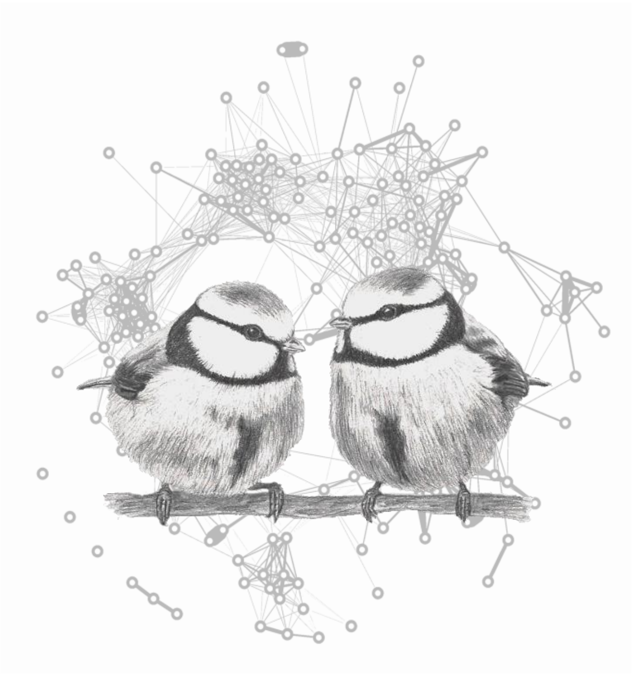
The link between social environment and patterns of extra-pair paternity



Dissertation

vorgelegt an der
Fakultät für Biologie
der Ludwig-Maximilians-Universität
München

durchgeführt am
Max-Planck-Institut für Ornithologie
Seewiesen

vorgelegt von
Kristina Beck
Juli 2020

1. Gutachter: **Prof. Dr. Bart Kempenaers**

2. Gutachterin: **Prof. Dr. Gisela Grupe**

Tag der Abgabe: **28.07.2020**

Tag der mündlichen Prüfung: **25.11.2020**

Contents

Summary

Social interactions with conspecifics are a key element of an individual's environment. Each individual differs in who and how frequently they interact with, resulting in unique social environments. These differences in sociality can have important consequences for an individual's reproduction. However, we still know relatively little about the link between the social environment and variation in mating behaviour.

Here, we investigate extra-pair matings – a common alternative mating behaviour in socially monogamous bird species. Extra-pair matings refer to sexual behaviour outside the social pair bond and can lead to extra-pair paternity. The patterns of extra-pair paternity can vary extensively among individuals and has been the focus of several studies in the past decades. Yet, our understanding of why extra-pair paternity varies among individuals remains limited. In this work, we aim to link variation in extra-pair paternity with characteristics of the social environment before (**Chapter 1, 2**) and during breeding (**Chapter 3, 4**), in a passerine model species, the blue tit (*Cyanistes caeruleus*).

More specifically, we quantify the social environment of each individual during the non-breeding season by monitoring their foraging associations at bird feeders, using PIT-tag technology and social network analysis. We explore three different perspectives of the social environment (i.e., the dyadic relationships, the direct and indirect social environment) and relate this to patterns of extra-pair paternity in the subsequent breeding season (**Chapter 1, 2**). First, we examine whether the social relationship strength between females and males predicts their likelihood to become extra-pair partners (**Chapter 1**). Second, we quantify whether aspects of an individual's direct and indirect social environment influence its future paring success (**Chapter 2**).

Next, we examine the direct social environment of individuals during breeding, using a long-term dataset of more than ten breeding seasons. Here, we quantify the social environment based on the spatial proximity of breeding pairs, whereby we define all direct breeding neighbours as an individual's direct social environment. First, we investigate causes of within-individual variation in extra-pair paternity (**Chapter 3**). Here, we examine whether extra-pair paternity is a repeatable trait in females and males. Following, we test whether within-individual changes in extra-pair paternity between breeding seasons relate to between-year changes in the direct social breeding environment (**Chapter 3**).

Lastly, we test a prediction of a proposed framework by Eliassen and Jørgensen (2014). The framework suggests that extra-pair copulations can incentivize males to shift focus from their own

brood towards neighbouring nests in which they may sire extra-pair young. This would imply that changes in male behaviour can lead to more “cooperative” breeding environments and thus increased fitness of whole nests or neighbourhoods. We test whether having extra-pair young or breeding in a neighborhood with a higher prevalence of extra-pair paternity is associated with increased breeding success and survival (**Chapter 4**).

Our findings reveal that the unique social environment that individuals experience before breeding can influence future (extra-pair) mating patterns. First, we show that females and males with stronger foraging associations are more likely to become i) social partners, ii) close breeding neighbours and iii) extra-pair partners (**Chapter 1**). Further, we generate new knowledge on the dynamics of pair formations by showing that social pairs likely get established earlier than extra-pair partners (**Chapter 1**). Second, we find that characteristics of the direct and indirect social environment influence male mating success. Male blue tits that move more often between different social groups are more likely to breed in the subsequent breeding season (**Chapter 2**). Further, among those individuals that bred, adult males that associated with more females prior to breeding were more likely to sire extra-pair young (**Chapter 2**).

We show that extra-pair paternity is to some extent a repeatable trait in females and males. Individual-level changes in the direct social breeding environment do not explain changes in extra-pair paternity in females (**Chapter 3**). In adult males, do changes into a less competitive environment lead to an increased extra-pair siring success (**Chapter 3**). However, most of the observed within-individual variation in extra-pair paternity remains unexplained.

Lastly, we find no evidence that nests containing extra-pair young or nests simply located in breeding environments with a higher prevalence of extra-pair paternity have higher breeding success and increased male survival (**Chapter 4**). However, there was some indication that female survival increases when they breed in an environment with a higher prevalence of extra-pair paternity (**Chapter 4**).

In sum, our findings reveal that the social environment that individuals experience prior to breeding is an important determinant of future (extra-pair) mating patterns (**Chapter 1, 2**). We provide evidence that extra-pair paternity is, at least to some extent, influenced by both individual-specific traits and the social environment (**Chapter 1, 2, 3**). Although, we speculate that extra-pair paternity will remain a trait that is difficult to predict. Finally, we show that having extra-pair young or breeding in an environment with a high prevalence of extra-pair paternity is unlikely to increase fitness of whole nests (**Chapter 4**).

General introduction

Animal social structure

Already back in 1878, Alfred Espinas highlighted in his work “Des sociétiés animals” that animal societies are not a random collection of individuals but that they emerge from the repeated interactions among its members. Each individual interacts differently with its’ conspecifics resulting in unique social environments. In the past years, research increasingly showed that animal social structure and the unique social environment that each individual experiences are important determinants for various ecological and evolutionary processes (Sayigh et al. 1999; Croft et al. 2016; Webber and Vander Wal 2019; Cantor et al. 2019).

The three levels of animal sociality

In 1976, Robert Hinde published a conceptual framework to analyse the social organization of animal societies. Hinde distinguishes three levels of sociality: interactions, relationships and social structure. His framework is based on a bottom-up approach whereby interactions between two individuals build the fundamental base. Interactions between individuals can be differently attributed (e.g. as agonistic, affiliative or sexual interaction) and can differ in space and time. The patterns of interactions can depend on the phenotypic traits of its actors such as their age, relatedness or mating status. For instance, certain age groups may interact more frequently with each other (i.e. assortative interactions). The sum of interactions between two individuals over a certain period of time then defines their relationship, the second level of Hinde’s framework. This can for example depict dominance relationships or social pair bonds. Finally, the sum of relationships among all members of a population defines the third level, the social structure. This framework made a huge contribution to the study of animal social structure and is, up to this day, frequently used and expanded by researchers.

Social network analysis

Hinde’s framework allows to classify animal social structure, but how to correctly quantify and analyse the different levels of sociality? The answer was brought by social network analysis. First used by sociologists and psychologists (Scott 1988), social network analysis soon became the predominant tool for the study of animal sociality. In social networks, individuals can be depicted by nodes and the connections between individuals are represented by edges. Each node (i.e. individual) can carry different phenotypic traits such as age, sex or body condition. The edges between nodes can simply refer to the presence or absence of a connection or describe the strength of a social relationship between two individuals (e.g. how much time two individuals spent together). Social networks can describe different types of relationships (e.g. cooperative, competitive or sexual) and usually represent only one type at a time. The sum of all combined connections between individuals of a population allows to quantify the overall social structure. Thus, social network analysis is an ideal tool to study the different levels of sociality, ranging from characteristics of relationships between two individuals to the overall population social structure. Most importantly, the use of social network analysis not only allows to display the social life of animals but to test hypothesis (Wey et al. 2008; Croft et al. 2011; Croft et al. 2016; Webber and Vander Wal 2019). This ability has led to a major increase in research over the last two decades (Webber and Vander Wal 2019), linking characteristics of the social structure with various ecological and evolutionary processes. For instance, the social structure has been repeatedly shown to influence the transmission of disease (Hamede et al. 2009; Silk et al. 2017) and information (Aplin et al. 2012; Farine et al. 2015; Firth et al. 2016), cooperation (Voelkl and Kasper 2009; Carter et al. 2020), competition (Araújo et al. 2008; Farine and Sheldon 2015), dispersal (Blumstein et al. 2009; Cozzi et al. 2018) and mating (Oh and Badyaev 2010; Psorakis et al. 2012; Fisher et al. 2016; Firth et al. 2018; Sabol et al. 2020), ultimately shaping individual fitness (Formica et al. 2012; Alberts 2019; Sabol et al. 2020) and selection acting on phenotypic traits (Oh and Badyaev 2010; Formica et al. 2011; Farine and Sheldon 2015).

Mating systems

Mating systems are influenced by two main factors, the spatiotemporal distribution of males and females, and the extent to which each sex invests in parental care (Emlen and Oring 1977). Depending on the number and identity of reproductive partners, mating systems are classified into monogamy, polygyny, polyandry, promiscuity and polygamy (Emlen and Oring 1977). Species are usually assigned to one typical mating system. However, mating systems are by far not static and can vary within species.

Social structure and mating systems

Variation in mating behaviour can be caused by several factors, whereby the social environment plays a key role in shaping mating systems. The social environment of an individual captures important features influencing mating behaviour including the number and phenotypic composition of potential mating partners and competitors and their rates of interactions, ultimately affecting patterns of mate choice, reproductive success and the extent of sexual selection (Jirotkul 1999; Oh and Badyaev 2010; Formica et al. 2012; Grant and Grant 2019; Heinsohn et al. 2019; Niemelä et al. 2019). The relationship between an individual's social environment and mating behaviour can be investigated from three different perspectives: the dyadic relationship, the direct social environment and the indirect social environment (Figure 1, Maldonado-Chaparro et al. 2018).

The dyadic relationship: A female-male pair (i.e. dyad) builds the fundamental base of a mating system. Speaking in social network terms, the presence of a connection between a female and a male can indicate that they copulated or that they formed a breeding pair. A pair can also be characterised based on their propensity to interact or associate with each other across a variety of other contexts (e.g. courtship, foraging, allo-preening etc.). The amount of time that a pair spent together in any of these contexts can define the strength of their social relationship (see second level in Hinde's framework) and can be a predictor of future mating outcomes. For instance, in many species, females and males form social relationships already long before the breeding season and the strength of these relationships has been shown to predict the formation of breeding pairs (Psorakis et al. 2012; Teitelbaum et al. 2017; Firth et al. 2018) and the spatial proximity during breeding (Firth and Sheldon 2016).

Direct environment: A focal individual's direct social connections to females and males defines its direct (local) social environment (see red nodes in Figure 1). The direct connections capture the local density of association partners and thus the availability of mates and the magnitude of competition (Formica et al. 2012; Niemelä et al. 2019; Sabol et al. 2020). Individuals with more social connections, particularly to the opposite-sex, may be more likely to mate than individuals with less connections or than individuals located in same-sex biased environments where competition is high. The direct connections also depict the phenotypic environment a focal individual is embedded in. A focal individual's phenotypic fit to the direct environment can predict the experienced selection pressure (West-Eberhard 1979; Moore et al. 1997) and ultimately it's mating tactics (Jirotkul 2000) and its success in copulations (Formica et al. 2011; Wey et al. 2015; Ziv et al. 2016), pairing (Oh and Badyaev 2010) or territory acquisition (Farine and Sheldon 2015).

Indirect environment: A focal individual is also indirectly connected to the association partners of its' direct connections ("friends of its' friends" (Brent 2015), see blue nodes in Figure 1). Continuatively, an individual can be indirectly connected to everybody else in the population. Here, social network measures of an individual's centrality within a group can depict the extent of indirect connections and have been shown to influence an individual's success in pairing (Oh and Badyaev 2010) or reproduction (McDonald 2007). In species where females mate multiply, a male's reproductive success will not only depend on its' direct competitors, but also on the female's connections to potential mates influencing pre- and post-copulatory competition (McDonald and Pizzari 2016; McDonald and Pizzari 2018). Further, a focal individual's mating behaviour may depend on the mating behaviour of the associates of its direct connections. For instance, in water striders (*Aquarius remigis*) the presence of hyper-aggressive males changed the mating behaviour of all other individuals present in a pond (Sih et al. 2014; Wey et al. 2015). Thus, mating behaviours could spread through a population leading to changes in the overall expressed mating system.

Taken together, research increasingly shows that the unique social environment is linked with variation in mating behaviour. However, there is many more aspects of mating behaviour that remain to be explored in relation to social factors.

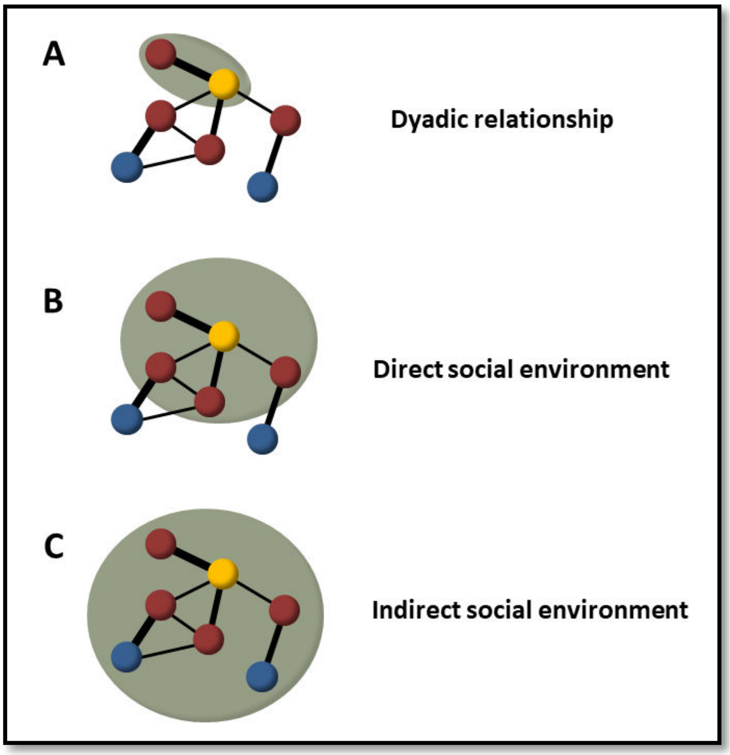


Figure 1. Three different perspectives of an individual's social environment represented in a simplified network. The focal individual is represented as yellow node. All connections to conspecifics are indicated as black edges and the size represents the strength of this connection (i.e. strength of the social relationship). Individuals directly connected to the focal individual are shown in red, individuals indirectly connected in blue. The grey circles represent in each of the three levels the aspect of interest, i.e. **A**: the dyadic relationship, **B**: the direct social environment and **C**: the indirect social environment.

Avian mating systems

Social monogamy is the predominant mating system in birds (more than 95% of species; Lack 1968, Bennett and Owens 2002). Birds form pair bonds that last at least for one breeding season and the pair cooperates in raising their brood together. However, when genetic tools became available to study the parentage of birds (Burke and Bruford 1987) it soon became evident that most socially monogamous species are not genetically monogamous. About 76% of all studied species engage in sexual behaviour outside of their pair bond, potentially leading to extra-pair paternity (Griffith et al. 2002; Brouwer and Griffith 2019). The frequency of extra-pair paternity varies notably between species, populations and even among individuals of the same population (Petrie and Kempenaers 1998; Griffith et al. 2002; Westneat and Stewart 2003; Brouwer and Griffith 2019). Since decades researchers are trying to find explanations for the observed variation in extra-pair paternity. But despite extensive effort, it remains puzzling why some individuals have extra-pair paternity while others do not.

Social structure and extra-pair paternity

Variation in extra-pair paternity has often been linked to differences in individual phenotypes. For instance, the tendency to engage in extra-pair behaviour may be genetically determined (Whittingham et al. 2006; Forstmeier 2007) or related to phenotypic traits such as age (Cleasby and Nakagawa 2012; Michálková et al. 2019), sperm quantity and quality (Moller and Briskie 1995; Knief et al. 2017; Girndt et al. 2019) and female body condition (Plaza et al. 2019). Next to individual differences, ecological factors have been proposed to influence variation in extra-pair paternity, with breeding synchrony (i.e. the overlap of the fertile period of females within a certain area in a given season) and breeding density (i.e. the number of individuals in a breeding area) as the most common ones examined (Dunn et al. 1994; Kempenaers 1997; Griffith et al. 1999; Chuang et al. 1999; Thusius et al. 2001; Schlicht et al. 2015a; Araya-Ajoy et al. 2015).

