



## Promiscuity, inbreeding and dispersal propensity in great tits

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Mating with relatives leads to inbred offspring, which are likely to experience reduced fitness owing to the expression of deleterious recessive alleles. Constraints in social mate choice do not always allow individuals to avoid pairing with kin. A possible means of inbreeding avoidance is to engage in extrapair copulations with unrelated extrapair individuals. In a population of great tits, *Parus major*, we tested whether broods of related partners were characterized by higher rates of extrapair paternity than neighbouring outbred broods. Contrary to our expectations, broods sired by related partners had about 60% lower rates of extrapair paternity relative to outbred broods. Parental status of female birds categorized as inbreeding, outbreeding locally born or outbreeding immigrant explained 29% of the variance in the proportion of extrapair young in their broods. Outbreeding locally born females and inbreeding females did not differ in rates of extrapair paternity, but had significantly fewer extrapair young than outbreeding immigrant females. Thus, the contrasting differences in the proportion of extrapair young in inbred and outbred great tit broods do not appear to be the consequence of inbreeding per se. Instead, variation in both promiscuity and inbreeding may reflect the operation of broad-scale effects caused by variation in large-scale dispersal behaviour.

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Mating with a close relative can considerably decrease offspring fitness (Lynch & Walsh 1998; Szulkin et al. 2007), and reports of inbreeding depression in natural populations have been documented across a wide range of taxa (Keller & Waller 2002). If inbreeding depression is severe, selection for the evolution of inbreeding avoidance is expected. However, because of possible constraints on social mate choice, such as timing of breeding, availability of nesting sites and/or availability of unpaired individuals, it may not always be possible to avoid pairing with related individuals. One way to avoid the negative effects of pairing with a genetically related mate would be to seek extrapair copulations (EPC), resulting in an elevated proportion of extrapair young (EPY) in the nest, and a reduced rate of inbreeding at the brood level. Consistent with this prediction, several studies have reported increased rates of extrapair paternity (EPP) when mating with relatives. Blomqvist et al. (2002) showed that the prevalence of EPP

increased with increasing genetic similarity between pair members in three species of shorebirds, providing support for the hypothesis that EPC functions as a means of inbreeding avoidance (but see Griffith & Montgomerie 2003 for a critique of some aspects of the study). Similarly, Eimes et al. (2005), Tarvin et al. (2005), Freeman-Gallant et al. (2006), Suter et al. (2007), Brouwer et al. (2011) and Varian-Ramos & Webster (2012) found increased occurrence of EPP with increasing genetic similarity of social mates in Mexican jays, *Aphelocoma wollweberi*, splendid fairy-wrens, *Malurus splendens*, Savannah sparrows, *Passerculus sandwichensis*, reed buntings, *Emberiza schoeniclus*, red-winged fairy-wrens, *Malurus elegans*, and red-backed fairy-wrens, *Malurus melanocephalus*, respectively. At the same time, several other studies (Kempnaers et al. 1996; Foerster et al. 2006; Stewart et al. 2006; Edly-Wright et al. 2007; Rubenstein 2007) failed to find such a directional relationship between EPP and social mate relatedness.

Although much debate focuses on identifying factors driving the evolution of promiscuity (Arnqvist & Kirkpatrick 2005; Griffith 2007; Cornwallis et al. 2010), the original idea that female promiscuity may principally evolve as a genetic corollary of male promiscuity (Halliday & Arnold 1987; Arnold & Halliday 1988; Forstmeier et al. 2011) or other correlated traits has until recently received little attention (but see Forstmeier et al. 2011). It is not impossible that propensity for promiscuity, instead of being the direct target of selection, is in fact a corollary of dispersal

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behaviour and/or exploratory behaviour (EB). Recent work on one great tit, *Parus major*, population from Wytham Woods (Oxfordshire, U.K.) has established specific links between propensity for dispersal and EB (Quinn et al. 2011), as well as EB and promiscuity (Patrick et al. 2012). Quinn et al. (2011) found a clear effect of natal origin (immigrant versus locally born) on EB, whereby EB was 11% higher among immigrants than locally born birds. In contrast, natal dispersal distance of birds born inside the study site did not influence EB, suggesting that an association between dispersal and EB existed at a between-population scale, but not within the main study site. In the same great tit population, Patrick et al. (2012) reported negative correlations between a male's EB and the paternity lost in its social nest. Moreover, other bird studies have reported a positive association between female EB and promiscuity (Duckworth 2006; Van Oers et al. 2008). Propensity for large-scale dispersal is thus a trait that is not only influencing the genetic structure of populations, but also covarying with behavioural traits such as EB (Quinn et al. 2011), which in turn has been found to covary with promiscuity (Duckworth 2006; Van Oers et al. 2008; Patrick et al. 2012). At the same time, natal dispersal distance within the study site has been shown to reduce the likelihood of inbreeding (Szulkin & Sheldon 2008a), which all in all reflects nonrandom covariation between those behavioural traits.

