *et al.* 2006). We studied sociable weavers at Benfontein, Kimberley, South Africa (28°52′S, 24°50′E), at 48 different colonies between 1993 and 2013. This study area covers approximately 15 km^2. GPS-coordinates were taken for each colony (n = 48) and a Cartesian two-coordinate system (UTM) was used to describe distance between colonies. Some colonies were abandoned (and sometimes subsequently re-occupied) or, more rarely, physically collapsed during the period of our study, partly explaining the variable number of colonies between years and analyses. Adults were captured at 6 – 30 colonies annually (except 2006 when only nestlings were ringed and 2007 when no birds were ringed), outside the breeding season at sunrise using mist-nets and were ringed with a numbered aluminium ring (6508 adult and juvenile birds in total) and, from 1999 (except 2007 and 2009), three colour rings for individual recognition in the field. Altwegg *et al*. (2014) found that capture of sociable weavers might have contributed to the observed decline in population size over 17 years of study (capture accounted for 7.1% of variance in survival), but that the estimated effect of researchers’ disturbance on movement between colonies appeared to be minimal. From 1998 (except 2007 and 2009), at most nests juveniles and nestlings were ringed with a numbered aluminium ring and a combination of three colour rings. In addition, the population has been subject to several small-scale experimental treatments, including nest protection against predation by snakes, food provisioning and within-colony brood switches (Covas *et al*. 2004; Spottiswoode 2009; Paquet *et al*. 2015a; Rat *et al*. 2015). However, the population genetic structure we describe here is unlikely to be affected by these experiments because the number of individuals included in these experiments is very small relative to the number of individuals used in our analyses. Additionally, these experiments were largely carried out after 2010, so analyses that used data from 2010 only were not affected.

Estimates of dispersal based on recapture of ringed birds

Male and female dispersal was estimated based on our long-term dataset of individuals captured and ringed between 1993 and 2013. Dispersal was defined as an individual recaptured at a different colony from where it was first captured or was known to have hatched. Dispersal frequency was estimated by dividing the number of birds that dispersed by the total number of birds initially ringed or subsequently recaptured. This dataset also allowed us to assess the age of individuals if they were ringed as a nestling or juvenile, or to estimate the minimum age if birds were first caught as adults. It is a common feature of cooperatively breeding species that individuals often disperse only as adults when breeding opportunities arise elsewhere (Ekman *et al.* 2004). However, here, we combine adults and juveniles in our analyses of dispersal because dispersal between colonies in sociable weavers may occur at any time after the first four months in an individual's lifetime, i.e. there is no single age group that disperses (see Results). In particular, it is important to note that inter-colony dispersal is not a prerequisite for reproduction because many birds recruit as breeders within their natal colony (Covas *et al*. 2002). Captured individuals with incomplete development of their black plumage throat patch were classified as juveniles (< 1 year-old, n = 78) because the black bib is fully developed only four months after fledging (Maclean 1973b). These birds were assumed to have hatched in the colony at which they were captured, because dispersal during the first four months of an individual's life was never observed during eight years of intense monitoring of colonies (RC, M. Paquet, CD & L. Broom, unpublished data).

Genetic analyses

Because our population is not closed, a pedigree is inevitably incomplete and the use of molecular markers to estimate relatedness and population genetic structure is essential. Recent evidence shows that molecular estimates are robust to severe reductions in genetic diversity and the limitations of using molecular marker-based relatedness estimates might not be so severe as previously thought (Robinson *et al.* 2013). Therefore, during capture, a small blood sample (*ca.* 50 μl) was collected by puncture of the brachial vein using a sterile needle and heparinised capillary tube, and was preserved in 1 ml of absolute ethanol. Genomic DNA was extracted from blood samples collected from 2004 onwards. Because sociable weavers are sexually monomorphic, sex was determined molecularly using the *P2-P8* sex-typing primers (Griffiths *et al.* 1998). For further details on molecular genetic analyses see van Dijk *et al.* (2014).

To assess the genetic structure of our population, including patterns of isolation by distance, we performed spatial autocorrelation analyses, i.e. regression analyses of Queller and Goodnight's (1989) r_{QG} estimate of pairwise genetic relatedness between pairs of individuals as a function of geographic distance, using SPAGeDi v. 1.4 (Hardy & Vekemans 2002). The natural logarithm (ln) of distance was used in these analyses. Additionally, we used the microsatellite allele size-based estimate of genetic differentiation R_{ST} (Slatkin 1995), as calculated in SPAGeDi, to describe the population genetic structure among individuals across colonies and within colonies in separate spatial autocorrelation analyses. We observed regular gene flow within our geographically restricted population of this relatively long-lived species (sociable weavers may live up to 16 years; Covas 2012), so that mutation rates are likely to be outweighed by gene flow and thus unlikely to influence R_{ST} estimates (Balloux & Lugon-Moulin 2002). Although we focus on R_{ST}-values, we follow the suggestion of Balloux and Lugon-Moulin (2002) and also analyse patterns of genetic differentiation using F_{ST}-values (Weir & Cockerham 1984). Values of pairwise R_{ST} (or F_{ST}), used to compare genetic diversity within and among colonies, were provided as R_{ST} / (1–R_{ST}) ratios (Rousset 1997).

Our population of sociable weavers consists of spatially, genetically and socially distinct colonies (Covas *et al.* 2006; van Dijk *et al.* 2014), which have previously been described as having meta-population characteristics (Marsden 1999; Altwegg *et al.* 2014), thereby providing a clear, *a priori* subdivision of our population. Additionally, although dispersal does occur, it takes place within a geographically restricted, environmentally homogeneous population, so that environmental gradients and ecology, other than social effects such as colony size, are unlikely to influence the population genetic structure in our study (Orsini *et al.* 2013). Furthermore, temporal sampling effects may arise because allele frequencies and, thus, the genetic composition of colonies and the population may vary over time due to demographic processes such as dispersal, mortality and recruitment

(Balloux & Lugon-Moulin 2002; Liebgold *et al*. 2013). We therefore also performed our spatial analyses of genetic structuring of our population within one 'snapshot' year (2010) in addition to our analyses based on all genotyped individuals (n = 1846 adults). We chose 2010 because this was the year with the largest number of individuals trapped and genotyped (n = 646 genotyped adults out of 697 captured in total at 23 colonies; mean ± SD number of individuals captured at colonies across years from 2004 onwards = 535.4 ± 183.0). Finally, we restricted our spatial autocorrelation analyses of relatedness and genetic differentiation for data originating from multiple years to females older than three years and males and individuals of unknown sex of more than four years of age (see Goudet *et al*. 2002; Fig. 1). The great majority of birds within these age classes are likely to be independent breeders because the mean ± SD age of male helpers at our study site is just 1.2 ± 0.4 years, while females only help as yearlings (Doutrelant *et al*. 2011). For our analyses concerning the population in 2010, we did not enforce this restriction, because the sample size from that single year is not large enough to allow meaningful analyses after such a restriction. Genetic relatedness and differentiation estimates were calculated with reference to genotypes from the entire population caught between 1993 and 2013 or, for the analyses of data from within one year, with reference to the population in 2010. We included only adults in our analyses of population genetic structure, which were assigned to the colony where they were trapped and sampled for blood as an adult. If a blood sample was taken from an individual as a nestling or juvenile, they were assigned membership of the colony where they were first observed as an adult.

Statistical analysis

Non-parametric tests were used to analyse dispersal frequency and dispersal distance and whether these depend on the sex or the age of the disperser or on the distribution of colonies, because neither dispersal frequency or dispersal distance were normally distributed. To test whether relatedness of dispersers to the rest of the colony was associated with dispersal, we focussed on the first dispersal event per individual only (most individuals dispersed only once). We calculated the difference between mean relatedness of the dispersing individual to the rest of the colony, and the mean relatedness of the entire colony. We did not use a mixed-model approach for these analyses with colony and individual identity as random factors, due to non-normality and heteroscedasticity of residuals from these models.

Analyses were performed at the level of individuals (r_{QG}) and spatially discrete groups (R_{ST} and F_{ST}). Statistical significance of mean observed r_{QG}-values, global R_{ST}-values, and global F_{ST}-values within colonies, and significance of the regression slope β of pairwise statistics on ln(distance) between colonies, was assessed using 10000 permutations of individuals among spatial positions. To test for an effect of the sex difference in dispersal strategies on fine-scale population genetic structure, we performed our spatial autocorrelation analyses of relatedness and genetic differentiation for males and females separately, with individuals permuted among spatial locations. To account for a potential clustering effect of nearby colonies, spatial analyses were also performed using 10 specified classes of equal distance (500 m) from the same colony (0 m) to the most distant colony (5000 m). Colonies were classified to each of these 10 distance intervals depending on the distance between each colony and the focal colony, and average relatedness and genetic differentiation estimates were then calculated for each set of predefined distance intervals. 500 m was chosen to generate enough variation in genetic structuring while maintaining a sufficiently large sample size of colonies to ensure meaningful analyses. It also ensured that the median distance of dispersal was larger than each distance class. We used a jackknife procedure over loci to estimate standard errors of genetic relatedness and differentiation estimates and of the slopes of their regression over ln(distance). All tests were two-tailed.