Factors such as the breeding synchrony and density already hint at the importance of the social environment when investigating variation in extra-pair paternity. Extra-pair paternity is inherently a social process resulting from the interactions between the traits of at least four individuals: the focal female or male, the focal individual's social partner, the extra-pair partner and its social partner (Westneat and Stewart 2003; Maldonado-Chaparro et al. 2018). Thus, variation in the social environment likely influences variation in extra-pair paternity (Maldonado-Chaparro et al. 2018). But, most studies that examined the breeding social structure took population averages (but see: Schlicht et al. 2015a), neglecting that each individual experiences a unique social environment. In addition, most research on extra-pair paternity only focused on the breeding environment (Dunn et al. 1994; Komdeur 2001; Thusius et al. 2001; Schlicht et al. 2015a). However in several species, individuals already associate with each other long before the actual reproduction. Thus, the unique social environment experienced prior and during breeding may both impact the future expression of extra-pair paternity.

In the presented work, we will explore the link between the individual-specific social environment and extra-pair paternity in a passerine bird, the blue tit (*Cyanistes caeruleus*).

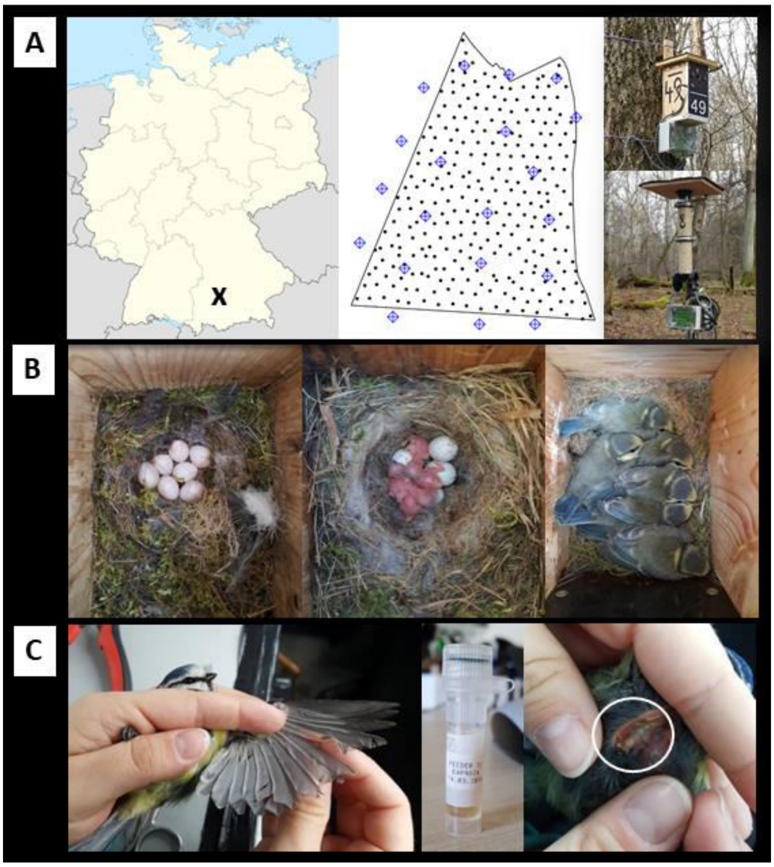
Study system

Blue tits are small, short-lived passerine birds and are a model species in behavioural ecology (Perrins 1979; Föger and Pegoraro 2004). During the breeding season (late March–June) blue tits form socially monogamous pairs and defend a territory against intruders. During winter (October–mid March), blue tits forage in large mixed-species flocks. For breeding, blue tits accept nest boxes in which they usually raise one brood, except for replacement clutches. Blue tits frequently engage in extra-pair matings and their broods show intermediate rates of extra-pair paternity (approx. half of the broods contain at least one extra-pair young, with 10–15% of young in a brood being extra-pair young, e.g. Kempenaers et al. 1992; Delhey et al. 2003). Since many years, research examined the variation of extra-pair paternity in blue tits showing that for instance adult and larger males, and close breeding neighbours are more likely to have extra-pair young (Schlicht et al. 2015b; Schlicht et al. 2015a). The relatively high rates of extra-pair paternity, the existence of previous research and the variation in their social structure during breeding and non-breeding make blue tits an ideal study species to explore the link between social environment and extra-pair paternity.

Here, we use data from a blue tit population located in southern Germany ("Westerholz", 48°08'26''N 10°53'29''E, ca. 40ha) whose breeding biology has been studied since 2007–present. The study area contains 277 nest boxes since 2007 and 20 bird feeders that were set up in the winter 2017/18 (October–mid March). The nest boxes (approx. 40m apart) and feeders (approx. 200m apart) are arranged in an even grid across the whole study site (Figure 2A) and are all equipped with radio-frequency identification (RFID) antennas (Loës et al. 2019a; Loës et al. 2019b). During each breeding season, nest boxes were checked at least once per week (from mid March onwards) to monitor nest-building activity and to determine laying onset (date of first egg), clutch size and the dates of hatching and fledging (Figure 2B).

Blue tits were caught either in spring as nestlings, or as adults during the provisioning phase of their young or in winter while sleeping inside a box or with mist-nets. From every blue tit, we took some standard measurements (e.g. tarsus length), took a small blood sample (ca. 10µl) for the paternity analysis and molecular sexing, and equipped each bird with a passive integrated transponder (PIT tag) that was implanted under the skin on the back (Figure 2C). Whenever a bird with a PIT-tag comes close to an RFID antenna (approx. 3cm), the tag gets activated and transmits a unique alphanumeric code. Together, with the information on the date, time and feeder/nest box identity this gets logged on a SD card. These data allowed us to examine the social environment during breeding, by quantifying the breeding neighbourhood constellation (i.e. who breeds next to whom), and the social environment prior to breeding by quantifying who associated with whom during foraging at bird feeders or when inspecting nest boxes together.

Figure 2. The study system. **A**: Left: Location of the study site in southern Germany (black cross). Middle: Map of the study site showing the location of the 277 nest boxes (as black dots) and 20 bird feeders (as blue diamonds). Right: Photo of a nest box and a feeder. **B**: Different nest stages, from eggs (left) until first hatchlings (middle) and finally fledglings (right). **C**: Bird processing: Taking a blood sample from the brachial vein (left), blood sample (middle) and a bird with an implanted transponder on its back (right, indicated by a white circle).



Aim of the thesis and chapter summary

The aim of this thesis is to improve our understanding of the variation in extra-pair paternity by generating novel insights into how the individual-specific social environment and the expression of extra-pair paternity are linked. We investigate the social environment prior and during breeding and explore it from three different perspectives (Figure 1). We examine the dyadic relationships between females and males formed prior to breeding and whether these can predict future extra-pair mating patterns (**Chapter 1**). Next, we explore an individual's direct and indirect social environment prior to breeding and whether this influences its future pairing success (**Chapter 2**). In addition, we quantify the direct social environment during breeding and examine whether within-individual variation in extra-pair paternity can be explained by changes in the individual's social breeding environment (**Chapter 3**). Finally, we explore whether the occurrence of extra-pair paternity has fitness consequences, potentially emerging from aspects of the social breeding environment (**Chapter 4**).

Social relationships established before breeding have been shown to translate into primary mating decisions, whereby stronger associated female-male pairs were more likely to become breeding partners (Psorakis et al. 2012; Teitelbaum et al. 2017; Firth et al. 2018). The strength of social relationships may also determine secondary mating decisions such as extra-pair matings. In **Chapter 1**, we quantify the relationship strength of birds by examining their foraging associations at bird feeders during winter (i.e. who forages with whom in the same flock and how often). Using social network analysis, we then ask whether female-male dyads with stronger relationships (i.e. that spent more time foraging together) are more likely to become i) social partners, ii) close breeding neighbours and iii) extra-pair partners. In addition, we explore and compare the temporal dynamics of social pair and extra-pair formations over the course of winter.

An individual's position within a social group–that is it's direct and indirect social connections–have been shown to influence reproduction in many species (Oh and Badyaev 2010; Formica et al. 2011; Wey et al. 2015; Ziv et al. 2016; Sabol et al. 2020). However, most studies examined polygynandrous mating systems and studies linking an individual's social position with pairing success in socially monogamous species are rare (but see Oh and Badyaev 2010). In **Chapter 2**, we quantify the direct and indirect social environment of female and male blue tits prior to breeding based on their foraging associations at bird feeders. We then calculate different social network metrics that represent an individual's social position within a group (i.e., its number of connections to potential mating partners and competitors, its average association strength to potential mates and its centrality) and examine whether these predict the likelihood to i) acquire a breeding partner and ii) have extra-pair young.

Extra-pair paternity has often been linked to aspects of the current breeding environment. However, studies usually took population averages, neglecting that each individual experiences a unique (social) environment. Further, past studies mostly focused on variation in extra-pair paternity among individuals instead of examining within-individual variation. For our understanding of the causes of the observed variation in extra-pair paternity it is crucial to disentangle individual from environmental effects. In **Chapter 3**, we aim to fill this gap by investigating the within-individual variation of extra-pair paternity in female and male blue tits. Using a long-term dataset on more than ten breeding seasons, we first examine whether extra-pair paternity is a consistent individual-specific trait. Second, we explore whether within-individual variation can be explained by changes in the individual breeding environment. We specifically focus on the social compounds of the direct breeding environment, capturing the number and phenotypic composition of potential mates and competitors, and the familiarity to those. Here, we define the direct social environment as the direct breeding neighbourhood based on spatial proximity. Following, the direct social environment includes all breeding neighbours that share a territory boundary with the focal individual and is not based on direct social associations (such as in **Chapter 1** and **2**).

Lastly, we explore in **Chapter 4** whether the occurrence of extra-pair paternity can influence brood success and adult survival. A proposed framework by Eliassen and Jørgensen (2014) suggested that extra-pair copulations may incentivize males (through paternity uncertainty) to extend focus from their own nest towards the entire breeding neighbourhood. For instance, extra-pair males may become less aggressive towards the female neighbour they mated with (Gray 1997a), or may even provide additional parental care or help with predator mobbing (Kempenaers 1993; Gray 1997b; Townsend et al. 2010). In such a scenario, extra-pair males may become more cooperative, potentially leading to “nicer” breeding neighbourhoods in which not only nests with extra-pair young but also nests simply located in such a neighbourhood should have fitness benefits. Here, we investigate whether nests containing extra-pair young or being located in a neighbourhood with a high prevalence of extra-pair paternity indeed have higher fitness (i.e. increased breeding success and adult survival) which may result from a more cooperative social breeding environment.

References

Alberts SC. 2019. Social influences on survival and reproduction: Insights from a long-term study of wild baboons. J Anim Ecol. 88(1):47–66.

Aplin LM, Farine DR, Morand-Ferron J, Sheldon BC. 2012. Social networks predict patch discovery in a wild population of songbirds. Proc R Soc London B Biol Sci. 279(1745):4199–4205.

Araújo MS, Guimaraes Jr PR, Svanbäck R, Pinheiro A, Guimarães P, Reis SF dos, Bolnick DI. 2008. Network analysis reveals contrasting effects of intraspecific competition on individual vs. population diets. Ecology. 89(7):1981–1993.

Araya-Ajoy YG, Dingemanse NJ, Kempenaers B. 2015. Timing of extrapair fertilizations: within-pair fertilization trade-offs or pair synchrony spillovers? Behav Ecol. 27(2):377-384.

Blumstein DT, Wey TW, Tang K. 2009. A test of the social cohesion hypothesis: interactive female marmots remain at home. Proc R Soc B Biol Sci. 276(1669):3007–3012.

Brent LJN. 2015. Friends of friends: are indirect connections in social networks important to animal behaviour? Anim Behav. 103:211–222.

Brouwer L, Griffith SC. 2019. Extra-pair paternity in birds. Mol Ecol. 28(22):4864–4882.

Burke T, Bruford MW. 1987. DNA fingerprinting in birds. Nature. 327(6118):149–152.

Cantor M, Maldonado-Chaparro A, Beck K, Carter G, He P, Hillemann F, Klarevas-Irby J, Lang S, Ogino M, Papageorgiou D. 2019. Animal social networks: revealing the causes and implications of social structure in ecology and evolution. EcoEvoRxiv.

Carter GG, Farine DR, Crisp RJ, Vrtilek JK, Ripperger SP, Page RA. 2020. Development of new food-sharing relationships in vampire bats. Curr Biol.

Chuang HC, Webster MS, Holmes RT. 1999. Extrapair paternity and local synchrony in the Black-throated Blue Warbler. Auk.:726–736.

Cleasby IR, Nakagawa S. 2012. The influence of male age on within-pair and extra-pair paternity in passerines. Ibis. 154(2):318–324.

Cozzi G, Maag N, Börger L, Clutton-Brock TH, Ozgul A. 2018. Socially informed dispersal in a territorial cooperative breeder. J Anim Ecol. 87(3):838–849.

Croft DP, Darden SK, Wey TW. 2016. Current directions in animal social networks. Curr Opin Behav Sci. 12:52–58.

Croft DP, Madden JR, Franks DW, James R. 2011. Hypothesis testing in animal social networks. Trends Ecol Evol. 26(10):502–507.

Delhey K, Johnsen A, Peters A, Andersson S, Kempenaers B. 2003. Paternity analysis reveals opposing selection pressures on crown coloration in the blue tit (Parus caeruleus). Proc R Soc London B Biol Sci. 270(1528):2057–2063.

Dunn PO, Whittingham LA, Lifjeld JT, Robertson RJ, Boag PT. 1994. Effects of breeding density, synchrony, and experience on extrapair paternity in tree swallows. Behav Ecol. 5(2):123–129.

Eliassen S, Jørgensen C. 2014. Extra-pair mating and evolution of cooperative neighbourhoods. PLoS One. 9(7):e99878.

Emlen ST, Oring LW. 1977. Ecology, sexual selection, and the evolution of mating systems. Science. 197(4300):215–223.

Espinas A V. 1878. Des sociétés animals. Germer Baillière, Paris, France. 1977. Arno Press New York, New York, USA Ed. 1:1877.

Farine DR, Aplin LM, Sheldon BC, Hoppitt W. 2015. Interspecific social networks promote information transmission in wild songbirds. Proc R Soc B Biol Sci. 282(1803):20142804.

Farine DR, Sheldon BC. 2015. Selection for territory acquisition is modulated by social network structure in a wild songbird. J Evol Biol. 28(3):547–556.

Firth JA, Cole EF, Ioannou CC, Quinn JL, Aplin LM, Culina A, McMahon K, Sheldon BC. 2018. Personality shapes pair bonding in a wild bird social system. Nat Ecol Evol. 2(11):1696–1699.

Firth JA, Sheldon BC. 2016. Social carry-over effects underpin trans-seasonally linked structure in a wild bird population. Ecol Lett. 19(11):1324–1332.

Firth JA, Sheldon BC, Farine DR. 2016. Pathways of information transmission among wild songbirds follow experimentally imposed changes in social foraging structure. Biol Lett. 12(6):20160144.

Fisher DN, Rodríguez-Muñoz R, Tregenza T. 2016. Comparing pre-and post-copulatory mate competition using social network analysis in wild crickets. Behav Ecol. 27(3):912–919.

Föger M, Pegoraro K. 2004. Die Blaumeise: Parus caeruleus. Westarp-Wiss.

Formica VA, McGlothlin JW, Wood CW, Augat ME, Butterfield RE, Barnard ME, Brodie III ED. 2011. Phenotypic assortment mediates the effect of social selection in a wild beetle population. Evolution. 65(10):2771–2781.

Formica VA, Wood CW, Larsen WB, Butterfield RE, Augat ME, Hougen HY, BRODIE III ED. 2012. Fitness consequences of social network position in a wild population of forked fungus beetles (Bolitotherus cornutus). J Evol Biol. 25(1):130–137.

Forstmeier W. 2007. Do individual females differ intrinsically in their propensity to engage in extra-pair copulations? PLoS One. 2(9):e952.

Girndt A, Cockburn G, Sánchez-Tójar A, Hertel M, Burke T, Schroeder J. 2019. Male age and its association with reproductive traits in captive and wild house sparrows. J Evol Biol. 32(12):1432–1443.

Grant PR, Grant BR. 2019. Adult sex ratio influences mate choice in Darwin’s finches. Proc Natl Acad Sci. 116(25):12373–12382.

Gray EM. 1997a. Do female red-winged blackbirds benefit genetically from seeking extra-pair copulations? Anim Behav. 53(3):605–623.

Gray EM. 1997b. Female red-winged blackbirds accrue material benefits from copulating with extra-pair males. Anim Behav. 53(3):625–639.

Griffith SC, Owens IPF, Thuman KA. 2002. Extra pair paternity in birds: a review of interspecific variation and adaptive function. Mol Ecol. 11(11):2195–2212.

Griffith SC, Stewart IRK, Dawson DA, Owens IPF, Burke T. 1999. Contrasting levels of extra-pair paternity in mainland and island populations of the house sparrow (Passer domesticus): is there an «island effect»? Biol J Linn Soc. 68(1):303–316.

Hamede RK, Bashford J, McCallum H, Jones M. 2009. Contact networks in a wild Tasmanian devil (Sarcophilus harrisii) population: using social network analysis to reveal seasonal variability in social behaviour and its implications for transmission of devil facial tumour disease. Ecol Lett. 12(11):1147–1157.

Heinsohn R, Olah G, Webb M, Peakall R, Stojanovic D. 2019. Sex ratio bias and shared paternity reduce individual fitness and population viability in a critically endangered parrot. J Anim Ecol. 88(4):502–510.

Hinde RA. 1976. Interactions, relationships and social structure. Man.:1–17.

Jirotkul M. 1999. Operational sex ratio influences female preference and male–male competition in guppies. Anim Behav. 58(2):287–294.

Jirotkul M. 2000. Male trait distribution determined alternative mating tactics in guppies. J Fish Biol. 56(6):1427–1434.

Kempenaers B. 1993. A case of polyandry in the blue tit: female extra-pair behaviour results in extra male help. Ornis Scand. 24(3):246–249.

Kempenaers B. 1997. Does reproductive synchrony limit male opportunities or enhance female choice for extra-pair paternity? Behaviour. 134(7):551–562.

