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Running title: Female-biased dispersal in black-throated tit

Sex-biased dispersal patterns of a social passerine: complementary approaches and evidence for a role of spatial scale

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ABSTRACT

Animal dispersal patterns have important implications for many biological processes, but measuring dispersal is challenging and often requires the use of complementary approaches. In this study, we investigated local-scale sex-biased dispersal pattern in a social bird, the black-throated tit (*Aegithalos concinnus*), in central China. Spatial genetic autocorrelation analyses suggested that significant fine scale genetic structure existed in males but not in females. Mark-recapture analyses of individuals ringed also showed that female offspring were more dispersive than male offspring, supporting genetic evidence of local female-biased dispersal. These results were contrary to a previous finding of male-biased long-distance dispersal in this species that was based on analyses of gene flow across the species' range in China. This implies that the species may potentially have a scale-dependent dispersal strategy, with females frequently dispersing further than males at the local level, but a proportion of males occasionally disperse long distances, contributing more to gene flow at a larger geographic scale. Long-distance dispersal by male black-throated tits may be induced by competition for resources or by unfavourable environmental conditions, warranting further investigation, but our findings increase evidence that geographic scale is an important factor to be considered when investigating animal dispersal patterns.

KEYWORDS: *Aegithalos concinnus* – black-throated tit – long-distance dispersal – mark-recapture – microsatellite – scale-specific dispersal – sex-biased dispersal – short-distance dispersal.

INTRODUCTION

Animal dispersal patterns are a major focus of research in evolutionary biology and ecology (Dieckmann *et al.*, 1999; Clobert *et al.*, 2001; Clobert *et al.*, 2012; Jønsson *et al.*, 2016) because they are essential to understand diverse processes, including population dynamics (Paradis *et al.*, 1999; Lowe, 2003), gene flow (Slatkin, 1985; Bohonak, 1999) and speciation (Belliure *et al.*, 2000; Bilton *et al.*, 2002). Dispersal strategies will depend on selective pressures such as availability of resources and mates, and the risk of inbreeding and competition with kin (Pusey, 1987; Dieckmann et al., 1999; Gandon, 1999; Perrin & Mazalov, 2000; Szulkin & Sheldon, 2008). When these selective pressures generate differing trade-offs between males and females of a species, sex-biased dispersal is expected to evolve (Lawson Handley & Perrin, 2007). For example, in many species with polygynous mating systems (e.g. most mammals) where female competition for resources and male competition for mates are usually intense, male-biased dispersal is observed (Greenwood, 1980; Dobson, 1982; Lawson Handley & Perrin, 2007). On the other hand, in many taxa exhibiting monogamous systems (e.g. most passerines) where males must defend a territory in order to pair up with a female and breed, males are expected to be more philopatric (Greenwood, 1980; Greenwood & Harvey, 1982; Clarke *et al.*, 1997).

A better understanding of the selection pressures driving sex differences in dispersal within and between species depends on accurate documentation of dispersal patterns, despite the inherent difficulties of doing so. Traditional methods, such as direct observation, capture-mark-recapture and radio-tracking techniques usually only allow researchers to work in finite areas, and fail to detect long-distance or infrequent dispersal, thus underestimating gene flow (Slatkin, 1985; Koenig et al., 1996; Prugnolle & De Meeûs, 2002). Genetic techniques, on the other hand, require less intensive field work and can effectively measure the extent of gene flow (Prugnolle & De Meeûs, 2002; Broquet & Petit, 2009; Woltmann *et al.*, 2012; van Dijk *et al.*, 2015; Lagerholm *et al.*, 2017). Genetic results may be consistent with those obtained by observational methods (Temple et al. 2006; Graham et al. 2017), but they sometimes reveal patterns that differ from those found through observation (Baker *et al.*, 2001; Li & Merilä, 2010; Blackmore *et al.*, 2011). Moreover, direct observations are more likely to reveal proximate causes of dispersal than genetic methods (Harris *et al.*, 2009). Therefore, it has been argued that these complementary approaches should be integrated to overcome potential biases of a single method (Nathan, 2001; Nathan et al., 2003; Cayuela et al., 2018).