Results

Dispersal frequency and distance

In total, 491 birds were known to have dispersed at least once from the colony of first capture. This represented 7.5% ($n = 6508$) of all juvenile and adult birds that were ringed, and 15.6% ($n = 3151$) of all birds that were recaptured at least once. Of the dispersing birds that were of known sex ($n = 231$), 34.2% were males and 65.8% were females (binomial test: $P < 0.001$). Thus there was a significant female bias in dispersal because the sex ratio of neither adults (52.2% were males; binomial test: $P =$

0.087, $n = 1579$) nor juveniles (53.4%; $P = 0.067$, $n = 743$) was different from parity in our study population (see also Doutrelant *et al.* 2004).

The median age at which males of known age moved to a different colony ($n = 21$ dispersing males of known age) for the first time was four years (inter-quartile range, IQR: 2–6, range: 1–12), whereas for females ($n = 51$) the median age was three years (IQR: 2–4, range: 1–8; Kruskal-Wallis rank-sum test: $\chi^2 = 3.515$, $df = 1$, $P = 0.061$). Including all individuals of known age ($n = 152$, including individuals of unknown sex) and all repeated observations of individuals that dispersed more than once ($n = 23$ individuals), the median age of dispersal was three (Fig. 1; $\text{median}_{\text{male}} = 4$, $\text{median}_{\text{female}} = 3$).

Birds that dispersed between colonies did so on average 1.17 ± 0.42 times (mean ± SD; range: 1–4, with 73 out of 491 birds dispersing twice, two three times and two four times), but among dispersing birds of known sex, there was no significant sex difference in the frequency of dispersal (Wilcoxon rank-sum test: $W = 4425$, $P = 0.986$, $n = 199$), with dispersing males moving on average 1.04 ± 0.21 (range 1–2) times and dispersing females 1.05 ± 0.21 (range 1–2) times. The distance for the second recorded dispersal event of those birds that dispersed at least twice was not different from that of their first move ($W = 3022$, $P = 0.937$, $n = 77$).

Considering all dispersal events, the median distance between the colony of origin and the destination colony was 721.9 m (IQR: 460.9–1019.7 m), with females (751.2 m, 530.8–1174.0 m, $n = 182$) dispersing further than males (641.5 m, 413.2–992.8 m, $n = 96$; $W = 7401$, $P = 0.036$, $n = 278$; Fig. 2 & 3). Dispersal distances must be determined in part by the distribution of other colonies (Fig. 3d), but the minimal distance between neighbouring colonies was just 215.8 m ± 133.4, so birds did not simply move to the nearest available colony (Fig. 4). The distance to the chosen colony was greater than the distance to the nearest colony ($W = 295858.5$, $P < 0.001$, $n = 566$ dispersal events) when all dispersal events were considered, and this was true for both males ($W = 8248.5$, $P < 0.001$, n

= 96) and females (W = 31034.5, $P < 0.001$, n = 182) in the subset of dispersers of known sex. Considering all dispersal events, dispersal distance decreased with age (χ^2 = 36.275, df = 21, P = 0.020, n = 491), but when we ran separate analyses for each sex, we found no effect of age on dispersal distance in either males (P = 0.158, n = 79), or females (P = 0.293, n = 152).

Dispersal and relatedness

Each individual was genotyped using 17 polymorphic microsatellite markers (multilocus averages across all genotyped individuals (n = 1846) and all colonies where individual genotypes were obtained (n = 33): 12.00 alleles, 4.07 effective alleles (Nielsen *et al*. 2003), allelic richness = 9.23, gene diversity corrected for sample size = 0.717, and individual inbreeding coefficient Fi = 0.020). None of these markers showed significant deviations from Hardy-Weinberg equilibrium or showed significant linkage disequilibrium after false-discovery-rate correction (van Dijk *et al*. 2014). In total, 163 alleles were detected. Heterozygotes were observed for males and females at all 17 loci, indicating they were autosomal in sociable weavers.

We investigated whether the decision of individuals to disperse from a colony was associated with their relatedness to other colony members. The mean relatedness of dispersers to the rest of their original colony, i.e. the colony they were first found in, did not differ significantly from the mean relatedness among all members of their original colony (Table 1a), showing that dispersers were randomly drawn from the original colony with respect to relatedness. In contrast, as expected, the mean relatedness of dispersers to the rest of their destination colony was significantly lower than mean relatedness among all members of their destination colony (Table 1a). Similarly, the relatedness of a disperser to members of its destination colony was lower than its relatedness to members of its original colony (Table 1a), showing that dispersers had a reduced chance of encountering relatives at their destination colonies.

When we ran separate analyses for each sex, we found qualitatively similar results for females, but not for males. In females, the difference between relatedness of dispersing females to their original colony and that among all members of the females' original colony was not different from zero (Table 1b). However, at the destination colony, the relatedness of dispersing females to other colony members was significantly lower than the relatedness among other colony members (Table 1b). For males, however, neither was different from zero (Table 1c). The relatedness of neither female (Table 1b) nor male (Table 1c) dispersers to members of their destination colony differed from their relatedness to members of their original colony. Critically, however, the relatedness of females to males at their original colony was significantly higher than that to males at their destination colony (Table 1d), whereas the relatedness of males to females at their original colony was not significantly different from that to females at their destination colony (Table 1d).

Overall, our results concerning individual dispersal by sociable weavers indicate male-biased philopatry, with females dispersing more often and greater distances than males and tending to disperse at an earlier age. Our results on the relatedness between dispersing birds and the rest of their original and destination colony indicate that these dispersal decisions by females, but not males, result in lower relatedness with potential mates.

Spatial analyses of relatedness

Mean colony-level relatedness, r_{QG}, was 0.026 ± 0.004 SE, which is similar to the value we reported previously for a subset of colonies in this population (0.032 ± 0.175 SD; van Dijk *et al.* 2014) and significantly higher than expected by chance under a null model of random association within the population among all individuals, among males, among females, and among males and females (Table 2).

The maximum distance between the 33 colonies containing genotyped individuals in our study population was 4872 m (mean ± SD = 1879 m ± 1079). We found strong support for isolation by distance, with pairwise relatedness decreasing with geographic distance between colonies across all categories of birds (Table 2). When we restricted these analyses to relatedness estimates from

2010 only, using birds of all age classes, including juveniles and young birds that had remained with their parents as helpers, our main results remained unchanged, except for pairwise individual relatedness between colonies for males, which did not decrease with distance (see Supporting Information).

When we performed spatial analyses of all genotyped females that were more than three year-old and all males that were more than four year-old plus birds of unknown sex (i.e. restricting the analysis to likely breeders) using 10 predefined classes of equal distance, we found that pairwise relatedness among all individuals was significantly higher than expected (based on permuted pairwise relatedness) among colonies up to 500 m distance, with a near-significant level of relatedness among individuals in colonies within a 1000 m radius. Beyond 1000 m, pairwise relatedness did not differ from that expected by chance (Fig. 5a). The spatial pattern for male-male relatedness showed that males within or among nearby colonies exhibited a higher relatedness than expected by chance, but such pairwise relatedness did not extend to ≥ 500 m (Fig. 5b). For females, however, we found a higher than expected relatedness among colonies within a 500 m radius, but not beyond (Fig. 5c). Finally, and importantly in terms of potential inbreeding risk, we found that the dyadic relatedness between males and females was significantly higher than expected by chance within a radius of 1000 m. At a radius of 3000 m and 4000 m, pairwise relatedness was marginally lower than expected (Fig. 5d).

Spatial analyses of genetic differentiation

Isolation by distance can lead to significant genetic differentiation (Frantz *et al.* 2009), and our analyses of global R_{ST} supported our finding of genetic structuring among colonies (Table 3). Global R_{ST} among 30 colonies was 0.021 ± 0.016 ($P = 0.025$, $n = 396$ birds), indicating that small but significant genetic variance within the population existed between colonies at a small spatial scale of ≤ 4872 m. This genetic differentiation was significant among males and between males and females, but showed only a non-significant trend among females (Table 3). However, our estimates of genetic differentiation were not related to the degree of geographic separation between colonies for all individuals, or among different combinations of males and females (Table 3). These results indicate that high philopatry with limited within-population gene flow has led to fine-scale population genetic structuring.

Despite the positive genetic structure that we found in terms of relatedness up to a distance of 1000 m between colonies (Fig. 5), when we defined ten equal distance intervals of 500 m, we found that pairwise genetic differentiation among groups of individuals was not significantly different from what is expected by chance at any distance interval (all $P > 0.119$). These results suggest that allelic diversity is maintained through regular dispersal between colonies.

We found qualitatively largely consistent results within our subset of data from 2010 (which was analysed separately to account for potential temporal sampling effects) and for analyses of F_{ST}-values, except that F_{ST}-values were negatively associated with geographic distance among all individuals (see Supporting Information).