Kempenaers B, Verheyen GR, Van den Broeck M, Burke T, Van Broeckhoven C, Dhondt A. 1992. Extra-pair paternity results from female preference for high-quality males in the blue tit. Nature. 357(6378):494–496.

Knief U, Forstmeier W, Pei Y, Ihle M, Wang D, Martin K, Opatová P, Albrechtová J, Wittig M, Franke A. 2017. A sex-chromosome inversion causes strong overdominance for sperm traits that affect siring success. Nat Ecol Evol. 1(8):1177.

Komdeur J. 2001. Mate guarding in the Seychelles warbler is energetically costly and adjusted to paternity risk. Proc R Soc London B Biol Sci. 268(1481):2103–2111.

Loës P, Skripsky P, Kempenaers B. 2019a. Github repository RFID-MS. doi:10.5281/zenodo.3516586.

Loës P, Skripsky P, Kempenaers B. 2019b. Github repository MOMO. doi:10.5281/zenodo.3516588.

Maldonado-Chaparro AA, Montiglio P, Forstmeier W, Kempenaers B, Farine DR. 2018. Linking the fine-scale social environment to mating decisions: a future direction for the study of extra-pair paternity. Biol Rev. 93(3):1558–1577.

McDonald DB. 2007. Predicting fate from early connectivity in a social network. Proc Natl Acad Sci. 104(26):10910–10914.

McDonald GC, Pizzari T. 2016. Why patterns of assortative mating are key to study sexual selection and how to measure them. Behav Ecol Sociobiol. 70(1):209–220.

McDonald GC, Pizzari T. 2018. Structure of sexual networks determines the operation of sexual selection. Proc Natl Acad Sci. 115(1):E53–E61.

Michálková R, Tomášek O, Adámková M, Kreisinger J, Albrecht T. 2019. Extra-pair paternity patterns in European barn swallows Hirundo rustica are best explained by male and female age rather than male ornamentation. Behav Ecol Sociobiol. 73(9):119.

Møller AP, Briskie J V. 1995. Extra-pair paternity, sperm competition and the evolution of testis size in birds. Behav Ecol Sociobiol. 36(5):357–365.

Moore AJ, Brodie III ED, Wolf JB. 1997. Interacting phenotypes and the evolutionary process: I. Direct and indirect genetic effects of social interactions. Evolution. 51(5):1352–1362.

Niemelä PT, Tiso S, Dingemanse NJ. 2019 Jan 1. Density-dependent costs and benefits of male mating success in a wild insect. bioRxiv.:733832. doi:10.1101/733832.

Oh KP, Badyaev A V. 2010. Structure of social networks in a passerine bird: consequences for sexual selection and the evolution of mating strategies. Am Nat. 176(3):E80–E89.

Perrins CM. 1979. British tits. HarperCollins.

Petrie M, Kempenaers B. 1998. Extra-pair paternity in birds: explaining variation between species and populations. Trends Ecol Evol. 13(2):52–58.

Plaza M, Cantarero A, Moreno J. 2019. An experimental increase in female mass during the fertile phase leads to higher levels of extra-pair paternity in pied flycatchers Ficedula hypoleuca. Behav Ecol Sociobiol. 73(12):161.

Psorakis I, Roberts SJ, Rezek I, Sheldon BC. 2012. Inferring social network structure in ecological systems from spatio-temporal data streams. J R Soc Interface. 9(76):3055–3066.

Sabol AC, Lambert CT, Keane B, Solomon NG, Dantzer B. 2020. How does individual variation in sociality influence fitness in prairie voles? Anim Behav. 163:39–49.

Sayigh L, Tyack P, Wells R, Solow A, Scott M, Irvine A. 1999. Individual recognition in wild bottlenose dolphins: a field test using playback experiments. Anim Behav. 57(1):41–50.

Schlicht L, Valcu M, Kempenaers B. 2015a. Spatial patterns of extra-pair paternity: beyond paternity gains and losses. J Anim Ecol. 84(2):518–531.

Schlicht L, Valcu M, Kempenaers B. 2015b. Male extraterritorial behavior predicts extrapair paternity pattern in blue tits, Cyanistes caeruleus. Behav Ecol. 26(5):1404–1413.

Scott J. 1988. Social network analysis. Sociology. 22(1):109–127.

Sih A, Chang AT, Wey TW. 2014. Effects of behavioural type, social skill and the social environment on male mating success in water striders. Anim Behav. 94:9–17.

Silk MJ, Croft DP, Delahay RJ, Hodgson DJ, Boots M, Weber N, McDonald RA. 2017. Using social network measures in wildlife disease ecology, epidemiology, and management. Bioscience. 67(3):245–257.

Teitelbaum CS, Converse SJ, Mueller T. 2017. Birds choose long-term partners years before breeding. Anim Behav. 134:147–154.

Thusius KJ, Dunn PO, Peterson KA, Whittingham LA. 2001. Extrapair paternity is influenced by breeding synchrony and density in the common yellowthroat. Behav Ecol. 12(5):633–639.

Townsend AK, Clark AB, McGowan KJ. 2010. The direct benefits and genetic costs of extrapair paternity in the cooperatively breeding American crow. Am Nat. 175:E1–E9.

Voelkl B, Kasper C. 2009. Social structure of primate interaction networks facilitates the emergence of cooperation. Biol Lett. 5(4):462–464.

Webber QMR, Vander Wal E. 2019. Trends and perspectives on the use of animal social network analysis in behavioural ecology: a bibliometric approach. Anim Behav. 149:77–87.

West-Eberhard MJ. 1979. Sexual selection, social competition, and evolution. Proc Am Philos Soc. 123(4):222–234.

Westneat DF, Stewart IRK. 2003. Extra-pair paternity in birds: causes, correlates, and conflict. Annu Rev Ecol Evol Syst. 34(1):365–396.

Wey T, Blumstein DT, Shen W, Jordán F. 2008. Social network analysis of animal behaviour: a promising tool for the study of sociality. Anim Behav. 75(2):333–344.

Wey TW, Chang AT, Fogarty S, Sih A. 2015. Personalities and presence of hyperaggressive males influence male mating exclusivity and effective mating in stream water striders. Behav Ecol Sociobiol. 69(1):27–37.

Whitehead H. 2008. Analyzing animal societies: quantitative methods for vertebrate social analysis. University of Chicago Press.

Whittingham LA, Dunn PO, Stapleton MK. 2006. Repeatability of extra-pair mating in tree swallows. Mol Ecol. 15(3):841–849.

Ziv EB, Ilany A, Demartsev V, Barocas A, Geffen E, Koren L. 2016. Individual, social, and sexual niche traits affect copulation success in a polygynandrous mating system. Behav Ecol Sociobiol. 70(6):901–912.

Chapter 1

Winter associations predict social and extra-pair mating patterns in a wild songbird

Kristina B. Beck, Damien R. Farine, Bart Kempenaers

Despite decades of research, our understanding of the underlying causes of within-population variation in patterns of extra-pair paternity (EPP) remains limited. Previous studies have shown that extra-pair mating decisions are linked to both individual traits and ecological factors. Here, we examine whether social associations among individuals prior to breeding also shape mating patterns, specifically the occurrence of EPP, in a small songbird, the blue tit. We test whether associations during the non-breeding period predict (1) future social pairs, (2) breeding proximity, i.e. the distance between breeding individuals, and (3) the likelihood that individuals have extra-pair young together. Individuals that were more strongly associated (those that foraged more often together) during winter tended to nest closer together. This, by itself, predicts EPP patterns, because most extra-pair sires are close neighbours. However, even after controlling for spatial effects, female-male dyads with stronger social associations prior to breeding were more likely to have extra-pair young. Our findings reveal a carry-over from social associations into future mating decisions. Quantifying the long-term social environment of individuals and studying its dynamics is a promising approach to enhance our understanding of the process of (extra-) pair formation.

Published as:

Beck KB, Farine DR, Kempenaers B. 2020. Winter associations predict social and extra-pair mating patterns in a wild songbird. Proc R Soc B. 287(1921):20192606.
https://doi.org/10.1098/rspb.2019.2606

PROCEEDINGS B

royalsocietypublishing.org/journal/rspb

Winter associations predict social and extra-pair mating patterns in a wild songbird

Kristina B. Beck[1], Damien R. Farine[2,3,4] and Bart Kempenaers[1]

[1]Department of Behavioural Ecology and Evolutionary Genetics, Max Planck Institute for Ornithology, Seewiesen, Germany
[2]Department of Collective Behaviour, Max Planck Institute of Animal Behavior, Konstanz, Germany
[3]Department of Biology, University of Konstanz, Germany
[4]Centre for the Advanced Study of Collective Behavior, University of Konstanz, Germany

KBB, 0000-0002-5027-0207; DRF, 0000-0003-2208-7613; BK, 0000-0002-7505-5458

Research

Cite this article: Beck KB, Farine DR, Kempenaers B. 2020 Winter associations predict social and extra-pair mating patterns in a wild songbird. *Proc. R. Soc. B* **287**: 20192606.
http://dx.doi.org/10.1098/rspb.2019.2606

Received: 7 November 2019
Accepted: 26 January 2020

Subject Category:
Behaviour

Subject Areas:
behaviour, ecology

Keywords:
extra-pair paternity, mating system, social network analysis, social environment, neighbourhood, *Cyanistes caeruleus*

Author for correspondence:
Kristina B. Beck
e-mail: kbeck@orn.mpg.de

Electronic supplementary material is available online at https://doi.org/10.6084/m9.figshare.c.4838778.

THE ROYAL SOCIETY
PUBLISHING

Despite decades of research, our understanding of the underlying causes of within-population variation in patterns of extra-pair paternity (EPP) remains limited. Previous studies have shown that extra-pair mating decisions are linked to both individual traits and ecological factors. Here, we examine whether social associations among individuals prior to breeding also shape mating patterns, specifically the occurrence of EPP, in a small songbird, the blue tit. We test whether associations during the non-breeding period predict (1) future social pairs, (2) breeding proximity (i.e. the distance between breeding individuals) and (3) the likelihood that individuals have extra-pair young together. Individuals that were more strongly associated (those that foraged more often together) during winter tended to nest closer together. This, by itself, predicts EPP patterns, because most extra-pair sires are close neighbours. However, even after controlling for spatial effects, female–male dyads with stronger social associations prior to breeding were more likely to have extra-pair young. Our findings reveal a carry-over from social associations into future mating decisions. Quantifying the long-term social environment of individuals and studying its dynamics is a promising approach to enhance our understanding of the process of (extra-)pair formation.

1. Introduction

Determining the factors that underlie variation in mating behaviour is crucial for our understanding of ecological and evolutionary processes such as sexual selection [1,2], cooperation [3,4] and population demographics [5,6]. In most socially monogamous bird species, some individuals engage in sexual behaviour outside the pair bond resulting in extra-pair paternity (EPP) [7,8]. However, the occurrence and frequency of EPP can vary drastically among individuals, even within the same population [7,9,10]. This variation has previously been linked to differences in individual traits (e.g. male body size [11]; female body condition [12]; male age [13]; sperm morphology [14]; male song characteristics [15]; male plumage [16]; but see [17,18]) or in ecological conditions (e.g. breeding synchrony [19]; breeding density [20]; but see [21,22]). Yet, despite much research, our ability to explain or predict patterns of EPP remains limited.

A major source of variation lies in the social environment. Individuals within a given population do not interact equally with all other members of that population, leading to heterogeneity in the number and quality of social associations. The individual-specific social surrounding should therefore determine important aspects of mating behaviour, such as mate availability, intra-sexual competition and mate choice [23–25]. Individuals usually interact with many more opposite-sex individuals than expressed in their social pair bond. Thus, the social environment probably includes potential extra-pair mates and may provide the substrate for future extra-pair copulations. For instance, a social surrounding including many opposite-sex members might favour extra-pair behaviour, and the frequency of social associations could be informative about who will mate with whom [23]. However, the effects of the social environment on patterns of EPP have rarely been investigated, despite potentially being able to give valuable insights into the expression of extra-pair behaviour [23,26].

A further limitation to our understanding of mating strategies revolves around the importance and timing of social associations with future (extra-pair) partners, including when decisions about (extra-pair) mating are made. Research on EPP has predominately focused on events or circumstances during the breeding season. For instance, several studies investigated the link between EPP and (a) local breeding density, reflecting the potential number of social associates [20,21,27], (b) the phenotypic composition of the breeding environment [26,28] or (c) associations of opposite-sex individuals during the female's fertile period (e.g. at nest-boxes [29]). However, for many animals, the breeding season is relatively brief and conditions can become suitable for breeding with short notice. By contrast, individuals can interact with others in different contexts for many months prior to breeding. Previous studies suggest that social associations among individuals before the breeding season can translate into the spatial breeding arrangement during spring [30] and potentially predict mating decisions, including social pair formation [31,32] and between-season divorce [33,34]. These findings suggest that social associations prior to breeding may also provide the opportunity for individuals to identify potential extra-pair mates or to form bonds with opposite-sex individuals other than the social mate.

Here, we examine whether social associations prior to the breeding season influence patterns of social and extra-pair mating in blue tits (*Cyanistes caeruleus*). Blue tits typically form socially monogamous pairs, but frequently engage in extra-pair mating (about half of the broods contain at least one extra-pair young and 10–15% of all offspring are sired by extra-pair males [35,36]). During winter, they forage in flocks including both conspecifics and heterospecifics [37]. Using PIT-tag technology and social network analyses in combination with parentage analysis, we quantified the birds' social associations during foraging events at local bird feeders during winter and monitored their breeding behaviour, including EPP, in the following spring.

We first test whether social associations at bird feeders predict the formation of future social pairs. Second, we examine whether winter associations can predict patterns of EPP. As extra-pair young are usually sired by close neighbours [21], we also test whether social associations at bird feeders during winter predict the observed spatial breeding arrangement—who nests nearby to who—and then examine whether these social associations predict patterns of EPP. Together, these analyses allow us to quantify the likelihood that a female–male dyad will have extra-pair young together while controlling for the two key factors known to influence EPP in blue tits (male age and breeding distance [21]). Our analyses include three variables representing the behaviour during the non-breeding phase: the arrival date of individuals in the local breeding area, the social association strength during foraging and the co-occurrence of individuals at nest-boxes. In blue tits, a larger difference in arrival date by previous social partners was associated with an increased likelihood of divorce [34]. In the context of this study, we predict (a) that a larger difference in arrival date between two opposite-sex individuals reduces the opportunity to interact and hence leads to a decreased likelihood of having extra-pair young together, and that (b) individuals with stronger social associations during foraging and those that (c) visited a nest-box together during winter will more likely become extra-pair partners. Third, we compare the association strength between social pairs, extra-pair partners and close neighbours. We predict that, if mating outcomes depend on winter social associations, the strength of those associations might be similar for within- and extra-pair partners. By contrast, if extra-pair mating is mainly the result of chance encounters during the fertile period, social pairs will show stronger winter associations than extra-pair partners. Finally, we calculate social networks for each month across the winter to investigate potential temporal patterns of the effects of the winter associations on the likelihood that a female–male dyad will become a social pair or extra-pair partners. Here, we predict that associations closer to the start of breeding are more meaningful in explaining mating patterns and that social pairs show stronger winter associations earlier on compared with extra-pair partners.

2. Materials and methods

(a) Study system

We studied a population of blue tits in a mixed-deciduous oak-dominated forest close to Landsberg am Lech, Germany (Westerholz, 48°08′26″N 10°53′29″E, approx. 40 ha). The study site contains 277 wooden nest-boxes since 2007 and 20 feeders that were put up in the fall of 2017. From November 2017 until mid-March 2018, the feeders provided food (crushed peanuts) ad libitum.

During the 2017 breeding season and the subsequent winter, we trapped blue tits and fitted them with a PIT-tag (transponder), which was implanted under the skin on the back, and a metal ring. We also scored age (yearling versus adult) and took a small (approx. 10 µl) blood sample for parentage analysis and sexing.

All nest-boxes and feeders were equipped with RFID antennas, such that each visit of a PIT-tagged blue tit was automatically recorded [38,39]. For each transponder detection, the bird's identity (unique transponder number), and the date and time were stored on a SD card. From these data, we then extracted information on the co-occurrence of individuals at feeders or nest-boxes and defined the timing of arrival into the study site as the first day an individual was detected (starting on 1 November 2017) either based on PIT tag detection or catching (following [34]). The data relevant for this study were collected between November 2017 and June 2018. For more details on the study system, see [40].

(b) Foraging associations

The detection of PIT-tagged blue tits at feeders created a temporal data-stream for each location and each day. We used the function 'gmmevents' from the R package 'asnipe' [41] in R (v. 3.5.1 [42]) to assign individuals to temporal clusters reflecting flocking events. This approach uses Gaussian mixture models [32] and generates social association data from sequential detections [43]. We then used the co-occurrence data to calculate the simple ratio index (SRI), defined as: $S_{AB} = x/x + y_{AB} + y_A + y_B$ [44,45]. Here, S_{AB} represents the association strength between individual A and B (i.e. the edge weight in the social network), x is the number of times both individuals co-occurred in the same flock, y_{AB} is the number of times they were both detected at the same time but not together, y_A is the number of times that A occurred in a flock without B over the time period where both individuals were known to be in the study site, and y_B is the number of times that B occurred in a flock without A over the period where both individuals were known to be in the study site. SRI values can range from 0 (two individuals never associated) to 1 (two individuals were always associated).

We created a non-directional weighted social network from the entire winter period including all individuals and ranked all the associates of a focal individual according to the association index SRI. For instance, if individual A has the following SRI values for three associates: $S_{AB} = 0$, $S_{AC} = 0.5$, $S_{AD} = 1$, the corresponding ranked values would be 1, 2 and 3. We then subtracted 1 from every ranked value and divided the new ranks by the maximum value (2 in our example). This resulted in a 'ranked' association index ranging from 0 (the individual with which the focal individual associated least) to 1 (the individual with which the focal individual associated the most). For each same- and mixed-sex dyad, we then calculated the average of the ranked association index from individual A to individual B and the ranked association index from individual B to individual A. From here on, we refer to this average value as the 'winter association strength'.