A critical distinction between genetic and observational approaches is the spatial scale at which dispersal can be detected (Koenig *et al.*, 1996; Dieckmann et al., 1999; Nathan, 2001; Bowler & Benton 2005), and a growing number of studies have revealed an unexpected role of geographic scale in dispersal patterns. For example, Fontanillas *et al.* (2004) found that dispersal in greater white-toothed shrews (*Crocidura russula*) was female-biased at the local scale (breeding-group level), but not at the larger scale (among local populations). Similarly, Gauffre *et al.* (2009) reported that local-scale dispersal was strongly male-biased in the common vole (*Microtus arvalis*), while long-distance dispersal was more balanced between sexes.

An effect of spatial scale on sex-biased dispersal patterns in birds has also been documented. In Siberian jay (*Perisoreus infaustus*), where male philopatry is observed at a fine spatial scale, Li and Merilä (2010) found strong genetic evidence for male dispersal across populations. In contrast, Cabanis's greenbuls (*Phyllastrephus cabanisi*) exhibit female-biased dispersal at small spatial scales, but not at the landscape level (Vangestel *et al.* (2013). These cases suggest that patterns and underlying mechanisms of sex-biased dispersal are not fully understood. They also demonstrate that combining direct observations and molecular methods may be necessary to overcome scale-dependent biases in dispersal studies and to reliably estimate gene flow resulting from long-distance dispersal.

In this study, we used both observational and genetic data to investigate local dispersal of a small passerine bird, the black-throated tit (*Aegithalos concinnus*). We also use our data to compare local dispersal with long-distance dispersal patterns reported in the literature (see below). The black-throated tit is distributed in South and East Asia, with most of its range occurring in Central and Southern China (Harrap, 2008; Zheng, 2017). Using samples collected across its distribution within China, Dai *et al.* (2013) found evidence for male-mediated gene flow and suggested long-distance male-biased dispersal to occur in this species. However, this male-biased dispersal pattern is contrary to that of the congeneric long-tailed tit (*A. caudatus*), which shows female-dispersal, at least at the local scale (Sharp *et al.*, 2008a; Sharp *et al.*, 2008b; Leedale *et al.*, 2018). Furthermore, the black-throated tit is a facultative cooperative breeder in which males typically provide help at a small proportion of nests of nestling stage (Li *et al.*, 2012), a behaviour that is commonly associated with male philopatry in other bird species (Cockburn *et al.*, 2017). Given this evidence, it is reasonable to expect a female-biased local dispersal pattern in black-throated tits. These apparently contradictory findings, coupled with the fact that male-biased dispersal is relatively rare in birds (Greenwood, 1980; Clarke et al., 1997), suggest that further evaluation of the dispersal pattern of black-throated tits at a finer spatial scale would be worthwhile.

METHODS

Study population

The black-throated tit (family Aegithalidae) is a small (5–8 g) passerine in which the sexes are monochromatic, albeit males are slightly larger than females (Li et al. 2010). The black-throated tit population that we studied is located in the Dongzhai National Nature Reserve of Henan province in central China (Fig. 1). The data used for this study were collected in the Baiyun Protection Station (ca. 4 km^2) and adjacent areas. The study area is mostly mountainous with coniferous and broadleaf trees and shrubs (Li et al., 2012). Black-throated tits are resident at our study site with a breeding season that usually lasts from late January/early February to late May/early June; they typically have one brood annually (Li et al., 2012). Clutch size is 5–8 eggs and only about one-third of nests are successful in producing fledglings (Li et al., 2012). Black-throated tits are socially monogamous with a low rate of extra-pair paternity (5.7% of nestlings, Li *et al.*, 2014). Offspring are sexually mature and start to breed as yearlings. Cooperative breeding behaviour exists in this population, but helpers, which are mostly males and occur at about 20% of nests during the nestling period, do not usually appear before that stage of breeding (Li et al., 2012). The origin of helpers is poorly understood, although at least some helpers are failed breeders that redirect their care to help other broods (J. Li, unpubl. data), as reported in the congeneric long-tailed tit (MacColl & Hatchwell, 2002).

During the breeding seasons of 2007–2014, black-throated tit nests were located by following adult birds, or by checking potential nesting sites along valleys in the study area (Fig. 1). Most nests were checked regularly every 1–3 days. Unmarked adults and fledglings were mist-netted, while nestlings were caught at the nest. All birds were banded with unique combination of colour rings and a numbered metal ring, and a small (20–50 μL) blood sample was taken by brachial venipuncture for genetic analyses.