Discussion

Sociable weavers live year-round and breed in large and permanent communal nests that may house tens to hundreds of individuals. We have used a combination of long-term capture data and population genetic analyses to investigate sex- and age-specific patterns of dispersal and their consequences for kin structure and genetic differentiation in this highly unusual social system. Our key findings are that: (i) male and female sociable weavers exhibit high levels of philopatry to their natal colony, with only 7.5% of all ringed birds and 15.6% of recaptured birds being observed to disperse to another colony; (ii) dispersal is female-biased, with females dispersing earlier and further than males; and (iii) these dispersal patterns are reflected in population genetic structure with isolation by distance in estimated relatedness and genetic differentiation among colonies, with both relationships being stronger among males than females.

The low dispersal estimates found here agree with previous studies that found low movement between colonies (Covas *et al*. 2002; Altwegg *et al*. 2014), confirming that sociable weavers are highly philopatric. However, as with any study on open populations, it is likely that these figures exclude birds that moved within the study area but were not recaptured and birds that dispersed away from the study area. Nonetheless, given the high number of colonies used in this study and the high recapture effort, it can be expected that a large proportion of the birds that moved were recaptured, and hence the low dispersal pattern described here is likely to provide a good indication of movement in this population.

Dispersal in sociable weavers, when it happens, is delayed relative to that of many other small passerine species, where it usually occurs during the first non-breeding season following fledging (Greenwood & Harvey 1982). Delayed dispersal is a widespread demographic trait among cooperative breeders (Ekman *et al.* 2004), resulting in the opportunity for helpers to gain direct and/or indirect fitness benefits by assisting breeders in subsequent breeding attempts (Cockburn 1998; Dickinson & Hatchwell 2004). However, with only 7.5% – 15.6% of birds known to have dispersed and > 60% of birds known to become a breeder in their natal colony (Covas *et al*. 2002), the frequency of dispersal exhibited by sociable weavers appears much lower than that observed for many other cooperatively breeding birds, where the majority of birds, especially females, usually disperse from their natal territory. For example, five studies of dispersal each on a different cooperatively breeding species have found dispersal to be up to 85% for males and to range from 54% to 100% for females (Blackmore *et al*. 2011; Sankamethawee *et al*. 2010; Temple *et al*. 2006; Double *et al*. 2005; Harrison *et al*. 2014). It is important to note, however, that in all the cases described above, dispersal entails movement away from the natal group, while in sociable weavers we have described dispersal as movement between colonies. The dispersal frequency we found is more similar to another colonial, but non-cooperatively breeding bird, the cliff swallow (*Petrochelidon pyrrhonota*), where 18.3% of males and 19.8% of females disperse to a non-natal colony (Brown & Brown 1992). The distinction between dispersal away from the natal group and dispersal between colonies is important, because in many cooperatively breeding species, dispersal from the natal group is often a prerequisite for reproduction to avoid inbreeding (Koenig & Haydock 2004) or to find a breeding vacancy (Emlen 1982). By contrast, in sociable weavers males and females may recruit as breeders within their natal colony, effectively dispersing from their natal group, but remaining within the colony. Thus, a colony of sociable weavers can be likened to the 'kin neighbourhoods' exhibited by a minority of cooperatively breeding species where, rather than existing in discrete family group, neighbours are closely related to each other as a consequence of limited natal dispersal, e.g. western bluebirds (*Sialia mexicana*; Dickinson *et al*. 2014), long-tailed tits (*Aegithalos caudatus*; Hatchwell *et al*. 2004) and rifleman (*Acanthisitta chloris*; Preston *et al*. 2013).

Sociable weavers' age of dispersal is around four years for males and three years for females. This estimated dispersal age might have been biased slightly upwards because some dispersers would not be found immediately after dispersal. Nevertheless, the estimated age at which sociable weavers were most likely to disperse generally coincides with the age at which they are expected to start breeding, i.e. three years for males and two years for females (Covas *et al.* 2004; RC, unpublished data). Once they start breeding, pairs of sociable weavers usually stay together for multiple years (Paquet *et al*. 2015b), so dispersal would be expected to occur prior to initial pair formation, as observed. This interpretation is supported by our finding that the relatedness of dispersers to the members of their destination colony was lower than to members of their original colony, especially when comparing the relatedness of dispersing females to male colony members. This again suggests that dispersal, at least in females, is related to finding a mate or breeding opportunity. This explanation might be less likely to account for the occasional dispersal of much older birds, for example, some > 7-year old birds (Fig. 1; 6 males and 4 females). Although we have no indication that dispersal of these birds was driven by the physical collapse of colonies (e.g. the branch supporting the nest falling down), such older birds may have lost their mate or close relatives in the colony, providing an incentive for dispersal. Other factors, such as food depletion or repeated nest failure due to predation (Marsden 1999, Brown *et al*. 2003), might drive such dispersal events by established breeders. In particular, nest predation by snakes is extremely high (an average of 70%, but over 90% in some colonies; Covas *et al*. 2008) and anecdotal evidence indicates that weavers may abandon colonies after long periods of repeated nest failure (RC & CD unpublished data).

Colony size of both the original and the destination colony may also be an important driver of dispersal, because it is likely to influence the availability of mates and other resources, such as food and nest chambers, as well as the level of competition between individuals for such resources. A previous study on the same population showed, consistent with our results, that sociable weavers disperse more often to nearby colonies than to colonies that are further away (Altwegg *et al*. 2014). Moreover, Altwegg *et al*. (2014) also showed that not just colony size per se, but trends of colony size (increasing or declining) at both colonies of origin and destination influence dispersal decisions in sociable weavers. Colony sizes and trends in colony size, however, are highly variable among the years included in our study and are thus unlikely to have influenced our results in a consistent manner.

The dispersal patterns that we have described would be expected to generate fine-scale population genetic structure. At a population level, we found that genetic relatedness did indeed decrease significantly with geographic distance between colonies, such that related individuals ($r > 0$) were clustered within and among colonies that are near each other. Although subtle, we found an important difference between males and females in such isolation by distance, which matched the observed sex difference in dispersal. Previous studies had described females-biased dispersal in this species (Doutrelant *et al*. 2004) and the resulting genetic structure at the colony level (Covas *et al*. 2006; van Dijk *et al*. 2014). Here, by analysing dispersal and genetic patterns on a larger number of colonies and investigating spatial effects, we found that relatedness among females, and, crucially, between males and females, was significant among colonies within a larger radius (≤ 1000 m) than was relatedness among males (< 500 m), reflecting female-biased dispersal.

Such within- and between-colony relatedness in sociable weavers generates within-population kin neighbourhoods and an opportunity for kin selection to operate. This is likely to have important consequences for a range of cooperative behaviours including cooperative breeding, which is largely directed towards kin within nuclear families (Covas *et al.* 2006), communal nest-building behaviour (van Dijk *et al.* 2014), and potentially other 'cryptic' kin-directed behaviours (Hatchwell 2010). Here we have shown that significant levels of relatedness extend between colonies that are near each other, which could also influence social dynamics among near-neighbours (Temple *et al.* 2006; Kurvers *et al.* 2014). For example, neighbouring colonies occasionally forage or move together (REvD & RC unpublished data), creating opportunities for kin-directed alarm calls or nepotistic resource sharing among relatives from these colonies.

Such spatial clustering of relatives also has important consequences in terms of mate choice. Firstly, spatially clustered kinship generates a risk of potentially deleterious inbreeding (Keller & Waller 2002; Blyton *et al*. 2015). Previous studies on cooperatively breeding birds have shown that dispersal by either both sexes or, more commonly, by females can be an efficient mechanism to avoid inbreeding (Walters *et al.* 2004; Blackmore *et al.* 2011; Nelson-Flower *et al.* 2012). Pied babblers (*Turdoides bicolor*), for example, disperse twice as far from natal groups as from non-natal groups, thus moving outside the range within which an inbreeding risk exists (Nelson-Flower *et al.* 2012). We found that although dispersal is female-biased, thereby reducing the risk of inbreeding (Greenwood 1980; Johnson & Gaines 1990; Lebigre *et al*. 2010; Clutton-Brock & Lukas 2012), most females remain in their natal colony and even females that do disperse do not move far and so are likely to encounter related individuals at their destination colonies. The risk of incestuous pairings actually occurring will depend on the rules governing mate choice and on the costs of inbreeding (Keller & Waller 2002). Moreover, in addition to sex-biased dispersal, there may be active discrimination against kin as mates via kin recognition (Komdeur & Hatchwell 1999). Consistent with the possibility that kin recognition mechanisms may serve to reduce inbreeding risk, a previous study found that paired males and females were not significantly related to each other (Covas *et al.* 2006). Future studies will need to quantify the incidence of inbreeding relative to the risk of choosing a related partner under alternative mate choice rules.