Given no clear understanding of the selective pressures driving promiscuity patterns in an inbreeding avoidance context, it is worth noting that dispersal is never introduced as a possible factor mediating the covariance between social-pair relatedness and promiscuity at the brood level. In the context of large fitness costs of inbreeding depression reported in the population (Szulkin & Sheldon 2007; Szulkin et al. 2007), we asked whether male and female great tits paired with relatives avoid inbreeding by increasing their proportion of EPY in the brood. We further tested whether the relationship between promiscuity and inbreeding can be explained by observed parental propensity to disperse at a between- or within-population scale; in this paper we discuss this in the light of evidence on promiscuity, dispersal and inbreeding accumulated in the population.

## METHODS

### Field Work

The nestbox population of great tits from Wytham Woods (also referred to as 'Wytham'), Oxfordshire, U.K. (1°20'W 51°46'N), breeds in 1021 nestboxes distributed across 385 ha of mostly deciduous forest at variable densities. It has been monitored continuously since 1947, and the number of great tit nestboxes, as well as the standard fieldwork protocol, has remained constant since 1964. More details on population characteristics can be found in Szulkin et al. (2007). All nestboxes were checked at regular intervals throughout the breeding period to establish hatch date and clutch size; parents were caught (for identification purposes) and ringed (if caught for the first time) 8–13 days after their offspring hatched, and nestlings were ringed on day 15 after hatching (hatching = day 1). We define 'locals' as birds born in Wytham Woods and breeding in the same location. 'Immigrants' are birds born outside the study area, and recruited into the Wytham breeding population thereafter, which usually occurs in the autumn/winter preceding their first breeding season. While the study site is isolated from other woodland by surrounding agricultural and urban landscapes, some great tits are undoubtedly breeding around Wytham in gardens, hedgerows and small woodlots. However, it is estimated that they constitute only a small fraction (6%) of all immigrant birds coming into Wytham to breed

(Verhulst et al. 1997). Immigrant birds are easily identified, as all Wytham-born offspring are ringed before fledging (as described above); individuals caught as adults without a ring are therefore considered immigrants to the population. The majority of immigrants breeding in Wytham are expected to have dispersed >2 km (Verhulst et al. 1997), which is a noticeable distance given that the median natal dispersal distance (i.e. distance between place of birth and place of first reproduction) within Wytham is 528 m for males and 788 m for females, respectively (Szulkin & Sheldon 2008a). Movement between successive breeding sites (breeding dispersal) is limited as the majority of birds reoccupy their previous territory and range between a median distance of 50 and 143 m (Harvey et al. 1979).

Birds were caught, ringed and released unharmed under British Trust for Ornithology ringing licences. Blood samples of young offspring and adults were collected (in the nest or at the time of catching, respectively) under U.K. Home Office Project Licence PPL no. 30/2409.

### Sampling Design

A key aim of this study was to test for differences in the proportion of EPY among inbreeding and outbreeding great tit pairs, siring offspring with  $f \geq 0.03125$  and  $f = 0$ , respectively. We further used the concept of 'parental status' to describe one of the following three situations: (1) inbreeding: mating with a relative and siring offspring with  $f \geq 0.03125$ ; (2) outbreeding local: born in Wytham Woods, and mating with an unrelated partner in Wytham Woods, siring offspring with  $f = 0$ ; (3) outbreeding immigrant: born outside of Wytham Woods, and mating with an unrelated partner in Wytham Woods, siring offspring with  $f = 0$ .

To identify inbred broods while still in the field, a social pedigree was built using all great tit breeding events occurring in Wytham and its vicinity from 1990 onwards. During the breeding seasons of 2005–2007 and 2009, we ran a pedigree analysis on alternate days throughout the season, using the identities of parents that had been trapped in the previous days to identify broods sired by relatives (siring offspring with an inbreeding coefficient  $f$  between 0.03125 and 0.25).

Rates of EPP are known to be affected by breeding density and synchrony (Griffith et al. 2002; Westneat & Stewart 2003). Wytham Woods is a heterogeneous habitat in terms of nestbox and breeding density (Wilkin et al. 2006), food availability, soil composition and altitude (Savill et al. 2010). Breeding sites are therefore of variable quality, and hatching asynchrony has been shown to be altitude dependent in this population (Wilkin et al. 2006). In consequence, it is possible that differences in extrapair mating strategies across the site may arise. To reduce spatial and temporal variables that could confound estimates of rates of EPP in inbreeding and outbreeding birds from our population, we matched focal inbred broods with outbred broods located in close spatial and temporal proximity. Thus, for each identified focal inbred brood with an inbreeding coefficient ranging from  $f = 0.03125$  to  $f = 0.25$  ( $N = 10$ ), we also blood-sampled two to five neighbouring broods whose parents were found to be unrelated to each other ( $N = 30$ ). Restrictions for outbred broods to be included as neighbours in the study were (1) to be as closely located to a focal inbred brood as possible, and (2) to hatch within 7 days of a focal inbred brood hatching date. This resulted in an average distance of 193 m between focal and neighbour broods, which is ca. eight times lower than the average distance between nestboxes in Wytham (1495 m, Szulkin et al. 2009), and a mean difference in hatching dates between inbred and outbred nests of 1.2 days ( $SD = 2.4$ ; see also the Results). None of the breeding parents bred more than once in the data set.

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