(c) Spatial overlap during foraging

We calculated the overlap in spatial activity of each dyad based on the amount of foraging locations that overlapped between the two individuals, as well as the amount of time they spent at these locations, following [30]. This resulted in a value from 0 (no overlap) to 1 (full overlap). For example, when individual A foraged 90% of the time at feeder 1 and 10% at feeder 2, and individual B foraged 90% at feeder 2 and 10% at feeder 1, their overlap in spatial activity would be 0.2 (10% overlap at feeder 1 and 10% overlap at feeder 2).

(d) Nest-box visits

For each female–male dyad, we quantified co-inspection of nest-boxes during winter (i.e. before the first signs of nest building in the population, which were on 14 March 2018). To find a meaningful definition for the co-occurrence of two individuals at a nest-box, we examined the nest-box visits of future social pair members during winter, because they likely perform nest inspections together. From all recorded visits and for each day and nest-box, we extracted the minimum time difference between the detection of the social female and the detection of her social mate. The minimum time difference between the nest-box visits of two future social partners was on average one minute (s.d. = 16 min, median = 0.02, range: 0–647 min; based on nest-box visits of 101 breeding pairs). Thus, we defined all visits of mixed-sex dyads that occurred within one minute as 'inspecting a nest-box together'. Because the majority of dyads did not visit a nest-box together or only rarely (599 dyads visited a nest-box together, approx. 0.4% of all possible mixed-sex dyads), we defined the co-occurrence at a nest-box as a binary variable (yes/ no).

(e) Spatial breeding arrangement

We examined the spatial breeding arrangement of birds using the R package 'expp' [46]. The package assigns territories to breeding pairs using Thiessen polygons. Based on this information, we determined the neighbourhood order of a focal pair to all breeding pairs in the study site, whereby first-order neighbours refer to neighbours sharing a territory border, second-order neighbours are those that have one territory in between them, and so on (for further details, see [21,46]). To calculate the neighbourhood order, we included all breeding birds, regardless of whether they had been present during winter. We recorded three cases of social polygyny (a male breeding with two females) during the 2018 breeding season. For these cases, we selected the female with whom the male settled first as 'social female' and assigned the territory accordingly. Further, we excluded five cases of replacement clutches (where either the same pair or the female or male bred again with a different partner after failure of the first clutch).

(f) Paternity analysis

During the 2018 breeding season, we collected blood samples from all nestlings and breeding adults that had not yet been sampled. We also collected and genotyped all unhatched eggs (provided sufficient DNA could be extracted) and all dead nestlings. Overall, we genotyped 1153 young out of 1238 laid eggs (93%). To assess parentage of all offspring, we used 8–11 microsatellite markers with on average 25 alleles per marker and compared the genotypes of putative parents and all offspring. We then determined how many extra-pair young each male sired with a given female and the number of extra-pair partners for both males and females. For a detailed description of the microsatellite markers and paternity analysis, see [36,40].

(g) Statistical analyses

For all analyses, we only included data of mixed-sex dyads where both individuals were present during winter (between November 2017 and mid-March 2018) and later bred in the study site. Presence in winter was necessary because some of the null models are based on the behaviour at bird feeders during this period (see below).

Social networks are based on non-independent observations of multiple individuals and thus network measures violate the assumptions underlying most parametric tests [47,48]. We used null models for hypothesis testing to account for non-independence of the data and for non-social factors (e.g. spatial preferences) that may affect the co-occurrence of individuals [47,49]. Specifically, we applied permutation tests by generating replicated datasets from the observed data in which the pattern of interest, in our case the associations among individuals, is randomized [47,49]. We then calculated the same test statistic for 1000 randomly generated datasets as for the observed data. If the value of the test statistic from the observed data fell outside the 95% range of values generated by the permutations, the effect was considered statistically significant. Details of each null model (i.e. for each hypothesis test) are given below.

(i) Do winter associations predict future social pairs?

We tested whether the winter association strength predicts whether a given female–male combination will become a social (breeding) pair, using a logistic matrix regression [50] with the 'netlogit' function of the R package 'sna' [51]. We included as the dependent variable whether a female–male combination ended up as a social breeding pair (yes/ no). The only explanatory variable was the winter association strength of each dyad. We examined the effect of winter association strength by performing 1000 permutations using a customized null model. We randomized the winter association strength across all dyads within the same neighbourhood order and randomized the association strength of social pairs within the first-order neighbours. Thus, we kept the spatial breeding structure of all individuals, but permuted the winter association strength among all opposite-sex conspecifics.

Some birds were only equipped with a transponder for part of the time during the study period. This means that they could have been part of the study population for an unknown period without having been detected, which may lead to a wrong representation of the social associations of these birds with others. Therefore, we repeated the analyses only including birds that had been equipped with a transponder prior to the start of the study.

(ii) Do winter associations predict spatial breeding arrangement?

We examined whether winter association strength predicts the breeding proximity of birds using a linear matrix regression with the 'netlm' function of the R package 'sna' [51] excluding social pairs from the dataset. We used a model with breeding proximity (i.e. the neighbourhood order, ranging from 1–5) of a dyad as the dependent variable and their winter association strength as well as their overlap in spatial activity during foraging as independent variables. We scaled all independent variables by dividing each value by two times the standard deviation to allow direct comparison of effect sizes among variables [52].

The breeding proximity of two individuals may simply reflect similar spatial preferences, and not the fact that they associated with each other (i.e. foraged together). To determine the effect of winter association strength, we performed 1000 permutations using a spatially restricted node permutation. We disentangled spatial and social effects by randomly reassigning the social network position of each individual to another individual that visited the same feeder before the start of the breeding season (i.e. the last feeder a bird was recorded at). For example, if individuals *A* and *B* were both recorded last at feeder 1, the social network positions of individuals *A* and *B* would be swapped. If only the preference for the same spatial location determines the associations of *A* and *B* with conspecifics, we would expect no difference between the observed and the permuted data. However, if individuals share the same spatial location but differ in their associations with other blue tits, the observed data will differ from the randomized data. Further, we repeated the analyses including only birds that had been equipped with a transponder before the start of the study.

Lastly, we compared the winter association strength between all neighbourhood orders. For each of the five neighbourhood orders, we determined the average winter association strength and calculated the difference in the means between all possible comparisons. We then randomly sampled the winter association strengths among the five orders, and again calculated the difference in the means between all order comparisons. We repeated this 1000 times and compared the differences calculated from the randomized data with the actual difference calculated from the observed data.

(iii) Do winter associations predict extra-pair paternity?

We examined whether we can predict the likelihood of a female–male combination to be classified as extra-pair partners from the winter association strength by performing a logistic matrix regression [50] using the 'netlogit' function [51]. We used the same dataset as described above (containing mixed-sex dyads and excluding social pairs). Whether a female–male combination had extra-pair young together (yes/ no) was the dependent variable. As independent variables, we included breeding distance (i.e. neighbourhood order, ranging from 1 to 5 [21]), male age (yearling versus adult [2]) and three factors describing the behaviour during winter: (1) winter association strength of each dyad, (2) the absolute difference in arrival time between members of each dyad and (3) whether both individuals inspected a nest-box together (yes/ no) during winter. We scaled all independent variables by dividing each value by two times the standard deviation [52]. We examined the effect of winter association strength using the same null model described in the section on social pairs.

We repeated the analyses on EPP on a smaller spatial scale, including only direct and second-order neighbours, because the majority of extra-pair sires bred within this neighbourhood (see results). We also repeated the analyses including only birds that had been equipped with a transponder before the start of the study.

Lastly, we examined whether the effect of winter association strength on EPP simply arises from the potential carry-over effects of the previous social breeding structure. We repeated the analyses with two datasets: (1) using dyads where both partners had bred in the study site in the previous season (2017) and (2) using dyads where at least one individual bred for the first time in the study site, which excludes the possibility of carry-over effects. If significant, this test provides evidence that the effect of winter social associations on patterns of EPP is not simply a by-product of the previous breeding associations.

(iv) Comparing the association strength between social partners, extra-pair partners and other close neighbours

We examined whether winter association strength differed between social pairs, extra-pair partners, direct neighbours and second-order neighbours. For each of the four categories of relationships, we determined the average winter association strength and calculated the difference in the means between all possible categories (e.g. social pairs, extra-pair partners, etc). Next, we randomly sampled the winter association strengths among the four categories and again calculated the difference in the means between all categories. We repeated 1000 times and inferred statistical significance by comparing the differences calculated from the randomized data to the actual difference calculated from the observed data.

(v) Temporal changes in the social network

The effect of winter association strength on the likelihood that a female–male dyad ends up as social pair or extra-pair partners may change during the study period. For example, associations closer to the start of breeding might be more meaningful in explaining mating patterns. Furthermore, the strength of the associations with the social (breeding) and the extra-pair partner may change over time. For example, social pairs may show stronger winter associations earlier on compared to extra-pair partners or the relative association strength of within- and extra-pair partners may change as birds anticipate the breeding season. To examine potential temporal differences in the effect of winter association strength, we created the same network as described above, but for each month separately (i.e. one network for November, December, January, February and 1–14 March). We then repeated the analyses to test whether winter association strength predicts whether a given female–male combination will become extra-pair partners or a social pair, as described in the sections (i) and (iii) above.

We also post-hoc split the winter into two halves (calculating one network for early winter: November–January) and one for late winter (February 1–14 March) and repeated all analyses as explained above.

3. Results

During the 5-month study, we recorded 30 205 flocking events at feeders (on average 15 per feeder per day including on average 4 individuals per flock, range = 1–42), comprising 563 individuals. Individuals were present on average 46 days (s.d. = 40.4, range: 1–138) and used 7.5 feeder locations (s.d. = 4.5, range: 1–20). From the 563 individuals recorded during winter, 221 (approx. 39%) bred in the subsequent spring. During the breeding season (14 March–25 June), we recorded 124 social pairs (excluding replacement clutches and cases of polygyny; see Materials and methods), i.e. 248 individuals (of which 221 (89%) were present during winter). Approximately 41% of nests contained at least one extra-pair young (range: 1–11 EPY per nest, mean = 2). In total, 59 dyads involving 95 individuals had extra-pair young ($N_{Females} = 49$, $N_{Males} = 46$). Of those 95 individuals, 64 (approx. 67%) were present during winter.

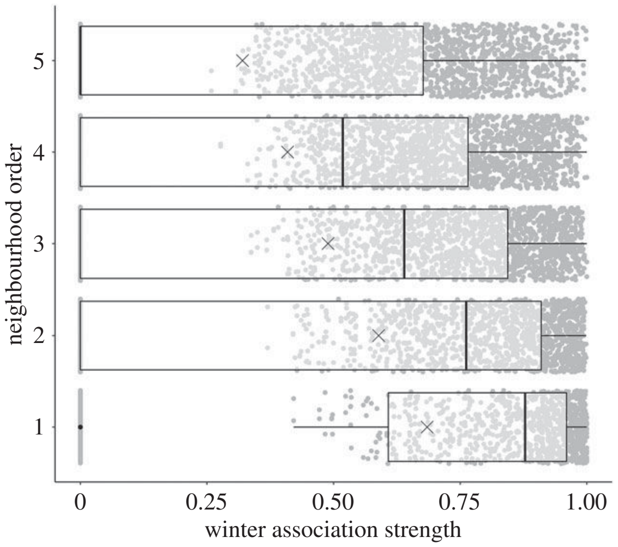


Figure 1. Relationship between breeding distance (neighbourhood order: 1 = direct neighbours, 2 = second-order neighbours, etc.) and winter association strength. Boxplots show the minimum values, lower quartile, median, upper quartile, maximum values and outliers (indicated as black dots). The mean is indicated by a cross. Grey points show all data. The mean winter association strength differed significantly between all neighbourhood order comparisons.

(a) Winter associations predict future social pairs

The association strength during winter was a significant predictor of whether a female–male dyad ended up as a social breeding pair ($N_{Dyads} = 12168$, $N_{Females} = 117$, $N_{Males} = 104$; estimate: 5.23, permutation test: $p < 0.001$). The results did not change qualitatively when the analysis only included individuals that had been equipped with a transponder before the start of the study ($N_{Dyads} = 7622$, $N_{Females} = 74$, $N_{Males} = 103$; estimate: 6.16, permutation test: $p < 0.001$).

(b) Winter associations predict spatial breeding arrangement

Individuals with a larger overlap in spatial activity during winter (estimate: −0.96, $p < 0.001$) and those with stronger winter associations during foraging (estimate: −0.17, permutation test: $p < 0.001$) ended up breeding closer together (figure 1). The results did not change qualitatively when the analysis only included individuals equipped with a transponder before the start of the study (electronic supplementary material, table S1). The mean winter association strength differed significantly between all neighbourhood orders (mean winter association strength: first order: 0.69 ± 0.38 s.d., second order: 0.59 ± 0.59 s.d., third order: 0.49 ± 0.39 s.d., fourth order: 0.41 ± 0.38 s.d., fifth order: 0.32 ± 0.36 s.d.; $p < 0.001$ for all comparisons; figure 1).

(c) Winter associations predict extra-pair paternity

Female–male dyads that were more strongly associated in winter were more likely to have extra-pair young together (mean winter association strength ± s.d.; EP partners: 0.75 ± 0.31, remaining neighbours: 0.32 ± 0.37; figure 2, table 1), independently of the spatial component (see corresponding null model). Further, female–male dyads that had visited a nest-box together before the breeding season were more likely to become extra-pair partners (percentage of pairs that visited a nest-box: EP partners: 23%, remaining neighbours: 2%; table 1), whereas the difference in arrival date did not have an effect (table 1).

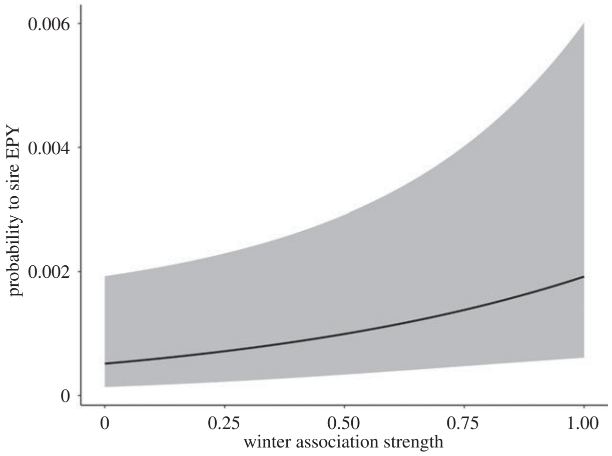


Figure 2. The predicted probability for a female–male dyad to have EPY together in the subsequent breeding season in relation to its winter association strength (while keeping all other independent variables constant at their mean values). The grey ribbon shows the 95% confidence interval from a generalized linear-mixed model including neighbourhood order, male age, box visit and difference in arrival as independent variables and including male and female identity as random effects.

The majority of nest-box visits were performed in late winter (January–mid-March). During this period, on average 13 unique dyads visited a nest-box on a given day (range: 1–37). During early winter (November–December), on average only 2 dyads visited a box on a given day (range: 1–4; electronic supplementary material, figure S1). Those birds that inspected a box did it on average with 2.3 other individuals (range: 1–8; excluding the future social partner). The number of partners with whom a bird visited a nest-box did not differ between faithful and unfaithful individuals (unfaithful: mean = 2.1, range: 1–7, faithful: 2.4, 1–8; Wilcoxon rank sum test: $W = 1288$, $p = 0.56$).

As in previous studies on blue tits, older males were more likely to sire extra-pair young (table 1) and the majority of extra-pair sires bred within the close neighbourhood (51% and 32% of extra-pair sires were first- and second-order neighbours, respectively). When the analysis was restricted to first- and second-order neighbours, the effect of winter association strength was similar in size, but no longer significant (table 1). The results did not change qualitatively when only individuals which had been equipped with a transponder before the start of the study were included (electronic supplementary material, table S2) or when running the analysis separately for dyads where both partners had bred in our study site in 2017 and for dyads where at least one bird was unfamiliar to the site. For both datasets, individuals with a higher association strength were more likely to have extra-pair young together (electronic supplementary material, table S3).

(d) Comparing the association strength between social partners, extra-pair partners and other close neighbours

Association strength was highest for social pairs and lowest for second-order neighbours (figure 3). Winter association strength did not differ significantly between social pairs (mean ± s.d.: 0.83 ± 0.30) and extra-pair partners (0.75 ± 0.31, permutation

Table 1. Results of logistic network regression models examining the effect of winter association strength on the likelihood of a female–male dyad to have extra-pair young together. The first model included all neighbourhoods (first to fifth order). The second model included only first- and second-order neighbourhoods. *p*-values inferred from the permutation tests are shown in italic.

	all neighbourhoods			first- and second-order neighbourhood		
	estimate	**exp(b)**	p	**estimate**	**exp(b)**	p
intercept	−6.34	0.002		−4.35	0.01	
neighbourhood order	−2.48	0.08	<0.001	−0.90	0.41	0.02
male age[a]	0.69	2.00	0.04	0.99	2.70	0.01
winter association strength	0.97	2.63	*0.01*	0.72	2.05	*0.06*
box visit[b]	0.40	1.50	0.01	0.66	1.93	0.01
difference in arrival time	0.53	1.70	0.16	0.19	1.21	0.65

[a] Adults compared with yearlings.

[b] Visiting a box together before the start of breeding (compared with no visit).