Genetic analyses for sex-biased dispersal

Total genomic DNA was extracted using a TIANamp Genomic DNA Kit (Tiangen, Beijing, China). The sex of each black-throated tit was determined with primers sex1'/sex2 (Wang *et al.*, 2010). Accuracy of the primers was validated in the field by examining for brood patches of adult birds (only female black-throated tits have brood patches during the breeding season). Eight microsatellite markers: Ase18, Ase37, Man13, Pca3, PmaD22 (Simeoni *et al.*, 2007), TG01040, TG04041 and TG01147 (Dawson *et al.*, 2010), which were previously used in a study of extra-pair paternity in black-throated tits (Li et al., 2014), were employed to examine sex-specific genetic structure. A total of 79 female and 105 male adult black-throated tits caught during the breeding seasons in 2007–2012 were genotyped. The microsatellite loci were amplified through polymerase chain reactions (PCRs) in three independent multiplex reactions for samples collected in 2007-2011 and, following a redesign of multiplexes, in two multiplex reactions for samples collected in 2012. The PCR conditions were same for all of the multiplex reactions (see Li et al., 2014 for details). Microsatellite genotypes were scored using software GeneMapper version 4.0 (ABI), and to ensure the quality of genotyping, all electropherograms were visually checked at least twice. Hardy–Weinberg equilibrium and linkage disequilibrium of the loci were examined with Genepop version 4.2 (Rousset, 2008). The loci showed no sign of deviation from Hardy–Weinberg equilibrium or of linkage disequilibrium after Bonferroni correction for multiple tests (Rice, 1989) (see Table S1 in supplementary materials for details of marker characteristics). G-tests for overall genic differentiation ($\chi^2 = 19.82$, df = 16, P = 0.228) and genotypic differentiation ($\chi^2 = 19.85$, df = 16, P = 0.227) did not provide evidence of temporal variation in genetic structure across years, so the samples were pooled for the following analyses.

The fine-scale dispersal patterns of black-throated tits were analysed by using spatial genetic autocorrelations (Smouse & Peakall, 1999; Peakall et al., 2003; Smouse et al., 2008). This approach is effective in detecting fine-scale genetic structure and sex-biased dispersal (Banks & Peakall, 2012). When there is a sexual difference in dispersal patterns, the philopatric sex will have greater proximity of relatives and therefore will show positive genetic structure at short-distance classes while the dispersive sex will not (Banks & Peakall, 2012). We conducted genetic spatial autocorrelation analyses in GenAlEx 6.5 (Smouse & Peakall, 2012). However, we previously calculated pairwise relatedness in ML-RELATE (Kalinowski *et al.*, 2006) as the genetic distance between individuals, even though GenAlEx has an internal function to calculate pairwise genetic distance. This was because the calculation of genetic distance in GenAlEx is not programmed to deal with missing genotypes (Smouse & Peakall, 1999), whereas ML-RELATE estimates robust maximum likelihood values of relatedness even in the presence of missing data (Milligan, 2003; Kalinowski et al., 2006). When estimating pairwise relatedness for individuals of each sex, reference allelic frequencies were calculated over the entire dataset. The geographic distance interval for autocorrelations analysis was set as 300 m because the median natal dispersal distances for female and male black-throated tit offspring were 630 m and 280 m, respectively (see Results). Based on the genetic and geographic matrices, an autocorrelation coefficient, r, was calculated. For each distance class, tests of significant genetic structure were performed by comparing the observed r with values obtained from 999 permutations and 999 bootstraps (Peakall et al., 2003). Significant positive genetic structure were inferred by the observed r being greater than the upper limit of the permuted 95% confidence intervals of the null hypotheses of no spatial structure, or by no overlap of the bootstrapped 95% confidence error bars with zero. In addition, overall correlogram significance was examined by the heterogeneity test. Also, to test for significance of sexual differences in genetic structure at each distance class, a 'T2' statistic was calculated using the 'multiple population' option in GenAlEx (i.e. a squared paired-sample t-test for heterogeneity between populations; see Smouse et al., 2008; Banks & Peakall, 2012), with females and males of each distance class treated as different populations.

Additionally, a Mantel test (Mantel, 1967), which compares the matrices of genetic distance (pairwise relatedness) and geographical distance, was conducted to verify the result obtained by the above analyses, despite its lower power (Peakall et al., 2003; Legendre & Fortin, 2010; Legendre *et al.*, 2015). The Mantel test was performed with 999 permutations for breeding females and males, respectively, in GenAlEx 6.5 (Smouse & Peakall, 2012). Again, different patterns of relationship between genetic and geographic distance may be expected between sexes if they differ in dispersal strategy, and the more philopatric sex would exhibit a stronger relationship between genetic and geographic distance (Woxvold *et al.*, 2006).