Secondly, as predicted by the optimal inbreeding or kin selection model, spatial clustering of kin facilitates mating with relatives, by which individuals may increase their inclusive fitness (Parker 1979; Lehmann & Perrin 2003; Kempenaers 2007). Any inbreeding costs (Szulkin *et al.* 2013) could be outweighed by potential fitness benefits of mating with (distant) relatives, such as enhanced breeding success and recruitment (Nelson-Flower *et al.* 2012; García-Navas *et al.* 2014), and through local adaptation to selection pressures such as predation, parasitism, or food availability. Previous studies on our study population of sociable weavers reported phenotypic sorting among colonies (Spottiswoode 2007), and suggested that fine-scale life-history variation between colonies might be adaptive (Spottiswoode 2009). Such structuring of fine-scale life-history and phenotypic variation might be facilitated by the limited dispersal and the structuring of genetic variation we present here.

In conclusion, we have shown that spatial analysis of fine-scale population genetics closely matches estimated patterns of male and female dispersal within our study population of sociable weavers. Such demographic information is difficult and time-consuming to obtain from field observations, yet of fundamental relevance for an understanding of a range of important biological processes. We found significant fine-scale genetic structure within this population, which is likely to have played an influential role in the evolution of the high levels of sociality observed in sociable weavers and/or to have emerged as a result of selection for sociality in this species. Importantly, we found that the average dispersal distance is such that the pairwise relatedness among males, among females and between the sexes is higher than expected by chance within and among nearby colonies, so that in addition to the opportunity for kin selection to operate, there may be a significant risk of inbreeding.

Acknowledgements

We are grateful to Jenny Kaden, Jamie Hutchison, Deborah Dawson and Terry Burke for conducting the molecular genetics analyses, which were performed at the NERC Biomolecular Analysis Facility at the University of Sheffield. We thank all people who helped with the fieldwork, especially Mark Anderson for data collected between 1993 and 1998, and Matthieu Paquet and Margaux Rat for their work during the breeding season. We also thank Res Altwegg for helpful discussion, and Morné du

Plessis, the late Phil Hockey, Peter Ryan and the Percy FitzPatrick Institute of African Ornithology provided important logistical and financial support. De Beers Consolidated Mines Ltd. kindly allowed us to live and work at their property Benfontein. This project received research permits from the Northern Cape Province's Department of Tourism, and Environment and Conservation and ethics approvals from the University of Cape Town, South Africa. Our research received funding from the Natural Environment Research Council (NERC, UK; NE/G018588/1 and NE/K015257/1) to BJH, the DST-NRF Centre of Excellence at the Percy FitzPatrick Institute of African Ornithology and the Portuguese Science and Technology Foundation (FCT PTDC/BIA-BEC/103818/2008) to RC, the CNRS and region Languedoc Roussillon to CD, St John's College, Cambridge, and the University of Cape Town to CNS, and the European MC-IRSES (FP7-PEOPLE-2012-IRSES; 'Cooperation' 318994) to RC, CD, REvD and BJH.

References

Altwegg R, Doutrelant C, Anderson MD, Spottiswoode CN, Covas R (2014) Climate, social factors and research disturbance influence population dynamics in a declining sociable weaver metapopulation. *Oecologia*, **174**, 413-425.

Avise JC (1996) Three fundamental contributions of molecular genetics to avian ecology and evolution. *Ibis*, **138**, 16-25.

Balloux F, Lugon-Moulin N (2002) The estimation of population differentiation with microsatellite markers. *Molecular Ecology*, **11**, 155-165.

Beckerman AP, Sharp SP, Hatchwell BJ (2011) Predation and kin-structured populations: an empirical perspective on the evolution of cooperation. *Behavioral Ecology*, **22**, 1294-1303.

Blackmore CJ, Peakall R, Heinsohn R (2011) The absence of sex-biased dispersal in the cooperatively breeding grey-crowned babbler. *Journal of Animal Ecology*, **80**, 69-78.

Blyton MDJ, Banks SC, Peakall R (2015) The effect of sex-biased dispersal on opposite-sexed spatial genetic structure and inbreeding risk. *Molecular Ecology*, **24**, 1681-1695.

Bourke AFG (2014) Hamilton's rule and the causes of social evolution. *Philosophical Transactions of the Royal Society B-Biological Sciences*, **369**, 20130362.

Brown CR, Bomberger Brown M (1992) Ectoparasitism as a cause of natal dispersal in cliff swallows. *Ecology*, **73**, 1718-1723.

Brown CR, Covas R, Anderson MD, Bomberger Brown M (2003) Multistate estimates of survival and movement in relation to colony size in the sociable weaver. *Behavioral Ecology*, **14**, 463-471.

Clutton-Brock TH, Lukas D (2012) The evolution of social philopatry and dispersal in female mammals. *Molecular Ecology*, **21**, 472-492.

Cockburn A (1998) Evolution of helping behavior in cooperatively breeding birds. *Annual review of ecology and systematics*, **29**, 141-177.

Cornwallis CK, West SA, Griffin AS (2009) Routes to indirect fitness in cooperatively breeding vertebrates: kin discrimination and limited dispersal. *Journal of Evolutionary Biology*, **22**, 2445-2457.

Covas R (2012) The benefits of long-term studies: 16-year old sociable weaver caught at Benfontein Game Reserve. Afring News 41:11-12

Covas R, Brown CR, Anderson MD, Bomberger Brown M (2002) Stabilizing selection on body mass in the sociable weaver *Philetairus socius*. *Proceedings of the Royal Society London B*, **269**, 1905-1909

Covas R, Dalecky A, Caizergues A, Doutrelant C (2006) Kin associations and direct vs indirect fitness benefits in colonial cooperatively breeding sociable weavers *Philetairus socius*. *Behavioral Ecology and Sociobiology*, **60**, 323-331.

Covas R, Doutrelant C, du Plessis MA (2004) Experimental evidence of a link between breeding conditions and the decision to breed or to help in a colonial cooperative bird. *Proceedings of the Royal Society London B*, **271**, 827-832.

Covas R, du Plessis MA, Doutrelant C (2008) Helpers in colonial cooperatively breeding sociable weavers *Philetairus socius* contribute to buffer the effects of adverse breeding conditions. *Behavioral Ecology and Sociobiology*, **63**, 103–112.

Covas R, Griesser M (2007) Life history and the evolution of family living in birds. *Proceedings of the Royal Society B*, **274**, 1349-1357.

Díaz-Muñoz SL, DuVal EH, Krakauer AH, Lacey EA (2014) Cooperating to compete: altruism, sexual selection and causes of male reproductive cooperation. *Animal Behaviour*, **88**, 67-78.

Dickinson JL, Ferree E, Stern CA, Swift R, Zuckerberg B (2014) Delayed dispersal in western bluebirds: Teasing apart the importance of resources and parents. *Behavioral Ecology*, **25**, 843-851.

Dickinson JL, Hatchwell BJ (2004) The fitness consequences of helping. In: *Cooperative breeding in birds* (eds. Koenig WD, Dickinson JL), pp. 48–66. Cambridge University Press, Cambridge, UK.

Dickinson JL, Koenig WD, Pitelka FA (1996) Fitness consequences of helping behavior in the western bluebird. *Behavioral Ecology*, **7**, 168-177.

Double MC, Peakall R, Beck NR, Cockburn A (2005) Dispersal, philopatry, and infidelity: Dissecting local genetic structure in superb fairy-wrens (*Malurus cyaneus*). *Evolution*, **59**, 625-635.

Doutrelant C, Covas R, Caizergues A, Du Plessis MA (2004) Unexpected sex ratio adjustment in a colonial cooperative bird: pairs with helpers produce more of the helping sex whereas pairs without helpers do not. *Behavioral Ecology and Sociobiology*, **56**, 149-154.

Doutrelant C, Dalecky A, Covas R (2011) Age and relatedness have an interactive effect on the feeding behaviour of helpers in cooperatively breeding sociable weavers. *Behaviour*, **148**, 1399-1417.

Edelaar P, Alonso D, Lagerveld S, Senar JC, Bjorklund M (2012) Population differentiation and restricted gene flow in Spanish crossbills: not isolation-by-distance but isolation-by-ecology. *Journal of Evolutionary Biology*, **25**, 417-430.

Ekman J, Dickinson JL, Hatchwell BJ, Griesser M (2004) Delayed dispersal. In: *Ecology and evolution of cooperative breeding in birds* (eds. Koenig WD, Dickinson JL), pp. 35-47. Cambridge University Press, Cambridge.

Emlen ST (1982) The evolution of helping: I. An ecological constraints model. *American Naturalist*, **119**, 29-39.

Emlen ST (1997) Predicting family dynamics in social vertebrates. In: *Behavioural ecology: an evolutionary approach* (eds. Krebs JR, Davies NB), pp. 228-253. Blackwell Science Ltd., Oxford.

Frantz AC, Cellina S, Krier A, Schley L, Burke T (2009) Using spatial Bayesian methods to determine the genetic structure of a continuously distributed population: clusters or isolation by distance? *Journal of Applied Ecology*, **46**, 493-505.