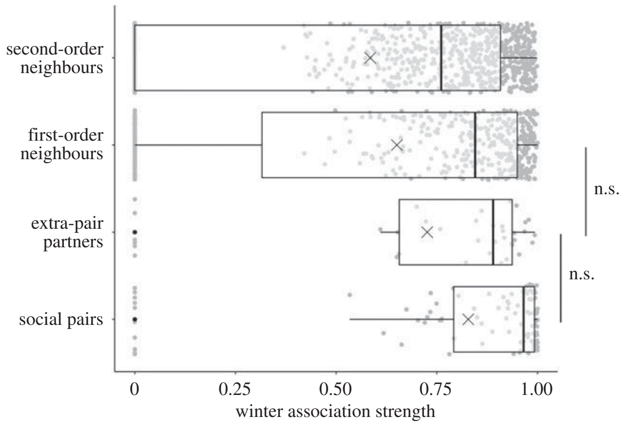


Figure 3. The winter association strength for different categories of female–male pairs. Boxplots show the minimum values, lower quartile, median, upper quartile, maximum values and outliers (indicated as black dots). The mean is indicated by a cross. Grey points show all data. Horizontal lines connect pair categories that do not differ significantly. Sample sizes for the different female–male dyads: $N_{Social\ pairs} = 99$, $N_{Extra\text{-}pair\ partners} = 37$, $N_{first\text{-}order\ neighbours} = 500$, $N_{second\text{-}order\ neighbours} = 937$.

test: $p = 0.18$; figure 3; electronic supplementary material, figure S2). However, the association strength also did not differ between extra-pair partners and direct neighbours (0.65 ± 0.39, permutation test: $p = 0.28$). Social pairs had significantly stronger associations compared to direct or second-order neighbours (0.58 ± 0.39, permutation test: both $p < 0.001$).

(e) Temporal changes in the social network

In general, the effect sizes of the association strength as predictor of mating increased as the breeding season approached (electronic supplementary material, figure S3). The strength of association in late winter (March) significantly predicted which female–male dyad ended up as extra-pair partners ($p < 0.001$), while the association strength earlier in winter (January–March) significantly predicted the likelihood of a dyad ending up as a social breeding pair (January: $p = 0.004$, February: $p = 0.007$, March: $p < 0.001$).

Effect sizes and p-values for analyses on social networks generated for the early (November–January) and late winter period (February–March) can be found in the electronic supplementary material (figure S4).

4. Discussion

It has been suggested that EPP emerges from the social interactions among multiple individuals (i.e. the focal male or female, their social partner and the potential extra-pair mate(s) [9,23]). Here, we provide extensive empirical support for this idea. We show that social associations during winter carry-over into the spatial breeding arrangement, whereby stronger associated individuals subsequently nested more closely together. This, by itself, will make it more likely that they end up becoming extra-pair mates, because extra-pair sires are typically close neighbours. However, independently of this spatial component, our results show that female–male dyads with stronger associations during winter are more likely to have extra-pair young together. Our study thus suggests that associations prior to breeding influence future mating behaviour.

The maintenance of social bonds with conspecifics can provide several benefits [53] such as reduced aggression [54], better access to information [55,56], increased opportunities for cooperation [57,58] or increased survival [59,60]. Thus, during a prolonged stationary period such as breeding, individuals might benefit from positioning themselves in a suitable social environment. Here, we show that associations during foraging prior to breeding carried over into the spatial breeding arrangement of blue tits (figure 1), similar to what has been found in the closely related great tit [30]. In great tits, familiarity with breeding neighbours increased reproductive success [61]. In cowbirds (*Molothrus ater*), females who spent more time with familiar individuals during the non-breeding phase laid more eggs in the subsequent breeding season [62]. Although the mechanisms underlying such effects are not yet clear, the potential benefits gained from having a familiar social surrounding during breeding may cause individuals to preferably nest closer to conspecifics they are more strongly associated with.

Familiarity to breeding neighbours may also facilitate opportunities for extra-pair matings. In many species, including blue tits, extra-pair young are mostly sired by neighbouring males (e.g. [29,63]). This raises the question whether EPP is simply the result of coincidental meetings between close neighbours or whether it emerges from social preferences for specific mating partners or is at least facilitated by previous social interactions. A previous study found no evidence that the proportion of familiar neighbours (i.e. familiar from previous breeding seasons) or the presence of a former social mate influenced the patterns of EPP [26]. Here we examined the associations among individuals that arose during the preceding non-breeding season. Our study shows that individuals that were more often foraging together in winter and those that visited a nest-box together were more likely to end up as extra-pair partners (figure 2 and table 1). Previously, Schlicht *et al.* [29] showed that the nest-box visits of males to neighbouring females during their fertile period also predicted the likelihood of having extra-pair young together, and our findings corroborate these results. Even though spatial proximity was the strongest predictor of the occurrence of EPP (the effect size for spatial proximity was more than double that of the winter association strength when considering all neighbourhoods, but effect sizes became more similar when only considering the close neighbourhood; table 1), our findings suggest that EPP does not only arise from spatial proximity and mating opportunities during breeding, but that they are also predicted by prior associations, especially those that took place closer to the start of the breeding season (electronic supplementary material, figure S3).

Winter social associations may simply reflect the preceding breeding social structure. However, when repeating the analyses only including dyads where at least one individual was not present, during the previous breeding season, the winter association strength still predicted extra-pair mating patterns. This indicates that winter social associations and their effect on EPP cannot solely be a consequence of the social structure during the previous breeding season. This finding makes logical sense, especially for short-lived species like the blue tit, as all individuals will necessarily experience a winter flocking period prior to first reproduction, and many individuals will reproduce only once in their life. However, our findings raise questions about whether the increased probability to have EPP with familiar individuals is due to mating preferences taking place prior to breeding (i.e. social associations are driven by extra-pair mate choice) or whether extra-pair matings are indirectly facilitated by other social processes (e.g. reduced aggression due to familiarity).

During winter, we found a clear negative gradient in the association strengths across what could be predicted as a spectrum of future reproductive engagement. Future social partners had the strongest association through to future second-order neighbours having the weakest. Importantly, the differences in winter association strength between future social pairs, extra-pair mates and close neighbours were small (figure 3), highlighting the substantial potential for reproductive outcomes to be shaped by over-winter associations. It could be that these results are explained by methodological limitations of our study. We measured associations exclusively based on foraging events and blue tits usually forage in flocks. Therefore, future social partners and neighbours (including future extra-pair partners) probably foraged together many times and hence may end up having similar association strengths. Information about fine-scale associations within flocks would help to conclusively show that social interactions with future extra-pair mates differ from other close neighbours. To fully understand whether and how prior social associations affect mating patterns, studies using more advanced tracking technologies [64] are needed to capture finer-scale patterns of social preferences. Furthermore, studies examining how differences in winter social structure (e.g. populations with varying levels of fission-fusion dynamics or with varying turn-over rates) affect future mating decisions would improve our understanding of mating patterns.

When and how individuals make mating decisions is still largely unknown. We assessed whether the importance of winter social associations as a predictor of future mating patterns changes over the season. Perhaps unsurprisingly, we find that the effects of social associations increased both for social pairs and extra-pair partners as the breeding season approached (electronic supplementary material, figure S3). For extra-pair partners, the effect of association was strongest in late winter, whereas the effect on social pairs was clear throughout the winter. While this pattern could simply be caused by lower statistical power at the beginning of the study (i.e. less individuals were present in November than in March), the conclusions seem robust. When we split the study period in early and a late winter, association strength in both periods significantly predicted future social pairs, whereas only the association strength in late winter predicted whether two individuals became extra-pair partners (electronic supplementary material, figure S4). These findings suggest that social pair bonds are established earlier than associations with extra-pair partners, thus providing new insights into the dynamics of different types of social relationships.

Ethics. Permits were obtained from the Bavarian government and the Bavarian regional office for forestry (LWF).

Data accessibility. Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.rv15dv44s [65].

Authors' contributions. All authors conceived the idea and designed the study; B.K. conducted the paternity analyses; K.B.B. and D.R.F. analysed the data with input from B.K.; K.B.B., D.R.F. and B.K. wrote the manuscript.

Competing interests. We declare we have no competing interests.

Funding. This work was supported by the Max Planck Society. D.R.F. received additional funding from the Deutsche Forschungsgemeinschaft (DFG grant FA 1402/4-1) and the DFG Centre of Excellence 2117 'Centre for the Advanced Study of Collective Behaviour' (ID: 422037984). K.B.B. is a PhD student in the International Max Planck Research School for Organismal Biology.

Acknowledgments. We are grateful to all people who contributed to data collection, in particular Agnes Türk, Andrea Wittenzellner, Carles Durà, Cécile Vansteenberghe, Friederike Böhm and Giulia Bambini. We thank Sylvia Kuhn and Alexander Girg for microsatellite genotyping; Peter Loës and Peter Skripsky for feeder and nest-box development and maintenance; Mihai Valcu for helpful comments on the analyses; and Daniel Costa and two anonymous reviewers for constructive comments on the manuscript. We thank the Bavarian regional office for forestry (LWF) for permission to work in Westerholz.

References

1. Webster MS, Pruett-Jones S, Westneat DF, Arnold SJ. 1995 Measuring the effects of pairing success, extra-pair copulations and mate quality on the opportunity for sexual selection. *Evolution (N. Y).* **49**, 1147–1157. (doi:10.1111/j.1558-5646.1995.tb04441.x)
2. Schlicht E, Kempenaers B. 2013 Effects of social and extra-pair mating on sexual selection in blue tits (*Cyanistes caeruleus*).

Evolution (N. Y) **67**, 1420–1434. (doi:10.1111/evo.12073)

3. Cornwallis CK, West SA, Davis KE, Griffin AS. 2010 Promiscuity and the evolutionary transition to complex societies. *Nature* **466**, 969–972. (doi:10.1038/nature09335)
4. Dillard JR, Westneat DF. 2016 Disentangling the correlated evolution of monogamy and cooperation. *Trends Ecol. Evol.* **31**, 503–513. (doi:10.1016/j.tree.2016.03.009)
5. Mobley KB, Jones AG. 2009 Environmental, demographic, and genetic mating system variation among five geographically distinct dusky pipefish (*Syngnathus floridae*) populations. *Mol. Ecol.* **18**, 1476–1490. (doi:10.1111/j.1365-294X.2009.04104.x)
6. Heinsohn R, Olah G, Webb M, Peakall R, Stojanovic D. 2019 Sex ratio bias and shared paternity reduce individual fitness and population viability in a critically endangered parrot. *J. Anim. Ecol.* **88**, 502–510. (doi:10.1111/1365-2656.12922)
7. Griffith SC, Owens IPF, Thuman KA. 2002 Extra pair paternity in birds: a review of interspecific variation and adaptive function. *Mol. Ecol.* **11**, 2195–2212. (doi:10.1046/j.1365-294X.2002.01613.x)
8. Brouwer L, Griffith SC. 2019 Extra-pair paternity in birds. *Mol. Ecol.* **28**, 4864–4882. (doi:10.1111/mec.15259)
9. Petrie M, Kempenaers B. 1998 Extra-pair paternity in birds: explaining variation between species and populations. *Trends Ecol. Evol.* **13**, 52–58. (doi:10.1016/S0169-5347(97)01232-9)
10. Westneat DF, Stewart IRK. 2003 Extra-pair paternity in birds: causes, correlates, and conflict. *Annu. Rev. Ecol. Evol. Syst.* **34**, 365–396. (doi:10.1146/annurev.ecolsys.34.011802.132439)
11. Kempenaers B, Verheyen GR, Dhondt AA. 1997 Extrapair paternity in the blue tit (*Parus caeruleus*): female choice, male charateristics, and offspring quality. *Behav. Ecol.* **8**, 481–492. (doi:10.1093/beheco/8.5.481)
12. Forstmeier W. 2007 Do individual females differ intrinsically in their propensity to engage in extra-pair copulations? *PLoS ONE* **2**, e952. (doi:10.1371/journal.pone.0000952)
13. Cleasby IR, Nakagawa S. 2012 The influence of male age on within-pair and extra-pair paternity in passerines. *Ibis (Lond. 1859)*. **154**, 318–324. (doi:10.1111/j.1474-919X.2011.01209.x)
14. Knief U *et al*. 2017 A sex-chromosome inversion causes strong overdominance for sperm traits that affect siring success. *Nat. Ecol. Evol.* **1**, 1177–1184. (doi:10.1038/s41559-017-0236-1)
15. Hasselquist D, Bensch S, von Schantz T. 1996 Correlation between male song repertoire, extra-pair paternity and offspring survival in the great reed warbler. *Nature* **381**, 229–232. (doi:10.1038/381229a0)
16. Yezerinac SM, Weatherhead PJ. 1997 Extra–pair mating, male plumage coloration and sexual selection in yellow warblers (*Dendroica petechia*). *Proc. R. Soc. Lond. B* **264**, 527–532. (doi:10.1098/rspb.1997.0075)
17. Rätti O, Hovi M, Lundberg A, Tegelström H, Alatalo RV. 1995 Extra-pair paternity and male characteristics in the pied flycatcher. *Behav. Ecol. Sociobiol.* **37**, 419–425. (doi:10.1007/BF00170590)
18. Hill CE, Akçay Ç, Campbell SE, Beecher MD. 2010 Extrapair paternity, song, and genetic quality in song sparrows. *Behav. Ecol.* **22**, 73–81. (doi:10.1093/beheco/arq171)
19. Stutchbury BJ, Morton ES. 1995 The effect of breeding synchrony on extra-pair mating systems in songbirds. *Behaviour* **132**, 675–690. (doi:10.1163/156853995X00081)
20. Westneat DF, Sherman PW. 1997 Density and extra-pair fertilizations in birds: a comparative analysis. *Behav. Ecol. Sociobiol.* **41**, 205–215. (doi:10.1007/s002650050381)
21. Schlicht L, Valcu M, Kempenaers B. 2015 Spatial patterns of extra-pair paternity: beyond paternity gains and losses. *J. Anim. Ecol.* **84**, 518–531. (doi:10.1111/1365-2656.12293)
22. Turjeman SF *et al*. 2016 Extra-pair paternity in the socially monogamous white stork (*Ciconia ciconia*) is fairly common and independent of local density. *Sci. Rep.* **6**, 27976. (doi:10.1038/srep27976)
23. Maldonado-Chaparro AA, Montiglio P, Forstmeier W, Kempenaers B, Farine DR. 2018 Linking the fine-scale social environment to mating decisions: a future direction for the study of extra-pair paternity. *Biol. Rev.* **93**, 1558–1577. (doi:10.1111/brv.12408)
24. Kokko H, Rankin DJ. 2006 Lonely hearts or sex in the city? Density-dependent effects in mating systems. *Phil. Trans. R. Soc. B* **361**, 319–334. (doi:10.1098/rstb.2005.1784)
25. McDonald GC, James R, Krause J, Pizzari T. 2013 Sexual networks: measuring sexual selection in structured, polyandrous populations. *Phil. Trans. R. Soc. B* **368**, 1–10. (doi:10.1098/rstb.2012.0356)
26. Beck KB, Valcu M, Kempenaers B. In preparation. Analysis of within-individual variation in extra-pair paternity in blue tits (*Cyanistes caeruleus*) shows low repeatability and little effect of changes in neighbourhood.
27. Van Wijk S, Bourret A, Bélisle M, Garant D, Pelletier F. 2016 The influence of iridescent coloration directionality on male tree swallows' reproductive success at different breeding densities. *Behav. Ecol. Sociobiol.* **70**, 1557–1569. (doi:10.1007/s00265-016-2164-5)
28. Roth AM, Firth JA, Patrick SC, Cole EF, Sheldon BC. 2019 Partner's age, not social environment, predicts extrapair paternity in wild great tits (*Parus major*). *Behav. Ecol.* **30**, 1782–1793.
29. Schlicht L, Valcu M, Kempenaers B. 2015 Male extraterritorial behavior predicts extrapair paternity pattern in blue tits, *Cyanistes caeruleus*. *Behav. Ecol.* **26**, 1404–1413. (doi:10.1093/beheco/arv076)
30. Firth JA, Sheldon BC. 2016 Social carry-over effects underpin trans-seasonally linked structure in a wild bird population. *Ecol. Lett.* **19**, 1324–1332. (doi:10.1111/ele.12669)
31. Teitelbaum CS, Converse SJ, Mueller T. 2017 Birds choose long-term partners years before breeding. *Anim. Behav.* **134**, 147–154. (doi:10.1016/j.anbehav.2017.10.015)
32. Psorakis I, Roberts SJ, Rezek I, Sheldon BC. 2012 Inferring social network structure in ecological systems from spatio-temporal data streams. *J. R. Soc. Interface* **9**, 3055–3066. (doi:10.1098/rsif.2012.0223)
33. Culina A, Radersma R, Sheldon BC. 2015 Trading up: the fitness consequences of divorce in monogamous birds. *Biol. Rev.* **90**, 1015–1034. (doi:10.1111/brv.12143)
34. Gilsenan C, Valcu M, Kempenaers B. 2017 Difference in arrival date at the breeding site between former pair members predicts divorce in blue tits. *Anim. Behav.* **133**, 57–72. (doi:10.1016/j.anbehav.2017.09.004)
35. Kempenaers B, Verheyen GR, Van den Broeck M, Burke T, Van Broeckhoven C, Dhondt A. 1992 Extra-pair paternity results from female preference for high-quality males in the blue tit. *Nature* **357**, 494–496. (doi:10.1038/357494a0)
36. Delhey K, Johnsen A, Peters A, Andersson S, Kempenaers B. 2003 Paternity analysis reveals opposing selection pressures on crown coloration in the blue tit (*Parus caeruleus*). *Proc. R. Soc. Lond. B* **270**, 2057–2063. (doi:10.1098/rspb.2003.2460)
37. Farine DR, Aplin LM, Sheldon BC, Hoppitt W. 2015 Interspecific social networks promote information transmission in wild songbirds. *Proc. R. Soc. B* **282**, 20142804. (doi:10.1098/rspb.2014.2804)
38. Loës P, Skripsky P, Kempenaers B. 2019 Github repository RFID-MS. (doi:10.5281/zenodo.3516586)
39. Loës P, Skripsky P, Kempenaers B. 2019 Github repository MOMO. (doi:10.5281/zenodo.3516588)
40. Schlicht L, Girg A, Loës P, Valcu M, Kempenaers B. 2012 Male extrapair nestlings fledge first. *Anim. Behav.* **83**, 1335–1343. (doi:10.1016/j.anbehav.2012.02.021)
41. Farine DR. 2013 Animal social network inference and permutations for ecologists in R using asnipe. *Methods Ecol. Evol.* **4**, 1187–1194. (doi:10.1111/2041-210X.12121)
42. R Development Core Team. 2018 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. http://www.r-project.org.
43. Psorakis I *et al*. 2015 Inferring social structure from temporal data. *Behav. Ecol. Sociobiol.* **69**, 857–866. (doi:10.1007/s00265-015-1906-0)
44. Cairns SJ, Schwager SJ. 1987 A comparison of association indices. *Anim. Behav.* **35**, 1454–1469. (doi:10.1016/S0003-3472(87)80018-0)
45. Hoppitt WJE, Farine DR. 2018 Association indices for quantifying social relationships: how to deal with missing observations of individuals or groups. *Anim. Behav.* **136**, 227–238. (doi:10.1016/j.anbehav.2017.08.029)
46. Valcu M, Schlicht L. 2013 R package 'expp'. See http://CRAN.R-project.org/package=expp.
47. Farine DR, Whitehead H. 2015 Constructing, conducting and interpreting animal social network analysis. *J. Anim. Ecol.* **84**, 1144–1163. (doi:10.1111/1365-2656.12418)
48. Croft DP, Madden JR, Franks DW, James R. 2011 Hypothesis testing in animal social networks.