Analysing sex-biased dispersal based on field observation

Based on recapture and re-sighting records, we estimated the linear distances of movements between breeding seasons by adults (i.e. breeding dispersal) and movements between natal site and first breeding site by offspring (i.e. natal dispersal). For individuals whose exact nest sites were unknown, their capture/re-sighting location was defined as their breeding site. This is reasonable given that (i) we have never observed breeders > 250 m away from their nest during breeding (J. Li, unpubl. data) and (ii) the average breeding season home range size in the closely related long-tailed tit, average breeding season home range size is ca. 2.0 ha (n = 20 pairs; F. Morland, personal communication). It should be noted that although population density may affect an individual's dispersal distance (Matthysen, 2005) and thus combining data across years could be problematic whenever there are yearly variations in breeding density, we are not aware of any change of population density during the study. We compared differences in dispersal distances between the two sexes and between natal and breeding dispersal using Mann–Whitney U tests, as not all of the distances conformed to normality.

For all statistical analyses, two-tailed P-values are reported and significance is declared when $P < 0.05$, unless otherwise stated.

RESULTS

Genetic evidence of sex-biased dispersal

For the 79 female and 105 male adult black-throated tits, spatial genetic autocorrelation analyses revealed significant positive genetic structure for male black-throated tits within a distance of 300 m (Fig. 2A), but not for females (Fig. 2B). Although within this distance the autocorrelation coefficient of males was not significantly different from that of females (male $r = 0.019$, female $r = 0.012$, $T2 = 0.27$, $P = 0.636$), the stronger and significant positive genetic structure of males suggest that male black-throated tits are more philopatric while female black-throated tits are more dispersive. Moreover, following the recommended α level (0.01) for significance of heterogeneity tests (Banks & Peakall, 2012), the correlogram is overall significant for males (Omega = 52.9, $P = 0.005$) but not for females (Omega = 40.3, $P = 0.045$).

Similarly, Mantel tests revealed a significant negative correlation between pairwise relatedness and geographical distance among breeding males (Mantel test, correlation = -0.056, P = 0.002), but not among females (Mantel test, correlation = -0.002, P = 0.455). These results corroborate the results of spatial genetic autocorrelation analyses.

Sex-biased dispersal from field observation

Between-year records of breeding sites were available for 11 adult females and 19 adult males. Among them, two females and three males each had breeding records for three consecutive years, resulting in a total of 35 breeding dispersal records (Fig. 3A). Breeding dispersal distances did not differ significantly between females and males, either analyzed with each bird's first-recorded breeding dispersal only (N_{female} = 11, N_{male} = 19; Mann–Whitney U = 77.0, P = 0.236; female vs. male median distance, 280 m vs. 200 m; Fig. 3B) or analyzed with all breeding dispersal records (N_{female} = 13, N_{male} = 22; Mann–Whitney U = 94.0, P = 0.094; female vs. male median distance, 280 m vs. 130 m; Fig. 3B).

A total of 294 individually banded nestlings fledged successfully from 52 nests, producing an equal sex ratio of 1.03:1 (male:female; Chi-Square test, χ^2 = 0.1, df = 1, P = 0.816). Additionally, 66 birds were banded as fledglings, including 18 males, 24 females and 24 of unknown sex. From the total of 336 sexed fledglings, more males (15/166, 9.0%) than females (8/170, 4.7%) recruited into the local breeding population, although their recruitment rates were not significantly different (Chi-square test, χ^2 = 2.4, df = 1, P = 0.136). Natal dispersal distances (i.e. distance from natal site to first breeding site) were known for seven females and 13 males (Fig. 4A), among which two female offspring and three pairs of male offspring were each from a same brood. Females dispersed significantly further than males either if all individuals were included in the analyses (median distance: 630 m vs. 280 m; Mann–Whitney U = 12.0, P = 0.008; Fig. 4B) or if just one individual was randomly selected for broods with two recruits (median distance: 605 m vs. 305 m; Mann–Whitney U = 10.0, P = 0.030; Fig. 4B). The natal dispersal distances of females (using one offspring from each brood) were greater than breeding dispersal distances of both adult females (using first breeding dispersal records; Mann–Whitney U = 6.5, P = 0.008) and males (using first breeding dispersal records; Mann–Whitney U = 12.0, P = 0.004). In contrast, the natal dispersal distance of young males (one offspring per brood) did not differ significantly from the breeding dispersal distances of either adult females (using first breeding dispersal records; Mann–Whitney U = 53.5, P = 0.916) or males (using first breeding dispersal records; Mann–Whitney U = 81.5, P = 0.535).