Frantz AC, Pope LC, Etherington TR, Wilson GJ, Burke T (2010) Using isolation-by-distance-based approaches to assess the barrier effect of linear landscape elements on badger (*Meles meles*) dispersal. *Molecular Ecology*, **19**, 1663-1674.

García-Navas V, Ferrer ES, Sanz JJ, Ortego J (2014) The role of immigration and local adaptation on fine-scale genotypic and phenotypic population divergence in a less mobile passerine. *Journal of Evolutionary Biology*, **27**, 1590-1603.

Gaston AJ (1978) The evolution of group territorial behavior and cooperative breeding. *American Naturalist*, **112**, 1091-1100.

Goudet J, Perrin N, Waser P (2002) Tests for sex-biased dispersal using bi-parentally inherited genetic markers. *Molecular Ecology*, **11**, 1103–1114.

Greenwood PJ (1980) Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour*, **28**, 1140-1162.

Greenwood PJ, Harvey PH (1982) The natal and breeding dispersal of birds. *Annual review of ecology and systematics*, **13**, 1-21.

Griffiths R, Double MC, Orr K, Dawson RJG (1998) A DNA test to sex most birds. *Molecular Ecology*, **7**, 1071-1075.

Hamilton WD (1964) The genetical evolution of social behaviour. *Journal of Theoretical Biology*, **7**, 1-52.

Hardy OJ, Vekemans X (2002) SPAGeDi: a versatile computer program to analyse spatial genetic structure at the individual or population levels. *Molecular Ecology Notes*, **2**, 618-620.

Harrison XA, York JE, Young AJ (2014) Population genetic structure and direct observations reveal sex-reversed patterns of dispersal in a cooperative bird. *Molecular Ecology*, **23**, 5740-5755.

Hatchwell BJ, Russell AF, MacColl ADC, Ross DJ, Fowlie MK, McGowan A (2004) Helpers increase long-term but not short-term productivity in cooperatively breeding long-tailed tits. *Behavioral Ecology*, **15**, 1-10.

Hatchwell BJ (2009) The evolution of cooperative breeding in birds: kinship, dispersal and life history. *Philosophical Transactions of the Royal Society B-Biological Sciences*, **364**, 3217-3227.

Hatchwell BJ (2010) Cryptic kin selection: kin structure in vertebrate populations and opportunities for kin-directed cooperation. *Ethology*, **116**, 203-216.

Heinsohn R, Dunn P, Legge S, Double M (2000) Coalitions of relatives and reproductive skew in cooperatively breeding white-winged choughs. *Proceedings of the Royal Society B-Biological Sciences*, **267**, 243-249.

Hewitt GM, Butlin RK (1997) Causes and consequences of population structure. In: *Behavioural Ecology: An Evolutionary Approach* (eds. Krebs JR, Davies NB), pp. 350-372. Blackwell Scientific Publications, Oxford.

Johnson ML, Gaines MS (1990) Evolution of dispersal: theoretical models and empirical tests using birds and mammals. *Annual review of ecology and systematics*, **21**, 449-480.

Keller LF, Waller DM (2002) Inbreeding effects in wild populations. *Trends in Ecology & Evolution*, **17**, 230-241.

Kempenaers B (2007) Mate choice an genetic quality: a review of the heterozygosity theory. *Advances in the Study of Behaviour*, **37**, 189-278.

Koenig WD, Haydock J (2004) Incest and incest avoidance. In: *Ecology and Evolution of Cooperative Breeding in Birds* (eds. Koenig WD, Dickinson JL), pp. 142-156. Cambridge University Press, Cambridge.

Koenig WD, Van Vuren D, Hooge PN (1996) Detectability, philopatry, and the distribution of dispersal distances in vertebrates. *Trends in Ecology & Evolution*, **11**, 514-517.

Kokko H, Johnstone RA, Clutton-Brock TH (2001) The evolution of cooperative breeding through group augmentation. Proceedings of the Royal Society London B, **268,** 187–196.

Komdeur J, Hatchwell BJ (1999) Kin recognition: function and mechanism in avian societies. *Trends in Ecology & Evolution*, **14**, 237-241.

Krams I, Krama T, Igaune K, Mänd R (2008) Experimental evidence of reciprocal altruism in the pied flycatcher. *Behavioral Ecology and Sociobiology*, **62**, 599-605.

Kurvers RHJM, Krause J, Croft DP, Wilson ADM, Wolf M (2014) The evolutionary and ecological consequences of animal social networks: emerging issues. *Trends in Ecology & Evolution*, **29**, 326-335.

Lebigre C, Alatalo RV, Siitari H (2010) Female-biased dispersal alone can reduce the occurrence of inbreeding in black grouse (*Tetrao tetrix*). *Molecular Ecology*, **19**, 1929-1939.

Lee J-W, Simeoni M, Burke T, Hatchwell BJ (2010) The consequences of winter flock demography for genetic structure and inbreeding risk in vinous-throated parrotbills, *Paradoxornis webbianus*. *Heredity*, **104**, 472-481.

Lehmann L, Balloux F (2007) Natural selection on fecundity variance in subdivided populations: Kin selection meets bet hedging. *Genetics*, **176**, 361-377.

Lehmann L, Perrin C (2003) Inbreeding avoidance through kin recognition: choosy females boost male dispersal. *American Naturalist*, **162**, 638-652.

Lehmann L, Rousset F (2010) How life history and demography promote or inhibit the evolution of helping behaviours. *Philosophical Transactions of the Royal Society B-Biological Sciences*, **365**, 2599-2617.

Leslie S, Winney B, Hellenthal G, *et al*. (2015) The fine-scale genetic structure of the British population. *Nature*, **519**, 309-314.

Liebgold EB, Gerlach NM, Ketterson ED (2013) Similarity in temporal variation in sex-biased dispersal over short and long distances in the dark-eyed junco, *Junco hyemalis*. *Molecular Ecology*, **22**, 5548-5560.

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

Maclean GL (1973a) The Sociable Weaver, Part 1: Description, distribution, dispersion and populations. *Ostrich*, **44**, 176-190.

Maclean GL (1973b) The Sociable Weaver, Part 3: Breeding biology and moult. *Ostrich*, **44**, 219-240.

Marsden RM (1999) *Coloniality in the sociable weaver* Philetairus socius, PhD thesis, University of Sheffield.

Nelson-Flower MJ, Hockey PAR, O'Ryan C, Ridley AR (2012) Inbreeding avoidance mechanisms: dispersal dynamics in cooperatively breeding southern pied babblers. *Journal of Animal Ecology*, **81**, 876-883.

Nielsen R, Tarpy DR, Kern Reeve H (2003) Estimating effective paternity number in social insects and the effective number of alleles in a population. *Molecular Ecology*, **12**, 3157-3164.

Orsini L, Vanoverbeke J, Swillen I, Mergeay J, De Meester L (2013) Drivers of population genetic differentiation in the wild: isolation by dispersal limitation, isolation by adaptation and isolation by colonization. *Molecular Ecology*, **22**, 5983-5999.

Painter JN, Crozier RH, Poiani A, Robertson RJ, Clarke MF (2000) Complex social organization reflects genetic structure and relatedness in the cooperatively breeding bell miner, *Manorina melanophrys*. *Molecular Ecology*, **9**, 1339-1347.

Papadopulos AST, Kaye M, Devaux C*, et al.* (2014) Evaluation of genetic isolation within an island flora reveals unusually widespread local adaptation and supports sympatric speciation. *Philosophical transactions of the Royal Society of London. Series B*, **369**, 20130342.

Paquet M, Covas R, Doutrelant C (2015a) A cross-fostering experiment reveals that prenatal environment affects begging behaviour in a cooperative breeder. *Animal Behaviour*, **102**, 251-258.

Paquet M, Doutrelant C, Hatchwell BJ, Spottiswoode CN, Covas R (2015b). Antagonistic effect of helpers on breeding male and female survival in a cooperatively breeding bird. *Journal of Animal Ecology,* doi:10.1111/1365-2656.12377

Parker GA (1979) Sexual selection and sexual conflict. In: *Sexual selection and reproductive competition in insects* (eds. Blum MS, Blum NA), pp. 123-166. Academic Press, New York.

Postma E, van Noordwijk AJ (2005) Gene flow maintains a large genetic difference in clutch size at a small spatial scale. *Nature*, **43**, 65-68.

Preston SAJ, Briskie JV, Burke T, Hatchwell BJ (2013) Genetic analysis reveals diverse kin-directed routes to helping in the rifleman *Acanthisitta chloris*. *Molecular Ecology*, **22**, 5027–5039.

Queller DC, Goodnight KF (1989) Estimating relatedness using genetic markers. *Evolution*, **43**, 258-275.

Rat M, van Dijk RE, Covas R, Doutrelant C (2015) Dominance hierarchies and associated signalling in a cooperative passerine. *Behavioral Ecology and Sociobiology*, **69**, 437-448.

Robinson SP, Simmons LW, Kennington WJ (2013) Estimating relatedness and inbreeding using molecular markers and pedigrees: the effect of demographic history. *Molecular Ecology*, **22**, 5779-5792.

