Animal Behaviour 106 (2015) 157–169

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Spatiotemporal and genetic contingency of extrapair behaviour in a songbird

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ARTICLE INFO

Article history:
Received 31 March 2015
Initial acceptance 28 April 2015
Final acceptance 11 May 2015
Available online 24 June 2015
MS. number: 15-00264

Keywords:
breeding synchrony
extrapair mating
genetic polygamy
'good genes'
Parus major

Multiple mating to obtain genetic benefits has been championed as the most likely cause of the evolution of polygamy. However, this assumption has been put into question by an increasing number of recent studies, most of which highlight the importance of considering ecological constraints to comprehend variation in extrapair (EP) behaviour. Here, we studied patterns of extrapair paternity (EPP) in the great tit, *Parus major*, using data from 11 nestbox plots that differed in population size and breeding conditions. Specifically, we analysed EPP rates in relation to socioecological variables that could influence the way individuals encountered one another in space and time, we tested whether adults engaged in EPP with more heterozygous, more compatible or phenotypically superior individuals than their social mates and we analysed whether extrapair offspring (EPO) were phenotypically or genetically superior to within-pair offspring. Our results do not provide support for the genetic benefit hypothesis from either the male or the female perspective. EPO were heavier than their within-pair paternal half-siblings, but there was no significant difference between EPO and their within-pair maternal half-siblings in terms of phenotypic quality. Regarding socioecological factors, we found a negative relationship between breeding synchrony and EPP rates both within and among plots, which suggests that males face a trade-off between mate guarding and obtaining EPP elsewhere. Our results show that most males engaged in EPP after the fertile period of their social female despite having to travel long distances: about half of the detected cases of EPP involved individuals from different woodlands. This study indicates that when and where to engage in EPP seem to be more relevant factors than with whom to do it and highlights the importance of considering spatiotemporal constraints at a landscape scale to achieve a better understanding of variation in EP mating behaviour.

Extrapair paternity (EPP) is a common reproductive strategy in many animal taxa (birds: Griffith, Owens, & Thuman, 2002; reptiles: Uller & Olsson, 2008; mammals: Cohas & Allainé, 2009). However, there is controversy about what prompts 'socially monogamous' individuals, especially females, to be 'unfaithful' (Akçay & Roughgarden, 2007; Forstmeier, Martin, Bolund, Schielzeth, & Kempenaers, 2011). When explaining the motivations of females to engage in extrapair copulations (EPC) several hypotheses have been raised, although during the last two decades a large body of research has focused on those related to the supposed genetic benefits of EPP (reviewed in Jennions & Petrie, 2000; Slayter, Mautz, Backwell, & Jennions, 2012). Genetic benefits are generally ascribed to three categories: (1) 'good genes', (2) genetic compatibility or (3) production of genetically diverse offspring. According to the 'good genes' hypothesis, females may gain additive genetic benefits if extrapair (EP) mates are of higher genetic quality than their social mates (Cohas, Yoccoz, Da Silva, Goossens, & Allainé, 2006; Hasselquist, Bensch, & von Schantz, 1996; Kempenaers et al., 1992). This hypothesis assumes that male characteristics, such as ornamental traits, but most commonly age and body size, are related to either fertilization success or paternity loss (e.g. Balenger, Johnson, & Masters, 2009; Canal, Potti, & Dávila,

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http://dx.doi.org/10.1016/j.anbehav.2015.05.020
0003-3472/

2011; Cleasby & Nakagawa, 2012). Following this reasoning, females should show a congruent response in their perception of 'top-quality' males and their EP mate choice preferences, in such a way that only a few males would monopolize all EPC. The 'genetic compatibility' hypothesis proposes that offspring viability and female fitness increase when females mate with males whose genomes best complement their own (Mays, Albrecht, Liu, & Hill, 2008). Hence, females may seek to engage in EPC with genetically compatible males (either the most dissimilar or with an optimal level of genetic similarity) in order to increase offspring genetic diversity and reduce the probability that deleterious recessive alleles are expressed and/or increase the probability of heterozygosity at genes experiencing some form of balancing selection (e.g. Brown, 1997; Fossøy, Johnsen, & Lifjeld, 2008; Leclaire, Nielsen, Sharp, & Clutton-Brock, 2013; Suter, Keiser, Feignoux, & Meyer, 2007; Varian-Ramos & Webster, 2012; Zeh & Zeh, 2003). Finally, polyandry may also constitute a female strategy to increase the variability of the genetic composition of their progeny and hence cope with environmental uncertainty and reduce the likelihood of disease ('bet-hedging' strategy sensu Yasui, 1998). Fluctuating natural selection may favour 'bet-hedging' strategies because these can increase the geometric mean fitness through reductions in the variance of mean fitness of each generation (Fox & Rauter, 2003; Williams, 1975).