One female and two male fledglings were recorded as breeders for the first time as two-year olds and thus were not included in the above analyses because the distances from natal site to first breeding site were unknown. For these birds, the female was found 960 m and the males 100 m and 4800 m away from their natal sites (Fig. 4A). When including these birds in the comparison of natal dispersal distances, females still dispersed significantly further than males either if all individuals of a brood were included in the analyses (median distance: 795 m vs. 280 m; Mann–Whitney U = 20.0, P = 0.010) or if just one individual was randomly selected from each brood with two recruits (median distance: 630 m vs. 305 m; Mann–Whitney U = 17.0, P = 0.035).

DISCUSSION

It has been suggested that neither observational nor genetic data alone are sufficient for studying sex-biased dispersal in animals (Lawson Handley & Perrin, 2007; Harris et al., 2009; Rollins *et al.*, 2012). At the scale of our study, the two approaches produced consistent results. Specifically, the results from mark-recapture, spatial genetic autocorrelation analysis and the less powerful Mantel test (Peakall et al., 2003; Legendre & Fortin, 2010; Legendre et al., 2015), were all consistent with the expected pattern that at a local scale, female black-throated tits dispersed further than males. Moreover, since our analysis of breeding dispersal distances of adults showed that there was no sex bias, and also that female adults were less dispersive than female fledglings, the current data support the idea that female natal dispersal is one of the drivers of the genetic structure in our study population. It should also be noted that the sex-specific genetic structure could also result from sex differences in mortality, a possibility that should be examined in future studies.

Black-throated tits are facultative cooperative breeders in which some nests are assisted by male helpers (Li et al., 2012). The female-biased local dispersal pattern of black-throated tits reported here is thus not only consistent with that of the congeneric long-tailed tit (Russell, 2001; Sharp et al., 2008a; Sharp et al., 2008b; Leedale et al., 2018), but also with what has been described in most other cooperatively breeding bird species, where helping is associated with male philopatry (Cockburn et al., 2017). However, our finding contrasts with the results of Dai *et al.* (2013), who found weak geographical structure amongst nuclear genetic markers, and a significant pattern of isolation by distance for a maternally inherited genetic marker (mitochondrial DNA sequences) using samples collected across the range of black-throated tits in China, leading them to conclude that dispersal in this species is male-biased. One possible reason for the inconsistent patterns obtained from nuclear and mitochondrial markers by Dai *et al*. (2013) could be due to some intrinsic differences between markers such as mutation rates and effective population sizes (Prugnolle & De Meeûs, 2002), but they have provided some evidence supporting ongoing male-biased gene flow among populations (see Dai et al., 2013 for details).

While results from Dai et al. (2013) would benefit from further investigation, an alternative explanation to these contrasting findings could be a scale-dependent sex-biased dispersal pattern, as observed in other species (Fontanillas et al., 2004; Gauffre et al., 2009; Li & Merilä, 2010; Yannic *et al.*, 2012; Vangestel et al., 2013). According to this explanation, black-throated tits may have the following dispersal strategies: at a local scale, female black-throated tits routinely disperse further than males who tend to be philopatric, whereas at a larger geographic scale, a proportion of males (but not females) disperse over longer distances (as evidenced by the two males in Fig. 3).