Rousset F (1997) Genetic differentiation and estimation of gene flow from F-statistics under isolation by distance. *Genetics*, **145**, 1219-1228.

Sankamethawee W, Hardesty BD, Gale GA (2010) Sex-bias and timing of natal dispersal in cooperatively breeding Puff-throated Bulbuls *Alophoixus pallidus*. *Journal of Ornithology*, **151**, 779-789.

Sharp SP, Simeoni M, Hatchwell BJ (2008) Dispersal of sibling coalitions promotes helping among immigrants in a cooperatively breeding bird. *Proceedings of the Royal Society B*, **275**, 2125-2130.

Slatkin M (1995) A measure of population subdivision based on microsatellite allele frequencies. *Genetics*, **139**, 457-462.

Spottiswoode CN (2005) Sociable weaver, *Philetairus socius*. In: *Roberts – birds of southern Africa* (eds. Hockey PAR, Dean WRJ, Ryan PG), pp. 1007–1010. Trustees of the John Voelcker Bird Fund, Cape Town.

Spottiswoode CN (2007) Phenotypic sorting in morpholgy and reproductive investment among sociable weaver colonies. *Oecologia*, **154**, 589-600.

Spottiswoode CN (2009) Fine-scale life-history variation in sociable weavers in relation to colony size. *Journal of Animal Ecology*, **78**, 504-512.

Sugg DW, Chesser RK, Dobson FS, Hoogland JL (1996) Population genetics meets behavioral ecology. *Trends in Ecology and Evolution*, **11**, 338-342.

Szulkin M, Stopher KV, Pemberton JM, Reid JM (2013) Inbreeding avoidance, tolerance or preference in animals? *Trends in Ecology & Evolution*, **28**, 205-211.

Taylor PD (1992) Altruism in viscous populations: an inclusive fitness model. *Evolutionary Ecology*, **6**, 352-356.

Temple HJ, Hoffman JI, Amos W (2006) Dispersal, philopatry and intergroup relatedness: fine-scale genetic structure in the white-breasted thrasher, *Ramphocinclus brachyurus*. *Molecular Ecology*, **15**, 3449-3458.

van Dijk RE, Kaden JC, Argüelles-Ticó A*, et al.* (2013) The thermoregulatory benefits of the communal nest of sociable weavers *Philetairus socius* are spatially structured within nests. *Journal of Avian Biology*, **44**, 102-110.

van Dijk RE, Kaden JC, Argüelles-Ticó A, *et al.* (2014) Cooperative investment in public goods is kin directed in communal nests of social birds. *Ecology Letters*, **17**, 1141-1148.

van Treuren R, Bijlsma R, Tinbergen JM, Heg D, van de Zande L (1999) Genetic analysis of the population structure of socially organized oystercatchers (*Haematopus ostralegus*) using microsatellites. *Molecular Ecology*, **8**, 181-187.

Walters JR, Cooper CB, Daniels SJ, Pasinelli G, Schiegg K (2004) Conservation biology. In: *Ecology and evolution of cooperative breeding in birds* (eds. Koenig WD, Dickinson JL), pp. 197-209. Cambridge University Press, Cambridge.

Wang C, Lu X (2014) Dispersal in kin coalition throughout the non-breeding season to facilitate fine-scale genetic structure in the breeding season: evidence from a small passerine. *Ethology*, **120**, 1-10.

Watts PC, Saccheri IJ, Kemp SJ, Thompson DJ (2007) Effective population sizes and migration rates in fragmented populations of an endangered insect (*Coenagrion mercuriale*: Odonata). *Journal of Animal Ecology*, **76**, 790-800.

Weir BS, Cockerham CC (1984) Estimating F-statistics for the analysis of population structure. *Evolution*, **38**, 1358-1370.

West SA, Pen I, Griffin AS (2002) Cooperation and competition between relatives. *Science*, **296**, 72-75.

Winker K, McCracken KG, Gibson DD, Peters JL (2013) Heteropatric speciation in a duck, *Anas crecca*. *Molecular Ecology*, **22**, 5922-5935.

Woxvold IA, Adcock GJ, Mulder RA (2006) Fine-scale genetic structure and dispersal in cooperatively breeding apostlebirds. *Molecular Ecology*, **15**, 3139-3146.

Author contributions

R.E.v.D. contributed to the design of the study, collected field data, performed all data analyses and wrote the first draft of the manuscript. R.C. managed the sociable weavers' long-term study and together with C.D. and C.N.S. collected the majority of field data. B.J.H. designed the study, collected field data and was the project's Principal Investigator. All authors contributed to writing the manuscript.

Data accessibility

The following data files are archived in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.gr7p0

Data on the date of capture and recapture of individuals and information on the colonies and the age at which sociable weavers were captured.

Microsatellite genotype data, data on the sex of individuals, and the UTM coordinates of the location of colonies of sociable weavers for all individuals genotyped for this study.

Microsatellite genotype data, data on the sex of individuals, and the UTM coordinates of the location of colonies of sociable weavers for individuals from 2010 genotyped for this study.

Supporting Information

Additional supporting information may be found in the online version of this article.

Supporting Information S1 Results of spatial autocorrelation analyses based on data from 2010 only, and based on F_{ST}-values

TABLE

Table 1 Mean relatedness, r, of dispersers to other colony members, concerning (a) all dispersers, (b) female dispersers, (c) male dispersers, and (d) male and female dispersers. Wilcoxon signed-rank (the V-value corresponds to the sum of ranks assigned to positive differences) and one-sample t tests were used to assess statistical significance with $\mu = 0$.

(a)

	Δr (mean ± SD)	V	P	n
r dispersers to original colony members versus r among all members of original colony	0.001 ± 0.079	11365	0.699	212
r dispersers to destination colony members versus r among all members of destination colony	-0.024 ± 0.077	8523	<0.001	225
r dispersers to destination colony members versus r dispersers to original colony	-0.017 ± 0.116	12679	0.027	207

(b)

	Δr (mean ± SD)		P	n
r dispersers to original colony members versus r among all members of original colony	-0.006 ± 0.078	$V = 2197$	0.759	95
r dispersers to destination colony members versus r among all members of destination colony	-0.022 ± 0.064	$t = 3.471$	0.001	99
r dispersers to destination colony members versus r dispersers to original colony	-0.020 ± 0.117	$V = 2497$	0.110	94

(c)

	Δr (mean ± SD)		P	n
r dispersers to original colony members versus r among all members of original colony	-0.005 ± 0.074	$t = 0.477$	0.635	53
r dispersers to destination colony members versus r among all members of destination colony	-0.003 ± 0.077	$t = 0.287$	0.776	61
r dispersers to destination colony members versus r dispersers to original colony	0.021 ± 0.129	$V = 554$	0.221	53

(d)

	Δr (mean ± SD)	V	P	n
r female dispersers to males at original colony versus r female dispersers to males at destination colony	0.024 ± 0.157	2676	0.037	91
r male dispersers to females at original colony versus r male dispersers to females at destination colony	-0.035 ± 0.174	462	0.060	52

Table 2 Mean colony-level relatedness estimates, r_{QG}, of sociable weavers for males and individuals of unknown sex aged > 4 years and females aged > 3 years. Relatedness estimates are shown among all individuals, within males, within females, between males and females, and the slope β of the regression between pairwise spatial and genetic distance (ln[geographic distance] *versus* r_{QG}) as a measure of spatial genetic structure. Statistical significance was based on two-sided tests using 10000 permutations of spatial group locations among spatial groups. A jackknife-procedure over loci was used to estimate standard errors. *n* indicates the number of individuals with the number of colonies in parentheses. $^{(*)}P < 0.10$, $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$

	r_{QG}			
	All	Males	Females	Males/Females
Colony	0.026 ± 0.004***	0.054 ± 0.010***	0.015 ± 0.005**	0.018 ± 0.005***
β ± SE	-0.008 ± 0.003***	-0.006 ± 0.004$^{(*)}$	-0.010 ± 0.031**	-0.010 ± 0.003***
n	396 (30)	196 (26)	177 (28)	373 (30)

Table 3 Mean genetic differentiation estimates, global R_{ST}, among colonies within a population of sociable weavers for males and individuals of unknown sex aged > 4 years and females aged > 3 years. Genetic differentiation estimates are shown among all individuals, within males, within females, between males and females, and the slope β of the regression between pairwise spatial and genetic distance (ln[geographic distance] *versus* global R_{ST}) as a measure of spatial genetic structure. Statistical significance was based on two-sided tests using 10000 permutations of spatial group locations among spatial groups. A jackknife-procedure over loci was used to estimate standard errors. *n* indicates the number of individuals with the number of colonies in parentheses. $^{(*)}P < 0.10$, $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$, n.s. = not significant