From the male perspective, the benefits derived from mating with multiple females seem to be more obvious: they can increase their number of descendants without the costs of having to rear them (Trivers, 1972; see also Noble, Keogh, & Whiting, 2013; Sousa & Westneat, 2013; Vedder, Komdeur, van der Velde, Schut, & Magrath, 2011). However, accumulating evidence suggests that males can also be 'choosy' under certain circumstances, for instance, when the costs of EPC increase (Edward & Chapman, 2011). Most paternity studies over the last 20 years have focused mainly on the female's perspective and, consequently, the male's role in this process has frequently been neglected. This bias has led to the misconception that females pursue EPC in a large number of species, for which behavioural evidence is weak (Westneat & Stewart, 2003). For this reason, the adoption of a multiplayer interaction scheme can provide a more reliable and comprehensive approach to studying the significance of EPP, particularly in those species in which it is not clear who promotes EP matings. This kind of approach, taking into consideration the perspective of both sexes, has rarely been applied in the context of genetic benefits studies.

In spite of the considerable amount of effort devoted to exploring the possible indirect benefits of EPC (mostly from the females' point of view), there is actually no consensus about its importance as a selective force driving EP mating behaviour (Parker & Birkhead, 2013; Reid, Arcese, Sardell, & Keller, 2011). A meta-analysis reported that both the 'good genes' and 'compatible genes' hypotheses failed to be supported in more than half of the species studied (Akçay & Roughgarden, 2007). This has prompted a resurgence of nonadaptive (Forstmeier, Nakagawa, Griffith, & Kempenaers, 2014) or new adaptive (Akçay & Roughgarden, 2007; Eliassen & Jørgensen, 2014) hypotheses in recent years and an increase in studies focusing on ecological constraints affecting EP matings such as breeding density and synchrony (e.g. Canal, Jovani, & Potti, 2012; Mayer & Passinelli, 2013; Rubenstein, 2007; Taff, Freeman-Gallant, Dunn, & Whittingham, 2013; Wang & Lu, 2014). In this regard, it has been suggested that one critical determinant of the incidence of EPP is the encounter rate, which largely depends on breeding density and the number of available mates in a certain time window (i.e. breeding synchrony). The influence of breeding synchrony is particularly controversial because it can be argued that EP matings should increase with high levels of breeding synchrony (since this allows females to assess multiple potential mates that are simultaneously displaying and thus reduce their search costs; simultaneous display hypothesis: Stewart, Westneat, & Ritchison, 2010; Stutchbury, 1998; Stutchbury & Morton, 1995) or decrease (as most males are engaged in mate-guarding duties resulting in a smaller pool of males available to pursue EPC; mate-guarding hypothesis: van Dongen & Mulder, 2009; Saino, Primmer, Ellegren, & Møller, 1997). At the intraspecific level, this relationship may depend on the different socioecological conditions experienced by individuals between populations and also within the same population. With regard to the former, remarkably few paternity studies consider multiple populations with contrasting socioecological conditions at a landscape scale. The few studies that analysed EPP patterns across populations involved a small number of populations (usually between two and four; Griffith et al., 2002) or populations in very similar ecological conditions (but see García-Navas, Ferrer, et al., 2014; Mayer & Passinelli, 2013 for exceptions). Fragmented landscapes, such as those of the Mediterranean region, are well suited for this kind of study because the size and connectivity of patchy populations have been linked to reduced breeding synchrony within and between populations (Banks, Piggott, Stow, & Taylor, 2007). In addition, certain environmental factors (e.g. conspecific density) may determine the reproductive strategies followed by each sex (for instance, in the case of males, to prioritize mate guarding versus EPC), which are expected to vary dynamically.

In the present study, we investigated patterns of paternity in relation to socioecological factors and examined the potential benefits of EPP from both the female and male perspective using a small passerine, the great tit, *Parus major*, as a model system. Our data come from 11 nestbox plots located in small and fragmented woodlands scattered within an area of 150 km^2 in Montes de Toledo, central Spain. Specifically, we first analysed the association between EPP rates and estimates of population size, breeding density and breeding synchrony in order to infer the phenology and spatial distribution of EP matings. We predicted that EPP rates are positively associated with population size and breeding density if increased proximity among individuals increases encounter rates and mating opportunities (García-Navas, Ferrer, et al., 2014; Mayer & Pasinelli, 2013; Westneat & Mays, 2005). According to the mate-guarding hypothesis, the demands of paternity defence constrain males from seeking EPC at the time when most potential EP partners are fertile (Saino et al., 1997). Under this assumption, we predicted that EPP rates are negatively associated with breeding synchrony at the plot level. On the other hand, the simultaneous display hypothesis suggests the opposite: that more synchronous breeding leads to higher EPP rates because the temporal clumping of mating opportunities facilitates mate choice allowing individuals to compare and choose the best option (Stutchbury & Morton, 1995). Second, we tested whether female and male great tits engage in EPP with more heterozygous, more compatible and/or phenotypically superior individuals than their social mates in order to gain genetic benefits for their offspring (Brown, 1997; Jennions & Petrie, 2000; Kempenaers et al., 1992). Finally, we tested whether extrapair offspring (EPO) are phenotypically or genetically superior to within-pair offspring (WPO).

METHODS

Study Species

In spite of being one of the most thoroughly studied species in the world, there is no conclusive evidence on whether EP matings constitute a female- or a male-driven strategy in the great tit (see Appendix Table A1 for a review). Previously, it has been