Long-distance dispersal events in animals have been increasingly reported (e.g. Blackmore et al., 2011; Jerina *et al.*, 2014; de Groot *et al.*, 2016; Hawley *et al.*, 2016; Cross *et al.*, 2017). Assuming that results from Dai et al. (2013) are robust, these results raise the question of why some male black-throated tits engage in long-distance dispersal. It has been hypothesized that long- and short-distance dispersal events are driven by different mechanisms (Ronce et al., 2001; Lawson Handley & Perrin, 2007; Ronce, 2007). Local dispersal may be sufficient to reduce the risks of inbreeding and kin competition, but in situations where vacant habitat and/or potential mates are limiting, an individual may have to travel farther to find a territory or mate (Perrin & Goudet, 2001; Lawson Handley & Perrin, 2007). In our study population, black-throated tits live in a broad range of habitats such as different types of forests and shrubland, and nest across different vegetation strata, from <0.5m in shrubs to >10m in the forest canopy (Li et al., 2012). This, along with the observations suggesting a lack of territorial behavior in the species, suggests that habitat limitation is not likely to be the reason for long-distance dispersal. On the other hand, male-biased dispersal is usually predicted to occur when local resource competition is less intense than mate competition (Perrin & Mazalov, 2000). This is often true for polygynous/promiscuous species, in which male reproductive success is constrained by access to females and local competition for access to mates drives male dispersal (Perrin & Mazalov, 2000; Yannic et al., 2012). In the polygynous red deer (*Cervus elaphus*), for example, males usually compete for females and male-biased dispersal is the norm, but in Spanish populations that have strong female-biased sex ratios, dispersal is not male-biased (Pérez-González & Carranza, 2009). Black-throated tits are socially monogamous and have a relatively low level of extra-pair paternity (Li et al., 2014) so competition for mates is not as intense as in polygynous or promiscuous species, but we found that in the winters following the banding of the two long-distance male dispersers in 2007 and 2008, the population sex ratios were both significantly male-biased (0.60 and 0.62 males, respectively; Li, 2010). Moreover, males were also overrepresented among samples reported in Dai et al.'s (2013) study, although it is not clear whether that reflected a male-biased sex ratio across populations or was a sampling artifact. Whatever the cause, the possibility that a lack of mating opportunities prompted some males to disperse further away cannot be excluded, and deserves further study.

Other mechanisms inducing long-distance dispersal may include environmental conditions, such as extreme weather. For example, in both black-winged stilt (*Himantopus himantopus*) (Figuerola, 2007) and glossy ibis (*Plegadis falcinellus*) (Santoro *et al.*, 2013) individuals disperse further following dry seasons, whereas in the Svalbard reindeer (*Rangifer tarandus plathyrynchus*) icing may immediately trigger longer dispersal (Stien *et al.*, 2010). During our study, there was heavy snow in January 2008, during which the number of freezing days and minimum temperatures were below the most extreme values recorded for the last 57 years (Gao, 2009; Wang *et al.*, 2009). Even though the two long-distance dispersal events reported here were found during the same year, we do not know whether they were causally related.

Costs such as energy and time investment and predation risks are likely to increase with dispersal distance (reviewed in Bonte *et al.*, 2012), and long-distance dispersal can also reduce the probability of beneficial social interactions with kin. In the cooperatively breeding long-tailed tit, males that disperse longer distances have a lower probability of helping and gain less indirect fitness (Green & Hatchwell, 2018).

If helping in black-throated tits is also a kin-selected behaviour, ~~as that in the congeneric long-tailed tit (Meade & Hatchwell, 2010; Hatchwell *et al.*, 2014),~~ future studies on their behaviour and ecology should investigate the fitness consequences of long-distance dispersal.

Conclusion

We have shown that dispersal of black-throated tits is female-biased at a local scale, which contrasts with the finding of Dai et al. (2013) that indicated male-biased gene flow at a regional scale. Assuming that both studies are representative of a general pattern, they suggest that the two sexes have different dispersal strategies: females regularly disperse a short distance from their natal area, while males have a bimodal dispersal pattern, either being philopatric or occasionally dispersing long distances, contributing to gene flow at a large geographic scale. This dispersal pattern adds to the few cases of birds and mammals exhibiting scale-specific sex-biased dispersal. However, long-distance dispersal is often hard to detect, so we advocate greater consideration of geographic scale using genetic approaches in future studies of dispersal patterns in natural populations.