Trends Ecol. Evol. **26**, 502–507. (doi:10.1016/j.tree.2011.05.012)

49. Farine DR. 2017 A guide to null models for animal social network analysis. *Methods Ecol. Evol.* **8**, 1309–1320. (doi:10.1111/2041-210X.12772)
50. Dekker D, Krackhardt D, Snijders TAB. 2007 Sensitivity of MRQAP tests to collinearity and autocorrelation conditions. *Psychometrika* **72**, 563–581. (doi:10.1007/s11336-007-9016-1)
51. Butts CT. 2008 Social network analysis with sna. *J. Stat. Softw.* **24**, 1–51. (doi:10.18637/jss.v024.i06)
52. Gelman A, Hill J. 2006 *Data analysis using regression and multilevel/hierarchical models*. Cambridge, UK: Cambridge University Press.
53. Cantor M *et al*. 2019 Animal social networks: revealing the causes and implications of social structure in ecology and evolution. EcoEvoRxiv
54. Temeles EJ. 1994 The role of neighbours in territorial systems: when are they 'dear enemies'? *Anim. Behav.* **47**, 339–350. (doi:10.1006/anbe.1994.1047)
55. Aplin LM, Farine DR, Morand-Ferron J, Sheldon BC. 2012 Social networks predict patch discovery in a wild population of songbirds. *Proc. R. Soc. B* **279**, 4199–4205. (doi:10.1098/rspb.2012.1591)
56. Firth JA, Sheldon BC, Farine DR. 2016 Pathways of information transmission among wild songbirds follow experimentally imposed changes in social foraging structure. *Biol. Lett.* **12**, 20160144. (doi:10.1098/rsbl.2016.0144)
57. Grabowska-Zhang AM, Sheldon BC, Hinde CA. 2012 Long-term familiarity promotes joining in neighbour nest defence. *Biol. Lett.* **8**, 544–546. (doi:10.1098/rsbl.2012.0183)
58. Carter GG, Wilkinson GS. 2013 Food sharing in vampire bats: reciprocal help predicts donations more than relatedness or harassment. *Proc. R. Soc. B* **280**, 20122573. (doi:10.1098/rspb.2012.2573)
59. Silk JB, Beehner JC, Bergman TJ, Crockford C, Engh AL, Moscovice LR, Wittig RM, Seyfarth RM, Cheney DL. 2009 The benefits of social capital: close social bonds among female baboons enhance offspring survival. *Proc. R. Soc. B* **276**, 3099–3104. (doi:10.1098/rspb.2009.0681)
60. Ekman J. 1990 Alliances in winter flocks of willow tits; effects of rank on survival and reproductive success in male–female associations. *Behav. Ecol. Sociobiol.* **26**, 239–245. (doi:10.1007/BF00178317)
61. Grabowska-Zhang AM, Wilkin TA, Sheldon BC. 2011 Effects of neighbor familiarity on reproductive success in the great tit (*Parus major*). *Behav. Ecol.* **23**, 322–333. (doi:10.1093/beheco/arr189)
62. Kohn GM. 2017 Friends give benefits: autumn social familiarity preferences predict reproductive output. *Anim. Behav.* **132**, 201–208. (doi:10.1016/j.anbehav.2017.08.013)
63. Komdeur J. 2001 Mate guarding in the Seychelles warbler is energetically costly and adjusted to paternity risk. *Proc. R. Soc. Lond. B* **268**, 2103–2111. (doi:10.1098/rspb.2001.1750)
64. Alarcón-Nieto G, Graving JM, Klarevas-Irby JA, Maldonado-Chaparro AA, Mueller I, Farine DR. 2018 An automated barcode tracking system for behavioural studies in birds. *Methods Ecol. Evol.* **9**, 1536–1547. (doi:10.1111/2041-210X.13005)
65. Beck KB, Farine DR, Kempenaers B. 2020 Data from: Winter associations predict social and extra-pair mating patterns in a wild songbird. Dryad Digital Repository. (doi:10.5061/dryad.rv15dv44s)

Supplementary material

Additional figures

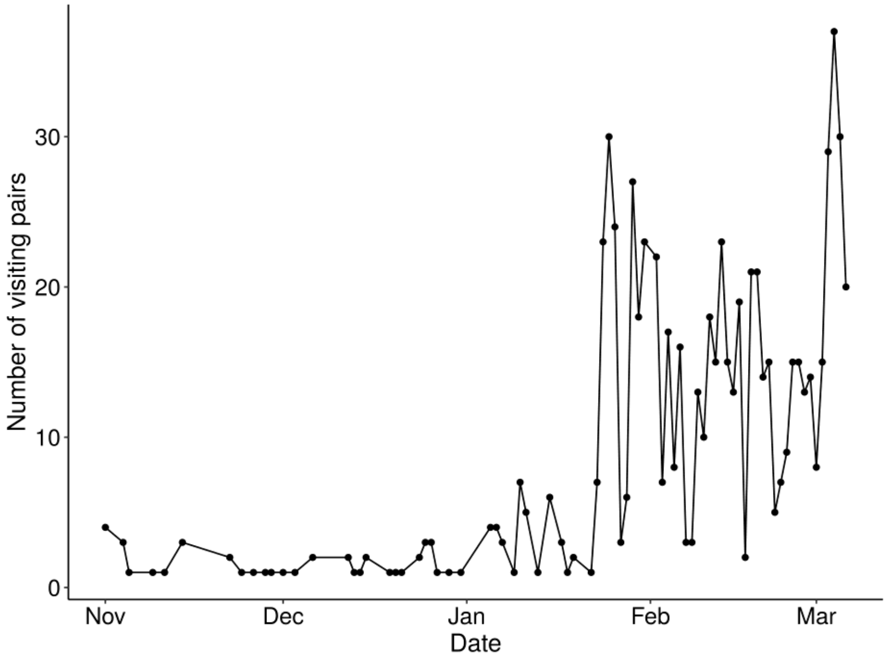


Figure S1. Plot showing the number of unique pairs that visited a nestbox together during the non-breeding phase (November – mid March). The y-axis represents the number of pairs that visited a nestbox and the x-axis represents the date on which the pair visited.

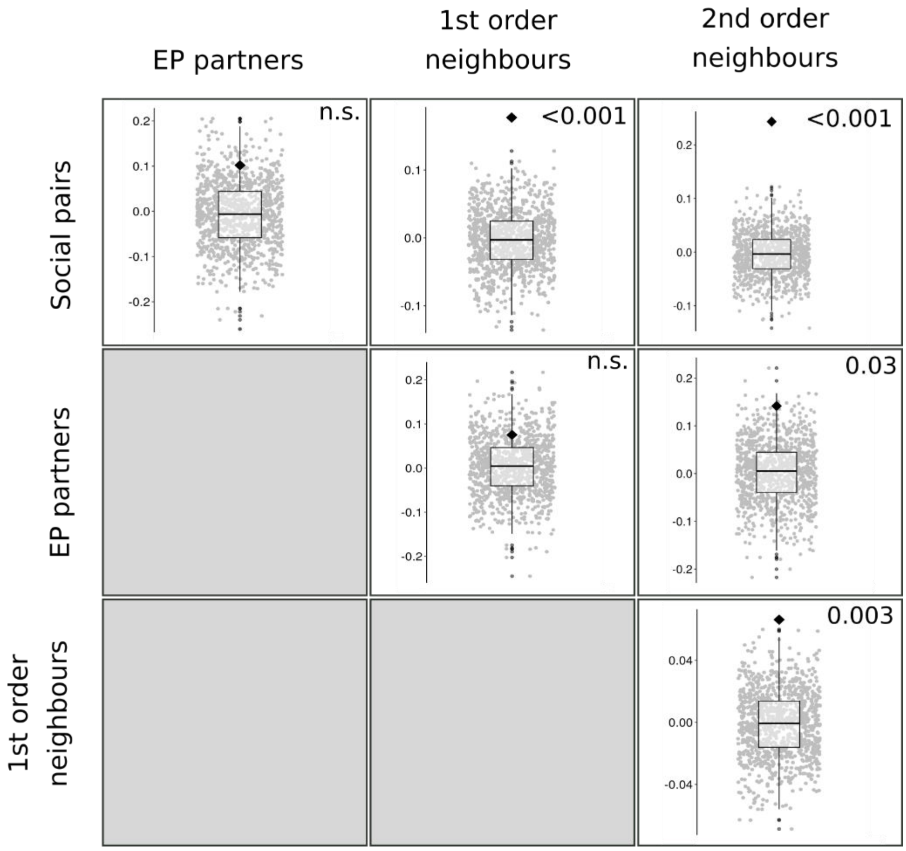


Figure S2. Figure showing the calculated difference in the mean association strength between different relationship categories (i.e., social pairs - extra-pair (EP) partners, social pairs – 1st order neighbours, social pairs – 2nd order neighbours, etc.). Boxplots and grey points represent the calculated differences between relationship categories generated from 1000 permutations. Boxplots show the minimum values, lower quartile, median, upper quartile, maximum values and outliers (indicated as black dots). The black diamonds represents the difference calculated from the observed data. The p value generated from the randomizations is shown for every relationship comparison in the upper right corner.

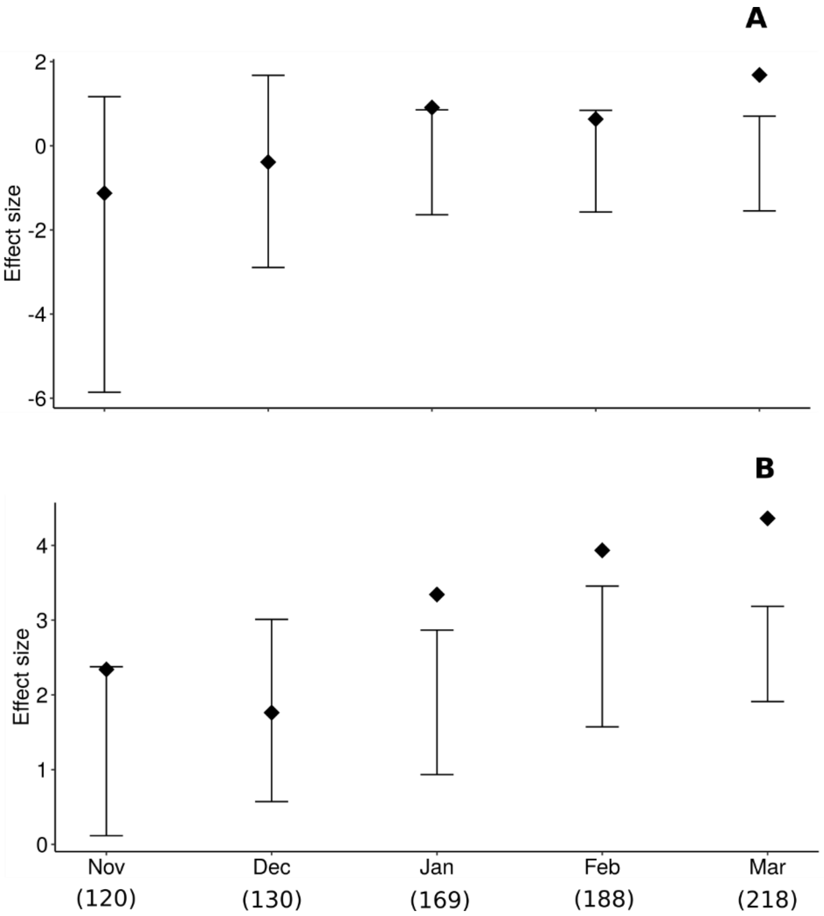


Figure S3. Effect sizes of the winter association strength during each month before breeding started on the likelihood to become extra-pair partners (A) or social (breeding) pairs (B). Bars indicate the 95% distribution range of the effect sizes generated from random sampling (permutation test); diamonds indicate the observed effect size. Numbers below each month indicate the sample sizes, i.e. the total number of individuals.

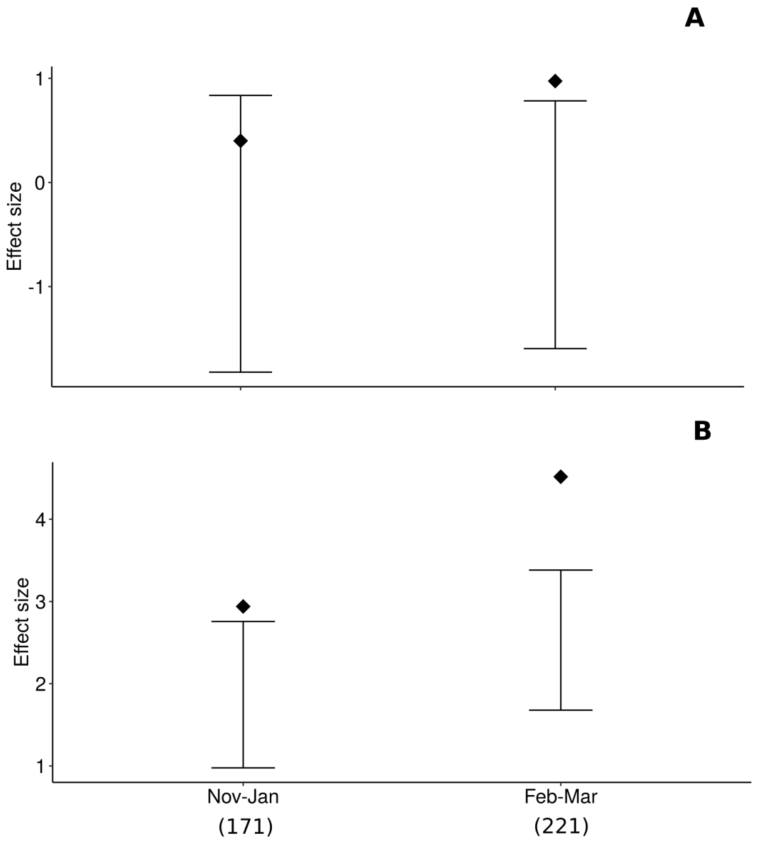


Figure S4. Effect sizes of the winter association strength during an early (November-January) and late (February-March) period before breeding started on the likelihood to become extra-pair partners (A) or social (breeding) pairs (B). Bars indicate the 95% distribution range of the effect sizes generated from random sampling (permutation test); diamonds indicate the observed effect size. P values inferred from the permutation tests for the early period: Extra-pair partners=0.44, Social pairs=0.02; late period: Extra-pair partners=0.03, Social pairs<0.001. Numbers below the time period indicate the sample sizes, i.e. the total number of individuals.

Additional tables

Table S1-S2 show the repeated analyses only including individuals which had been equipped with a transponder before the start of the study (N=177, 80% of the 221 individuals which were used for the analyses in the main text, N_{Dyads}=7834). For further details on the analyses see the descriptions within the main text.

Table S1. Results of the linear network regression model examining the effects of winter association strength and spatial overlap on the breeding proximity of individuals. High overlap in spatial activity and strong winter associations are both associated with breeding closer together. The P-value inferred from the permutation test is shown in italic.

	Estimate	**P**
Intercept	3.42	
Winter association strength	- 0.22	*< 0.001*
Overlap in spatial activity	- 1.00	< 0.001

Table S2. Results of logistic network regression models examining the effect of winter association strength on the likelihood of a female-male dyad to have extra-pair young together. The first model included all neighbourhoods (1st -5th order). The second model included only individuals that ended up as 1st or 2nd order neighbours. P-values inferred from the permutation tests are shown in italic.

	All neighbourhoods			**1st and 2nd order neighbourhoods**		
	Estimate	**Exp(b)**	**P**	**Estimate**	**Exp(b)**	**P**
Intercept	- 6.20	0.002		- 4.27	0.01	
Neighbourhood order	- 2.36	0.09	< 0.001	- 0.98	0.38	0.03
Male age*	0.46	1.59	0.20	0.83	2.29	0.06
Winter association strength	1.22	3.38	*0.01*	1.08	2.94	*0.03*
Box visit†	0.50	1.65	0.006	0.82	2.27	0.006
Difference in arrival time	0.62	1.85	0.16	0.28	1.32	0.58

*Adults compared to yearlings.
†Visiting a box together before the start of breeding (compared to no visit).