	R_{ST}			
	All	Males	Females	Males/Females
Population	0.021 ± 0.016*	0.048 ± 0.011**	0.028 ± 0.020$^{(*)}$	0.039 ± 0.058**
β ± SE	0.001 ± 0.004$^{\text{n.s.}}$	-0.006 ± 0.006$^{\text{n.s.}}$	-0.027 ± 0.040$^{\text{n.s.}}$	-0.014 ± 0.019$^{\text{n.s.}}$
n	396 (30)	196 (26)	177 (28)	373 (30)

FIGURES

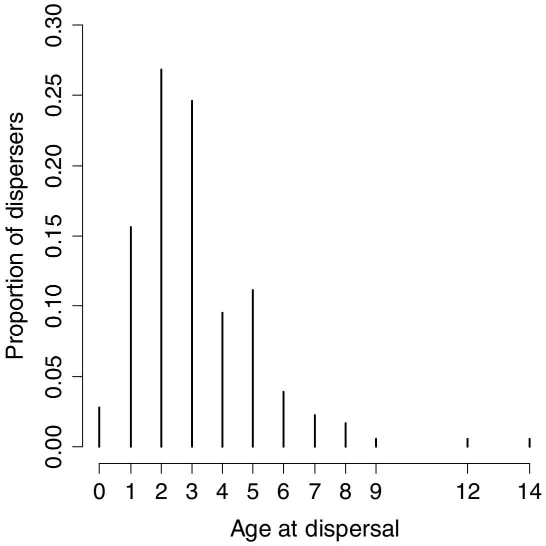


Fig. 1 The likelihood of dispersal against age (*n* = 180 dispersal events of 152 individuals of known age).

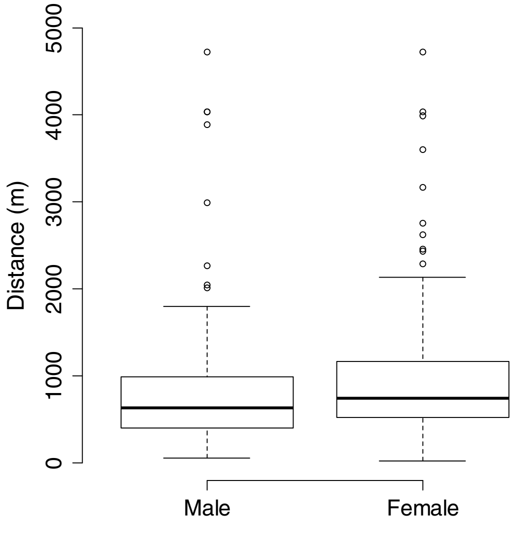


Fig. 2 Dispersal distance of males and females. Box plots indicate the median (thick line inside box), the interquartile range (box), the maximum and minimum values excluding outliers (dashed line from box), and outliers (dots).

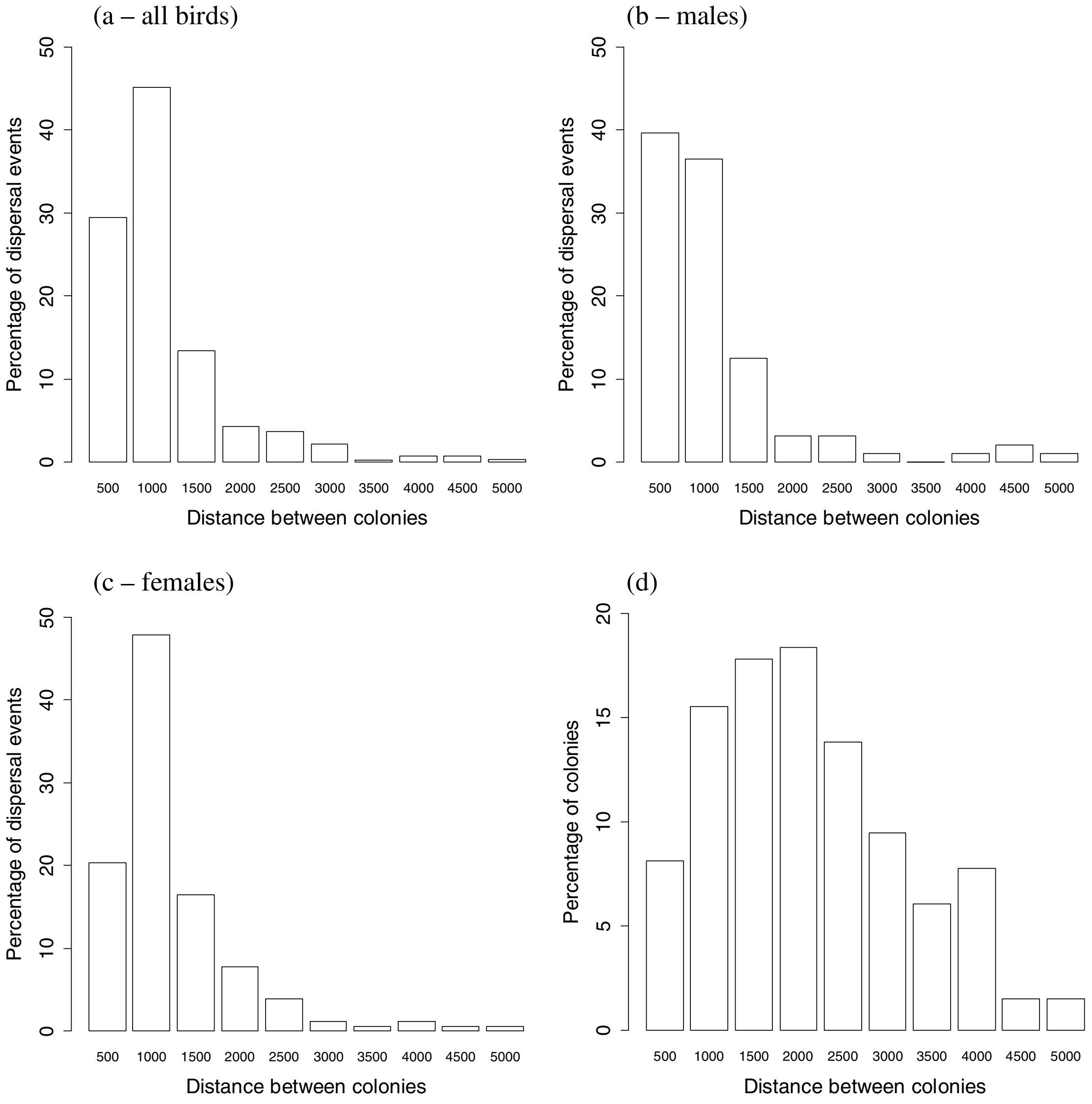


Fig. 3 The percentage of dispersal events per distance class. (a) all birds, (b) males, and (c) females. (d) The percentage of available colonies to disperse to from each colony per distance class. The values on the x-axis are the maximum distances for each distance class.