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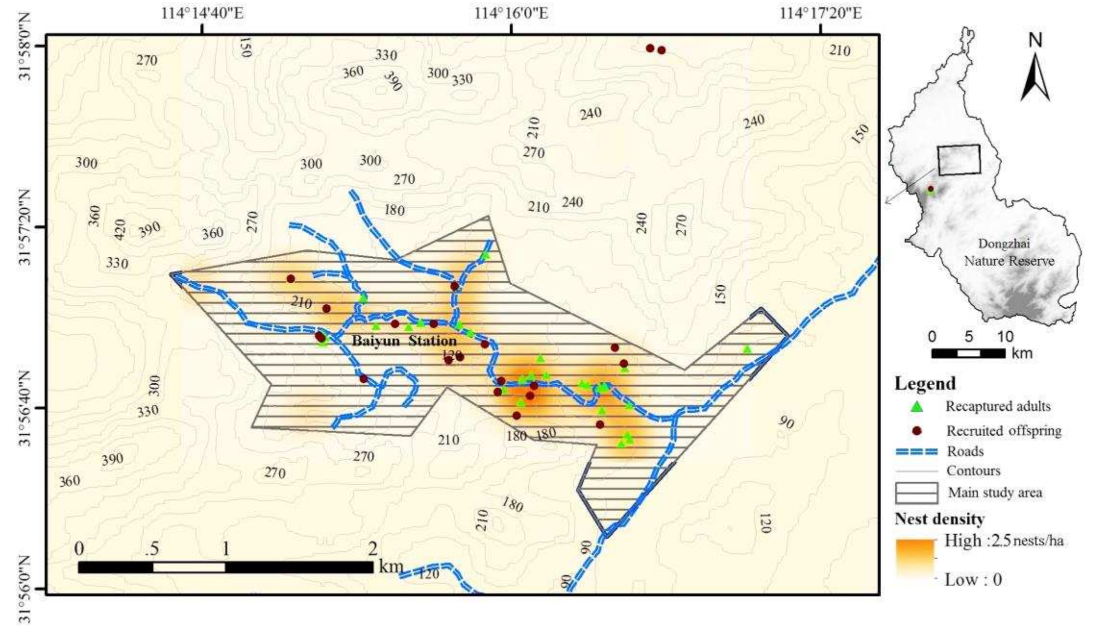

Figure 1. Map of the study area. Nest density reflects the sampling effort across the study area; it was calculated based on the nests found during the study, and does not represent the actual nest density of the population. Note that one adult and three offspring were recaptured further away from the main study area.

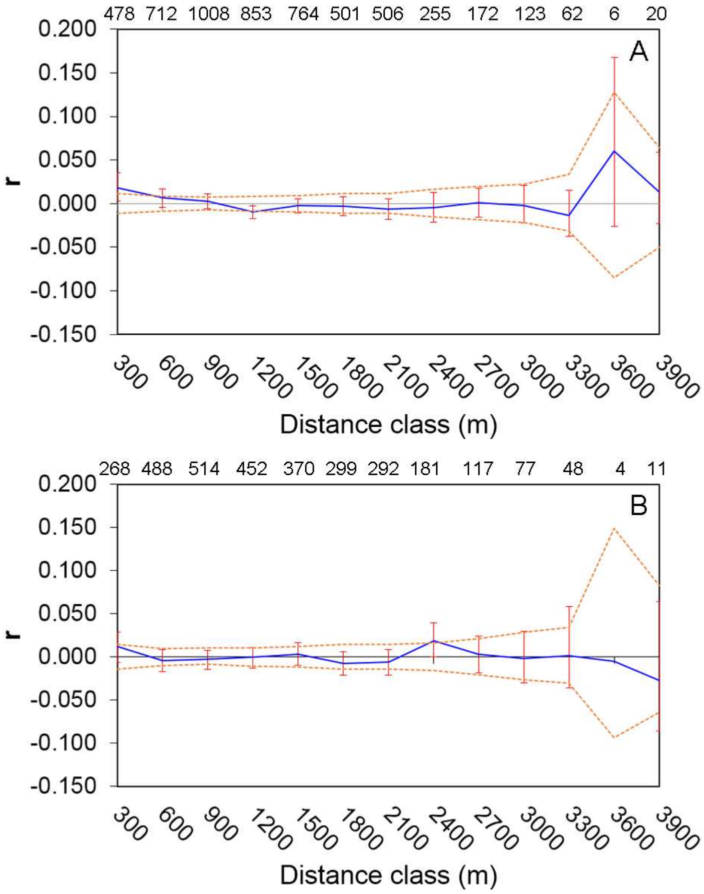

Figure 2. Correlograms showing the results of spatial genetic autocorrelation analyses of 105 male (A) and 79 female (B) black-throated tits. Significant positive genetic structure for each distance class is indicated by the observed r (blue solid line) being greater than the upper limit of the 95% confidence intervals (red dotted lines) of the null hypotheses of no spatial structure based on 999 permutations, and by no overlap of the bootstrapped 95% confidence error bars with zero. The number of comparisons for each distance category is shown above the figure.