Table S3. Results of logistic network regression models examining the effect of winter association strength on the likelihood of a female-male dyad to have extra-pair young together. The first model included only dyads where at least one individual was unfamiliar to the study site (N_{Dyads}=18034). The second model included only dyads where both individuals had been breeding in our study site in 2017 (Dyads familiar from previous season, N_{Dyads}=3164). Both models include all neighbourhoods (1st -5th order). P-values inferred from the permutation tests are shown in italic.

	Dyads unfamiliar from previous season			**Dyads familiar from previous season**		
	Estimate	**Exp(b)**	**P**	**Estimate**	**Exp(b)**	**P**
Intercept	- 6.83	0.001		- 5.59	0.004	
Neighbourhood order	- 2.20	0.11	< 0.001	- 2.79	0.06	< 0.001
Male age*	1.49	4.42	0.05		**	
Winter association strength	0.93	2.55	*0.05*	1.18	3.26	*0.03*
Box visit†	0.38	1.48	0.12	0.44	1.55	0.05
Difference in arrival time	0.86	2.35	0.14	0.51	1.67	0.32

*Adults compared to yearlings.
†Visiting a box together before the start of breeding (compared to no visit).
** Not applicable as all previously breeding birds are adults.

Chapter 2

Social network position predicts male mating success in a small passerine

Kristina B. Beck, Damien R. Farine, Bart Kempenaers

Individuals differ in the quantity and quality of associations with conspecifics. The resulting variation in the positions that individuals occupy within their social environment can affect several aspects of life history, including reproductive behaviour. While research increasingly shows how social factors can predict dyadic mating patterns (i.e. who will breed with whom), much less is known about how an individual's social position affects it's overall likelihood to acquire mating partner(s). We studied social networks of socially monogamous blue tits (*Cyanistes caeruleus*) to investigate whether the number and strength of connections to opposite-sex conspecifics, the ratio between same- and opposite-sex connections, and the tendency to move between social groups in the months prior to breeding affects individuals' success in acquiring 1) a breeding partner and 2) an extra-pair partner. After controlling for differences in spatial location, we show that males that moved more often between social groups were more likely to acquire a mate and adult males that associated with more females were more likely to sire extra-pair young. The number of female associates also predicted the proportion of familiar female breeding neighbours, suggesting that familiarity among neighbours may facilitate opportunities for extra-pair matings. In females, none of the social network metrics significantly predicted the likelihood of acquiring a social or extra-pair partner. Our study suggests that the positioning of males within their social environment prior to breeding can translate into future mating success, adding an important new dimension to studies of (extra-pair) mating behaviour.

Unpublished manuscript

Introduction

Within animal groups, individuals typically occupy different social roles or positions (Aplin et al. 2015; Williams et al. 2017; Blaszczyk 2018), which can have fitness-relevant consequences. Differences in individual sociality, characterised by variation in the number and strength of connections to conspecifics and the centrality within the group, have been linked to processes such as the acquisition of information (Aplin et al. 2012; Kulahci and Quinn 2019), the contraction of diseases (Godfrey et al. 2009; Hamede et al. 2009), competition for resources (Farine and Sheldon 2015; Fisher et al. 2016), and survival (Stanton and Mann 2012; Alberts 2019). One dimension of life histories where variation in social position is also important is mating behaviour. Here, the number and strengths of connections can ultimately shape reproductive outcomes and the strength of sexual selection (Ryder et al. 2009; Oh and Badyaev 2010; Formica et al. 2012; McDonald et al. 2013; McDonald and Pizzari 2018).

An individual's social position in the group can impact its mating behaviour in several ways. For instance, connections to conspecifics are fundamentally linked to mate availability, to the degree of intra-specific competition, and to the potential for sexual harassment (e.g., Jirotkul 1999; Le Galliard et al. 2005; Maldonado-Chaparro et al. 2018; Grant and Grant 2019; Niemelä et al. 2019). Social factors operating at the individual level can generate population-level patterns in terms of which individuals are most likely to breed and with whom they reproduce. For the latter, there is increasing evidence that female-male relationships established prior to breeding can predict dyadic mating patterns (i.e. who will reproduce with whom; Rodway 2007; Psorakis et al. 2012; Teitelbaum et al. 2017; Firth et al. 2018; Maldonado-Chaparro et al. 2018; Beck et al. 2020). The female-male relationships formed prior to breeding can also extend to the patterns of future extra-pair partners (Beck et al. 2020). However, while the links between prior female-male relationships and future dyadic mating patterns are becoming well-established, much less is known about whether an individual's social position can determine it's overall likelihood to breed.

Studies have often examined the relationship between position in the social environment and breeding success in the light of male-male competition. These studies show that not only the focal male's phenotype but also the composition of the social environment (i.e. the other males' phenotypes) influence it's future success in gaining copulations (Formica et al. 2011; Wey et al. 2015; Ziv et al. 2016) or in acquiring a territory (Farine and Sheldon 2015). Furthermore, it has been shown that more central or active individuals (in males: Formica et al. 2012; Sih et al. 2014; in females: Ziv et al. 2016) and those with a higher number of social connections (both sexes: Sabol et al. 2020) gain more copulations. However, many of these studies focused on polygynandrous systems (Formica et al. 2011; Formica et al. 2012; Sih et al. 2014; Wey et al. 2015; Ziv et al. 2016) or examined mating success indirectly through the acquistion of nest sites (Farine and Sheldon 2015). Rarely have studies examined how social factors that relate to the competition for mates contribute to gaining reproductive success in species that form prolonged pair bonds for breeding, i.e. socially monogamous species (but see Oh and Badyaev 2010).

Most bird species are socially monogamous with biparental care (Black and Hulme 1996). Thus, the acquisition of a suitable social partner is a critical component of an individual's fitness. This is particularly true for short-lived species that may only have one or a few opportunities for reproduction. Characteristics that are important in acquiring a social partner may also be important in enhancing overall fitness via extra-pair offspring. Many bird species frequently engage in sexual behaviour outside their pair bond resulting in extra-pair paternity (Brouwer and Griffith 2019). Thus, reproduction can involve two processes: the formation of a social pair bond and the acquisition of extra-pair partners.

Individual differences in social position may affect the overall likelihood to acquire a social and extra-pair partner. For instance, individuals connected to more conspecifics of the opposite sex (Sabol et al. 2020), and those experiencing less competition (relatively fewer same-sex connections) prior to breeding should be more likely to find mates. Further, individuals moving more frequently between social groups (i.e. that are more central) may be more likely to acquire a social (Oh and Badyaev 2010) and extra-pair partner. Social factors may also influence within- and extra-pair reproduction in different ways. For example, a high number of associates may allow individuals to find a more preferred social partner, and lead to both greater reproductive output and less extra-pair paternity in the brood (Ihle et al. 2015). Individuals also differ in how frequently they re-associate with others. Thus, one could predict that individuals with fewer but stronger social bonds should be more likely to find a social partner but less likely to acquire extra-pair partners.

In this study, we investigated whether an individual's social position prior to breeding predicts its future mating success in a socially monogamous bird, the blue tit (*Cyanistes caeruleus*). Blue tits form social pairs during the breeding season and frequently engage in extra-pair matings (Kempenaers et al. 1992; Delhey et al. 2003). In winter, blue tits forage in large mixed-species flocks and the social relationships established during this time have been shown to predict who will mate with whom in the subsequent breeding, including social and extra-pair partners (Beck et al. 2020). Here, we examined the link between an individual's overall success in acquiring either a breeding partner or an extra-pair partner and four measures of an individual's social position: (i) the number of opposite-sex associates, (ii) the average association strength to the opposite-sex associates, (iii) the sex ratio of all its associates, as a measure for intra-sexual competition, and (iv) the tendency to move between, and therefore connect, different social groups. We predict that individuals that have more opposite-sex connections, that have on average stronger association strengths, that experience less competition (i.e. an opposite-sex biased ratio), and those with a greater tendency to move between social groups will be more likely to acquire a social partner and will be more likely to have had extra-pair partners.

Methods

Study species and system

Blue tits are hole-nesting songbirds that form socially monogamous pairs which defend a territory during the breeding season whereas during the winter they forage in large mixed-species flocks (Perrins 1979; Farine et al. 2015). They only breed once per year, except for some replacement clutches. In blue tits extra-pair partners are usually close breeding neighbours and adult males are more likely to sire extra-pair young than yearling males (Schlicht et al. 2015).

We collected data from August 2017 until the end of June 2018 from a population located in southern Germany (48°08’26”N 10°53’29”E) that has been studied since 2007. The study site contains 277 nest boxes and during winter (November 2017 – mid March 2018) 20 bird feeders. We arranged the nest boxes (approx. 40m apart) and feeders (approx. 200m apart) in an even grid across the whole study site and equipped all of them with radio-frequency identification (RFID) antennas (Loës et al. 2019a; Loës et al. 2019b). During each breeding season, nest boxes were checked at least once per week (from mid-March onwards) to monitor nest-building activity and to determine laying onset (date of first egg), clutch size and the dates of hatching and fledging.

Birds were trapped, either at the nest (as nestlings or breeding adults the previous spring) or during winter using mist-nets. From every bird, we took a small blood samples (ca. 10µl) for the paternity analysis and molecular sexing (see section on extra-pair paternity), some standard measurements such as tarsus length and weight, and determined their age based on the colour of the wing coverts (yearling vs. adult (Svensson 1992)). In addition, birds were fitted with a metal ring and a uniquely coded passive-integrated transponder (PIT-tag), which was implanted under the skin on the back. This allowed us to record data on the occurrence of birds with a PIT-tag if coming close (approx. 3cm) to the antenna of one of the bird feeders or nest boxes. At every detection, we logged the bird’s identity, the date, and time on a SD card. For further details on the study system see (Schlicht et al. 2012).

Social network

We inferred the social position of individuals by creating a network based on the foraging associations of PIT-tagged birds at feeders during the last two month before breeding (01 February–14 March, where the first signs of nest-building have been detected). We selected this time window as foraging associations during this period have been shown to be important for future mating (Beck et al. 2020). We defined an association as two birds foraging together within the same flock. We assigned individuals to flocking events based on a temporal clustering using Gaussian Mixture Models (Psorakis et al. 2012) with the function “gmmevents” from the R package “asnipe” (Farine 2013) in the program R (Team 2018). From these co-occurrence data, we then inferred the association strength of each dyad by calculating the simple ratio index (SRI), ranging from 0 (never observed in the same flock) to 1 (always observed in the same flock) (Cairns and Schwager 1987; Hoppitt and Farine 2018). We created an undirected weighted network and derived for each individual the number of opposite-sex associates (i.e. the degree), the average association strength to the opposite-sex associates (i.e. the average of an individual's edge weights), the sex ratio by dividing the number of same-sex associates through the total number of associates and the betweenness centrality (Freeman et al. 1979) using the R package “igraph” (Csardi and Nepusz 2006). Betweenness represents the number of shortest paths between individuals that pass through the focal individual, and represents an individual’s tendency to move between different flocks.

Pairing success

We defined a bird as having successfully acquired a social partner if we detected it breeding in one of the nest boxes in our study site. We quantified breeding pairs based on the PIT-tag detections at nest boxes throughout the breeding season. Both, female and male visit their breeding box frequently from nest-building onwards until their young fledge. We defined individuals as having been unsuccessful in acquiring a social partner if they were still present in our study site (i.e. based on PIT-tag detections at the nest boxes) from the start of the breeding season onwards but have not been recorded breeding in one of our boxes. We defined the start of the breeding season as the day on which the first nest material was found inside a nest box (i.e. 14th of March). We cannot exclude the possibility that “unsuccessful” individuals bred elsewhere in natural cavities within our study site. However, we suspect that the number of such birds within the study site is small, because there is an excess of nest boxes (i.e. high-quality nest sites) and even during the highest-density seasons not all nest boxes were occupied. Further, we only recorded a single case of blue tits breeding in a natural cavity within our study site (since 2007), but we may have missed other cases.

Extra-pair paternity

We genotyped nestlings and adults using 14 microsatellite markers and one sex chromosome linked marker (ADCbm; ClkpolyQ; Mcμ4; PAT MP 2-43; Pca3, Pca4, Pca7, Pca8, Pca9; PK11, PK12; PmaTAGAn71; POCC1, and POCC6). Microsatellite amplifications were performed in multiplexed PCRs and primer mixes containing two to five primer pairs. We compared the genotypes of parents and their offspring using the software CERVUS (Kalinowski et al. 2007). This allowed us to determine whether the brood of a female contained extra-pair young and which males sired extra-pair young. For further information on the paternity analysis see the supplementary material (Table S1).

Statistical analyses

Pairing success

We examined the effect of an individuals' social network position on its' pairing success by fitting generalized linear models (GLMs) using the R package "lme4" (Bates et al. 2015). Analyses were performed separately for males and females and only included data from birds that were present during winter and that had been equipped with a transponder before the start of the winter study (01 February 2018). Further, we excluded birds that had bred in our study site in previous years to exclude any effects of experience. We included as dependent variable whether the individual had bred or not ("binomial error structure") and as explanatory variables the four social network measures: (1) the number of opposite-sex associates, (2) the average association strength to opposite-sex associates, (3) the sex ratio and (4) the betweenness centrality. Further, we included an individual's arrival time into the study site as this has been shown to affect the likelihood to breed (Gilsenan et al. 2020) and it's age (yearling vs adult) assuming that adult males may be more likely to breed. The arrival time of birds was defined as the first day an individual was recorded based on automated detection at a nest box or feeder (starting from 01 August 2017 following Gilsenan et al. 2020 until the end of our winter study period on 14 March 2018). We standardised each variable by subtracting the mean and dividing two-times the standard deviation using the "standardize" function of the R package "arm" (Gelman 2008; Gelman and Su 2018). Correlation coefficients among all fixed effects were below the threshold ($r<0.5$, Dormann et al. 2013).

Extra-pair paternity

We examined the effect of an individuals' social network position on extra-pair paternity by fitting GLMs using the R package "lme4" (Bates et al. 2015). We analysed the data separately for males and females and only included data from birds that had been equipped with a transponder before the start of the study, that were present during winter and later bred in the study site. We included as dependent variable whether the individual had extra-pair young or not ("binomial error structure") and as explanatory variables the four social network measures as described above in the section on pairing success. For males, we only included adults (i.e. older than one year) as yearlings are much less likely to sire extra-pair young (Schlicht and Kempenaers 2013) (here only three yearlings sired extra-pair young). We standardised all explanatory variables and checked for correlations (all r<0.5) as described in the section on pairing success.

Null models

We used node permutations (Farine and Whitehead 2015; Farine 2017) to determine the effect of our social network measures on the likelihood to acquire a breeding partner or extra-pair partner. In node permutations, the identity of each node is randomized, breaking the link between the social network metrics and the individual identity (Farine 2017). We first performed an unrestricted permutation by randomly swapping the network position of same-sex individuals. Following, we performed a spatially restricted node permutation. This location-specific null model allowed us to control for potential confounding effects that may influence our social network metrics and thus their effect on the dependent variable. At the same time this allowed us to partially differentiate between patterns arising from social versus spatial effects. For instance, certain habitat configurations (e.g. vegetation, density, presence of predators etc.) in the location where an individual preferably forages may influence the social network metrics. In such a case, individual differences in network metrics may not necessarily arise from differences in social behaviour but simply from differences in spatial condition. We determined for each individual its' preferred feeder as the one that the individual most often visited. Ideally, we would then have swapped the network positions of those same-sex individuals that preferably foraged at the same feeder. However, as some feeders were only preferred by few individuals (6 feeders with less than 3 individuals), performing randomizations within each feeder location would not be meaningful. Thus, we clumped the bird feeders into spatial clusters, each containing at least 10 individuals. This resulted in five distinct clusters (each comprising 3-5 feeders, Figure S1). Following, we only swapped the network position of those same-sex individuals that preferably foraged in the same spatial cluster.

We repeated the node permutations for the unrestricted and the location-specific null model 1000 times and after each permutation, we repeated the GLM as described above in the sections on *paring success* and *extra-pair paternity*, and compared the coefficient of the slope from the observed data to the distribution of coefficients from 1000 models fitted to the randomised data. Cases where the observed value lays outside the 95% range of the distribution of randomised values indicated a statistically significant effect. If the observed data differ from the location-specific null model, differences in the network metrics and their potential effect on mating success are likely caused by differences in social behaviour rather than spatial effects.

Post-hoc analyses

We found that males associating with more females during winter were more likely to sire extra-pair young (see Results). Individuals breeding in neighbourhoods with higher densities are usually more likely to have extra-pair young (Schlicht et al. 2015). Thus, we examined whether the number of female associates translated into i) the number of neighbours and ii) the proportion of familiar females (familiarity defined as having associated during winter) within the close neighbourhood in the subsequent breeding season. We investigated the breeding neighbourhood of birds using the R package "expp" (Valcu and Schlicht 2013). The package assigns territories to breeding pairs using Thiessen polygons. Based on this information, we determined the neighbourhood order of a focal pair to all breeding pairs in the study site, whereby 1st order neighbours refer to neighbours sharing a territory border, 2nd order neighbours refer to those that have one territory in between them, and so on (for further details on the method see Valcu and Schlicht 2013; Schlicht et al. 2015). For our analyses we only focused on the close neighbourhood (i.e. 1st and 2nd direct neighbours) because this is where most extra-pair young are sired (Schlicht et al. 2015; 51% and 32% of extra pair sires were 1st and 2nd order neighbours, respectively). We fitted GLMs using the R package "lme4" (Bates et al. 2015) and included as dependent variable i) the number of direct neighbours in the close neighbourhood ("poisson error structure") and ii) the proportion of familiar females ("binomial error structure"). As explanatory variable we included the number of female associates during winter. We examined the effect of the number of female associates by performing node permutations as described above.