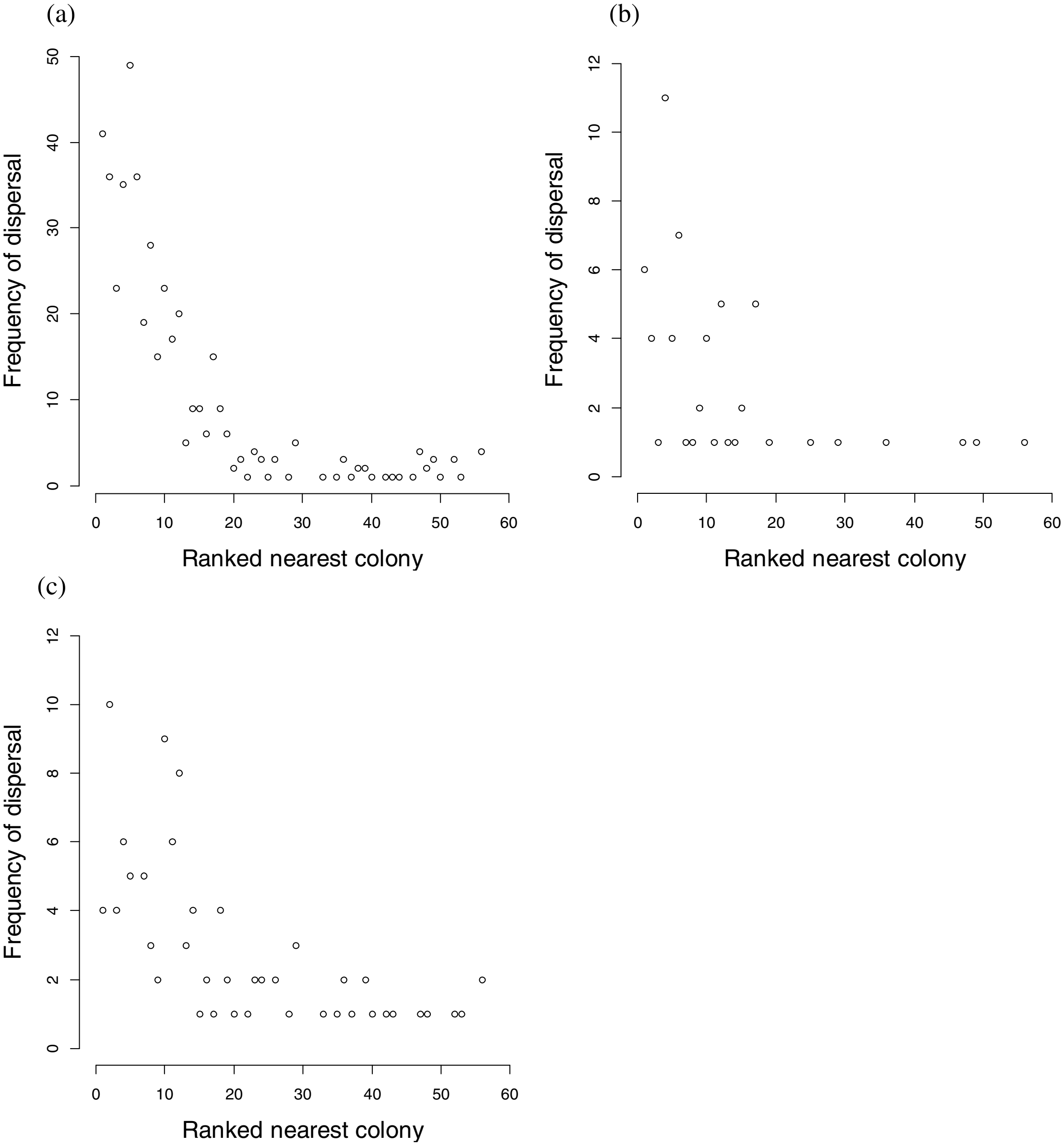
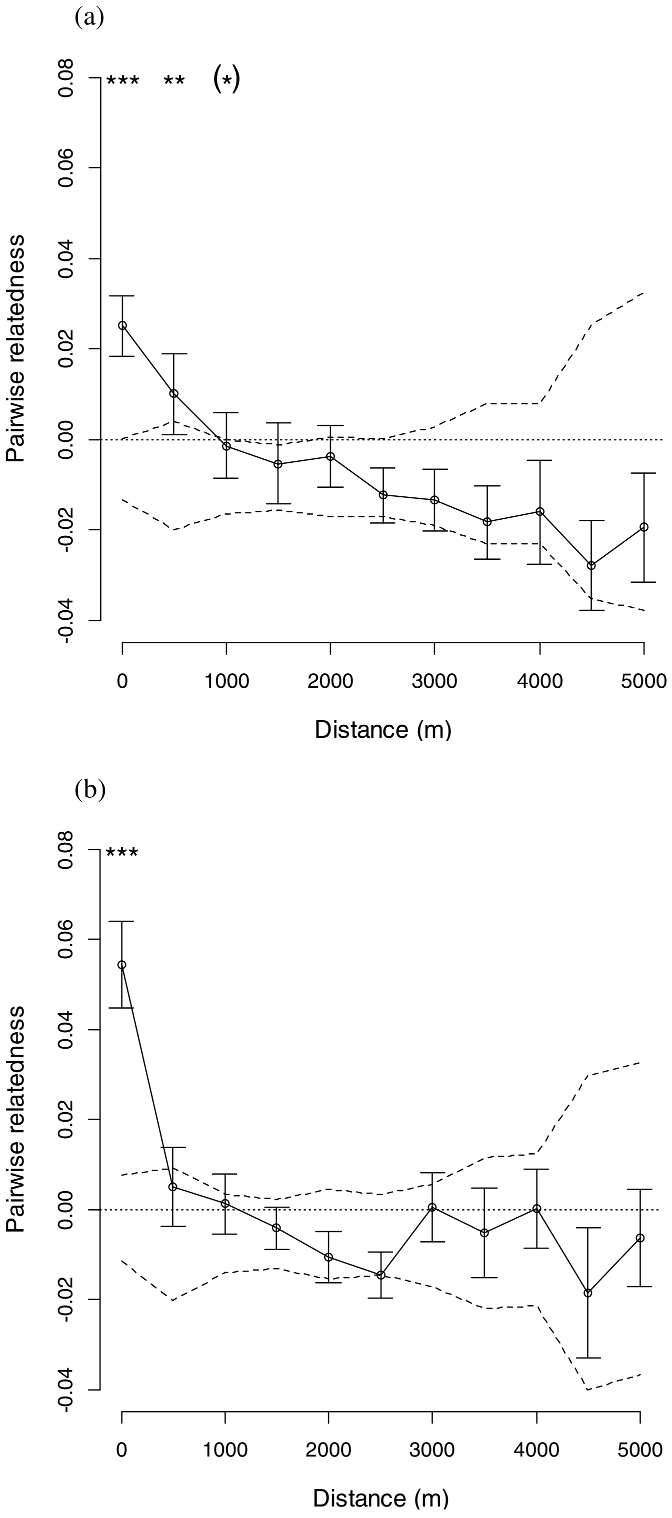


Fig. 4 The frequency of dispersal to the 1st, 2nd, … xth nearest colony to the colony of origin. (a) All known dispersers, (b) male dispersers, and (c) female dispersers.


(a)
*** ** (*)
Pairwise relatedness
0.08
0.06
0.04
0.02
0.00
-0.02
-0.04
0
1000
2000
3000
4000
5000
Distance (m)
(b)
***
Pairwise relatedness
0.08
0.06
0.04
0.02
0.00
-0.02
-0.04
0
1000
2000
3000
4000
5000
Distance (m)

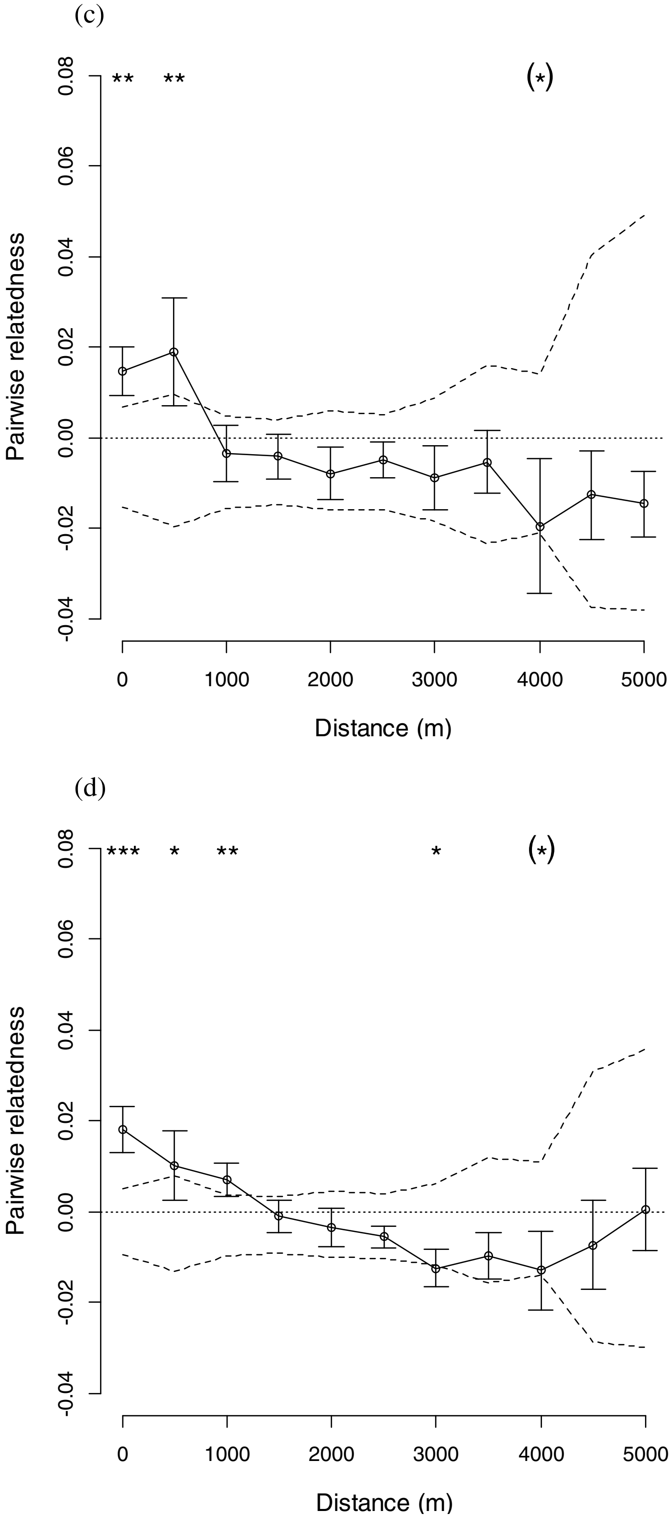


Fig. 5 Pairwise relatedness ± SE over 11 classes of maximum distance between colonies. (a) Among all individuals, (b) within males, (c) within females, and (d) between males and females. Distance class 0 represents within-colony relatedness. Dashed lines indicate the 95% confidence intervals, and the dotted lines $r = 0$. $^{(*)}P < 0.10$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$