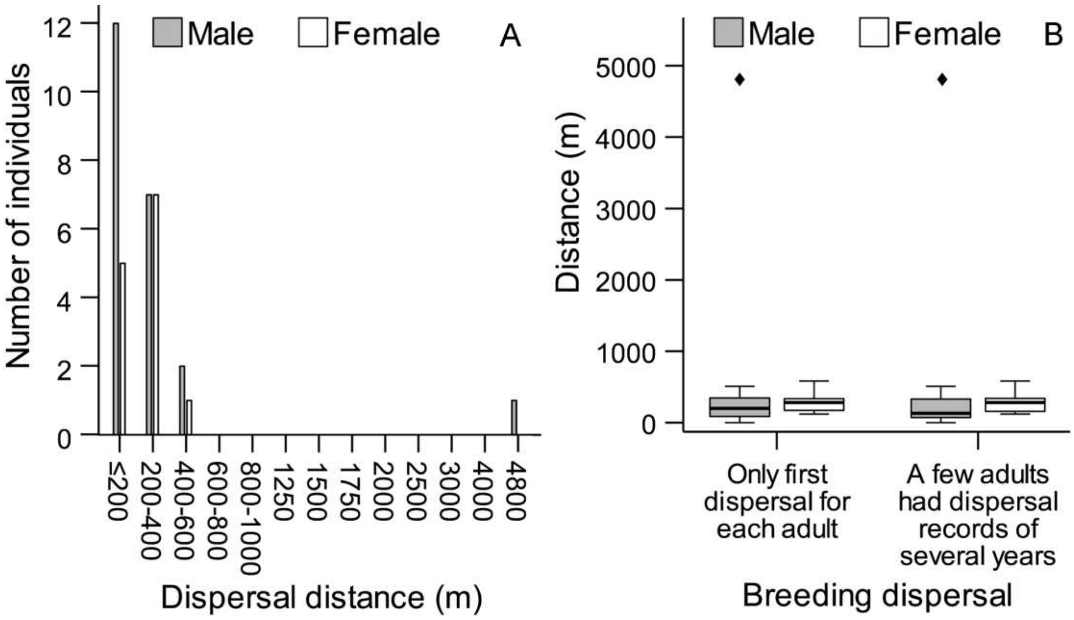

Figure 3. Frequency distribution (A) and box-plots (B) of breeding dispersal distances of adult black-throated tits (n = 35 breeding dispersal events from 30 individuals).

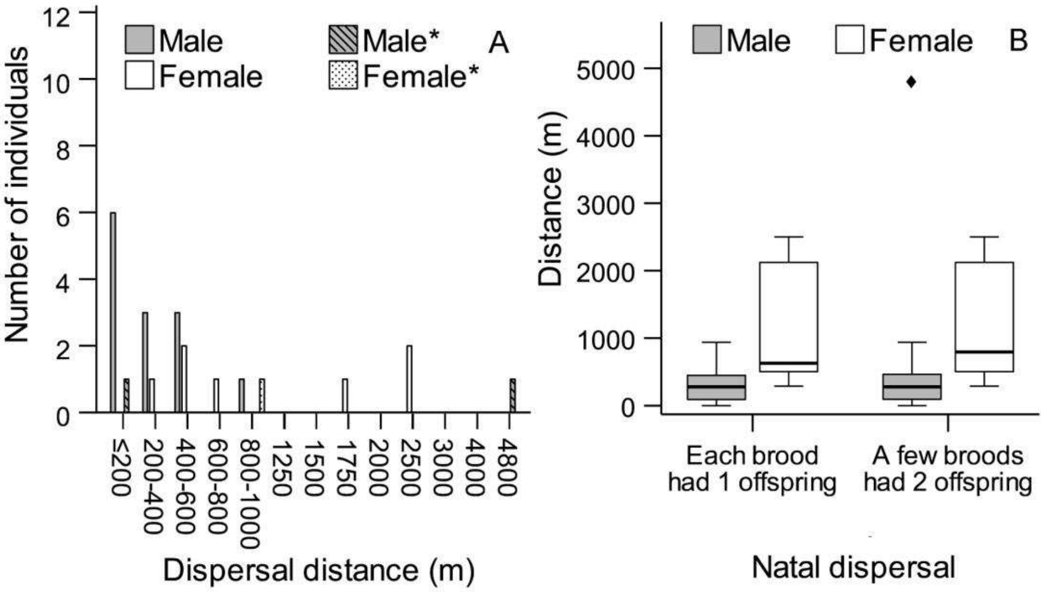

Figure 4. Frequency distribution (A) and box-plots (B) of natal dispersal distances by juvenile black-throated tits. A - includes 20 individuals' natal dispersal events and one female (960 m) and two males' dispersal (100 m and 4800 m) from their natal sites to second breeding sites (indicated by hatched bars and *). B – box-plots as described in Figure 3.