In addition, we examined whether the number of associates could be one of the underlying reasons for the increased extra-pair siring success in adult blue tits (Schlicht and Kempenaers 2013). For this, we performed a Wilcoxon rank sum test comparing the number of female associates between adult and yearling males.

Results

During winter, we recorded 13095 flocking events at feeders (on average 19 per feeder per day), comprising 452 individuals. Individuals on average were recorded on 24 days (sd=15.10, range: 1–48) and used 6 different feeder locations (sd=3.43, range: 1–17). From the 452 individuals, 221 (48.89%) were recorded breeding in one of our nest boxes.

Pairing success

We included 119 males (46 successfully paired, 73 did not pair) and 93 females (41 successfully paired, 52 did not pair) into the analysis on pairing success. We found that yearling males, and those arriving earlier and with a greater betweenness centrality (i.e. a greater tendency to move between different flocks) were more likely to breed in the subsequent spring (mean betweenness centrality±sd: breeding individuals: 1180.53±2748.19; not breeding: 180.17±504.43; Fig. 1A, Table 1). A juvenile male with an average betweenness centrality of 566.90 had a 47% probability to acquire a breeding partner (while keeping all other independent variables at their mean values; adult males: 25%; Fig. 1A). The effect of betweenness centrality on pairing success remained unchanged when controlling for spatial location (Figure 2A, Table 1). Our data on the betweenness centrality included one strong outlier (see Figure 1A) but the effect was still present when repeating the analysis after excluding this individual (Table S2). In females, none of the network metrics predicted the likelihood of pairing success but yearlings were more likely to breed than adults (Table 1).

Table 1. Results of the models examining the effect of the number of opposite-sex associates, the average association strength, the sex ratio, the betweenness centrality, age (yearling vs adult) and the arrival time on the likelihood to acquire a mate in males (N=119) and females (N=93). Significant *P* values are shown in bold and the *P* values for the four network metrics that were inferred from 1000 random permutations are shown in italic. *P* values derived from the unrestricted null model are indicated by a triangle (Δ) and values derived from the location-specific null model with an asterisk (*).

	Males			**Females**		
Fixed effect	**Estimate ± SE**	**z**	***P***	**Estimate ± SE**	**z**	***P***
Intercept	-0.48 ± 0.22	-2.14		-0.29 ± 0.24	-1.23	
Number of associates	-0.37 ± 0.50	-0.74	*0.44* $^{\Delta}$ *0.41* *	-0.35 ± 0.61	-0.58	*0.52* $^{\Delta}$ *0.51* *
Average association strength	0.28 ± 0.48	0.58	*0.53* $^{\Delta}$ *0.55* *	-0.28 ± 0.51	-0.54	*0.60* $^{\Delta}$ *0.59* *
Sex ratio	-0.20 ± 0.47	-0.43	*0.66* $^{\Delta}$ *0.66* *	0.59 ± 0.52	1.14	*0.26* $^{\Delta}$ *0.29* *
Betweenness centrality	**2.10 ± 0.91**	**2.32**	***0.01*** $^{\Delta}$ ***0.02*** *	0.70 ± 0.61	1.15	*0.27* $^{\Delta}$ *0.26* *
Age (adult)	**-1.00 ± 0.47**	**-2.13**	**0.03**	**-1.68 ± 0.60**	**-2.82**	**0.01**
Arrival time	**-1.48 ± 0.49**	**-3.04**	**0.002**	-1.08 ± 0.57	-1.89	0.06

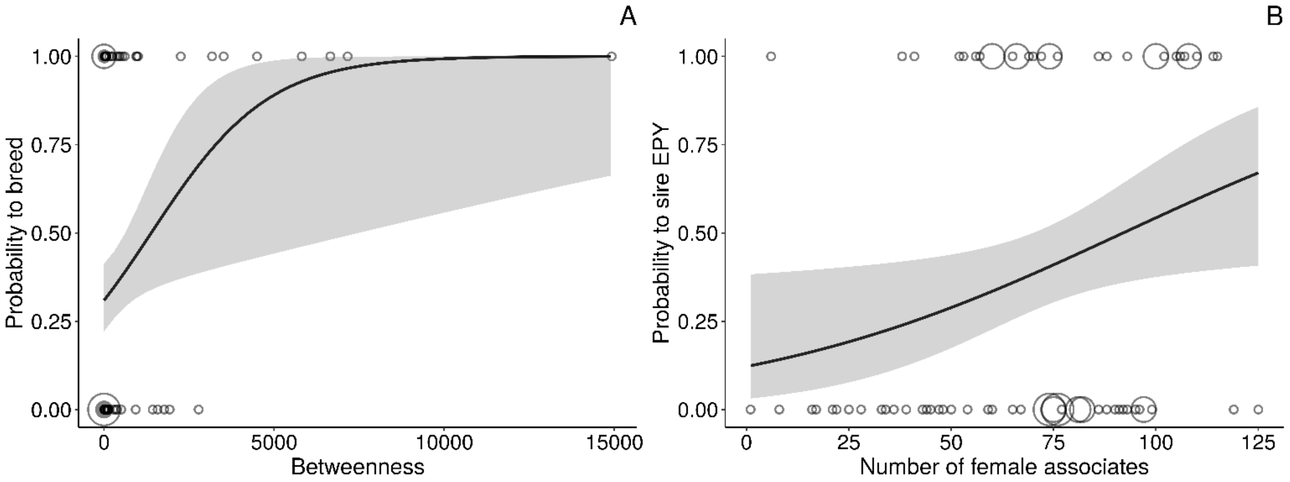


Figure 1. The predicted probability that a male bred in relation to the betweenness centrality (A) and the predicted probability that an adult male sired extra-pair young (EPY) in relation to the number of female associates (B). Nodes show the raw data and node size represent the number of individuals (A: N=1-30, B: N=1-3). The grey ribbon shows the 95% confidence interval from the generalized linear model described in the main text while keeping all other independent variables constant at their mean values (results in Table 1 and 2).

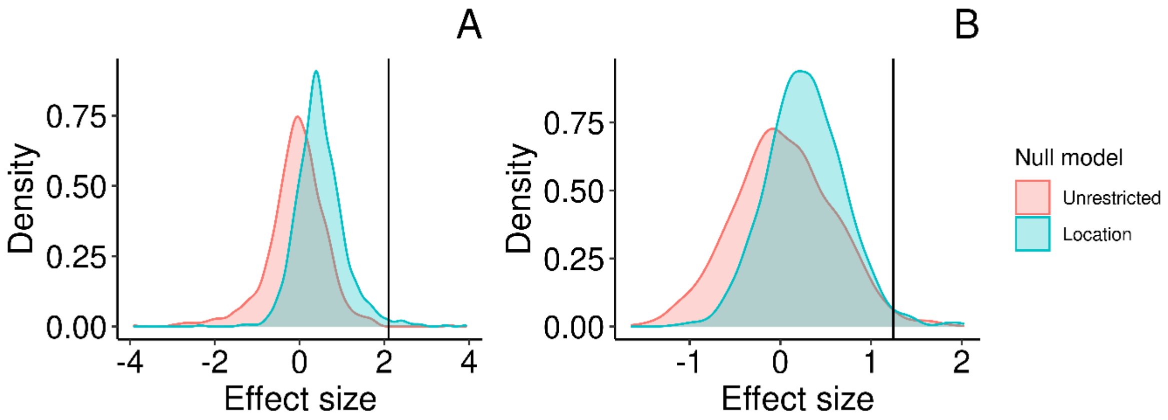


Figure 2. Distribution of the effect sizes of the observed and randomized data for males. The left panel shows the effect size of the betweenness centrality on pairing success (A) and the right panel shows the effect size of the number of female associates on extra-pair siring success (B). The black line indicates the effect size of the observed data (see also Table 1, 2). The density plots show the distribution of effect sizes generated with the unrestricted null model (red) and the location-specific null model (blue).

Extra-pair paternity

For our analysis on extra-pair paternity, we included 81 adult males (excluding 34 yearlings from the total 115 males) and 95 females. Of those, 32 adult males (and 3 yearlings) and 36 females had extra-pair young. Males that associated with more females during winter were more likely to sire extra-pair young, even when controlling for spatial location (mean number of female associates±sd: individuals having extra-pair young: 78.03±26.32; no extra-pair young: 63.94±29.58; Fig. 1, 2B, 3, Table 2). An adult male with an average number of 69.51 female associates had a 38% probability to acquire an extra-pair partner (while keeping all other independent variables constant at their mean values). The average association strength to females, the sex ratio and betweenness centrality did not predict extra-pair paternity (Table 2). The number of female associates did not differ between adult and yearling males (Table S3) and did not translate into having more neighbours during breeding but did lead to a greater proportion of familiar females within the close neighbourhood (Table S4). In females, none of the examined social network metrics predicted extra-pair paternity, although the effect of the number of male associates is also positive (Table 2).

Table 2. Results of the models examining the effect of the number of opposite-sex associates, the average association strength, the sex ratio and the betweenness centrality on the likelihood to acquire extra-pair young in adult males (N=81) and females (N=95). *P* values are inferred from 1000 random permutations and values derived from the unrestricted null model are indicated by a triangle (Δ) and values derived from the location-specific null model with an asterisk (*).

	Males			**Females**		
Fixed effect	**Estimate ± SE**	**z**	***P***	**Estimate ± SE**	**z**	***P***
Intercept	-0.48 ± 0.24	-1.20		-0.55 ± 0.23	-2.45	
Number of associates	**1.25 ± 0.57**	**2.19**	**0.02 Δ 0.02 ***	0.93 ± 0.53	1.74	0.08 Δ 0.07 *
Average association strength	0.64 ± 0.53	1.22	0.22 Δ 0.23 *	-0.02 ± 0.46	-0.05	0.96 Δ 0.96 *
Sex ratio	0.23 ± 0.53	0.43	0.66 Δ 0.74 *	0.91 ± 0.50	1.82	0.07 Δ 0.08 *
Betweenness centrality	-0.40 ± 0.53	-0.75	0.47 Δ 0.54 *	-1.14 ± 0.78	-1.47	0.10 Δ 0.10 *

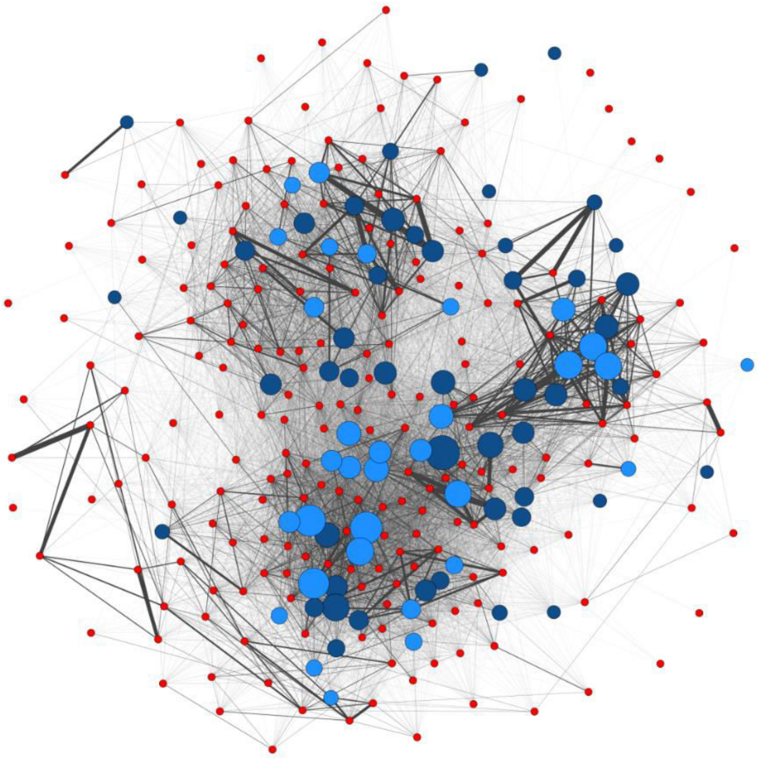


Figure 3. Social network representing all males included in the analysis on extra-pair paternity (N=81) and their connections to females during the study period. Females are shown in red and males in blue. Light blue indicates males that sired extra-pair young, dark blue shows males that did not. Node size in males represents their degree (i.e. larger nodes indicate a higher number of female connections); node size in females is kept constant. The thickness of lines between nodes represents the edge weight (i.e. thicker lines indicate stronger associations).

Discussion

Research increasingly acknowledges that animal social structure can affect various ecological processes and fitness outcomes (Croft et al. 2016; Webber and Vander Wal 2019; Cantor et al. 2019). Despite a considerable amount of research on the link between social effects and mating behaviour, few studies examined how social factors contribute to gaining reproductive success in socially monogamous species that form pair bonds for breeding. Here, we demonstrate that the social position of male blue tits during winter has consequences for their success in acquiring 1) a breeding partner and 2) extra-pair partner(s). Males with a greater tendency to move between flocks (a higher betweenness centrality) were more likely to breed than males that moved less. Further, adult males that were connected to more females during winter were more likely to sire extra-pair young in the subsequent breeding season, relative to males with fewer female associates. This suggests that the acquisition of a breeding partner probably follows different mechanisms than the acquisition of extra-pair partners. In females, none of the investigated social network metrics significantly predicted mating success.

Individuals can actively modify their social environment in order to increase mating success (Jirotkul 2000; Oh and Badyaev 2010; Formica et al. 2011). For instance, in house finches (*Carpodacus mexicanus*), males with a less elaborate plumage changed social groups more frequently (i.e. expressed a higher betweenness centrality) compared to more elaborate males (Oh and Badyaev 2010). This increased the relative attractiveness of less elaborate individuals to other males, leading to an increased pairing success (Oh and Badyaev 2010). Here, we found that male blue tits that moved more frequently between flocks were also more likely to subsequently be observed breeding (Fig.1A, Table 1). This could be the case if a higher betweenness centrality increases an individuals' opportunities to find a suitable social partner or if it increases the likelihood of a male to acquire a territory. Similar processes as found in the house finches may explain our findings, but this warrants further exploration.

Variation in extra-pair paternity has often been linked to characteristics of the breeding environment such as the breeding density (Westneat and Sherman 1997; Thusius et al. 2001; Schlicht et al. 2015) or synchrony (Stutchbury and Morton 1995; Chuang et al. 1999; Thusius et al. 2001). However, recent evidence suggests that extra-pair paternity does not only arise from conditions during breeding, but could be linked to pre-breeding associations between females and males (Maldonado-Chaparro et al. 2018; Beck et al. 2020). Here, we report that a male's success in gaining extra-pair young increased when he associated with more females prior to breeding (Fig. 1B, 3, Table 2). This finding raises the question of how more connections during winter translate into an increased likelihood to sire extra-pair young. If more associates lead to higher densities in the breeding neighbourhood this may result in more potential extra-pair partners. However, we found no such effect (Table S4). Instead we show that having more female associates translated into a higher proportion of familiar females within the close breeding neighbourhood (Table S4). Whether familiarity among neighbours facilitates extra-pair copulations still needs investigation. Also, a male's number of female connections was strongly correlated with its number of male connections and thus it's overall degree. Therefore, we cannot disentangle whether the increased success in gaining extra-pair young is caused by the greater availability of females or simply due to some males being more social than others.

Our findings show that the social features that predict a male's success in acquiring a social and extra-pair partner differ (i.e. betweenness centrality versus number of female associates). Thus, the acquisition of a future social partner may follow different processes than the acquisition of extra-pair partners. A study on the same population suggested that social partners get established earlier in winter than associations with future extra-pair partners (Beck et al. 2020). For social partners it might be beneficial to bond early in order to assess the compatibility of the future partner and in order to synchronize their behaviours (Spoon et al. 2006; Griggio and Hoi 2011; Ihle et al. 2015). Moving more frequently between social groups may facilitate to find a (suitable) breeding partner. Extra-pair matings may not require a prolonged pair formation process during winter but might simply arise from increased opportunities to engage in extra-pair copulations during breeding. As mentioned above, we speculate that familiarity between breeding neighbours might lead to an increase in extra-territorial visits (e.g. through active mate preference or decrease aggression) and thus increases opportunities for extra-pair copulations.

Individual differences in social network metrics may not necessarily result from differences in social behaviour, but may be affected by other factors such as the habitat configuration (He et al. 2019). Some individuals might for instance prefer to forage at sites with high densities of conspecifics that can lead to a higher number of social associates compared to individuals mostly foraging at low density sites. In our study, we controlled for the potential effect of spatial location, but the effect of our network measures on the likelihood to gain a breeding partner or extra-pair partner remained present. This suggests that the differences in individual social position are not simply due to spatial effects. However, the location-specific null model did create larger effect sizes than the unrestricted null model (mean effect size from 1000 permutations±sd: analysis on pairing success: unrestricted=-0.08±0.62, location-specific=0.46±0.56; analysis on extra-pair paternity: unrestricted=0.03±0.53, location-specific=0.29±0.43). Thus, the spatial location likely contributes, at least to some extent, to the observed effect.

The relationship between mating success and social network position may also result from underlying phenotypic traits that themselves directly influence mating success as well as network position. For instance, in the closely related great tit (*Parus major*), differences in personality have been linked to variation in extra-pair paternity (Van Oers et al. 2008) and to differences in social position (Aplin et al. 2013). Thus, it is important to disentangle whether the relation between mating success and social network position results from underlying phenotypic traits that directly influence both mating success and network position. Otherwise social position may be erroneously detected as target of selection. The link between extra-pair paternity and the number of prior associates could for example arise if females preferably associate with higher quality males. We tested whether the number of female associates differed with male age—a factor strongly influencing patterns of extra-pair paternity (Cleasby and Nakagawa 2012)—but found no support for such an effect (Table S3). More research is needed on the factors underlying individual social network position, and how position is linked to other phenotypic traits affecting mating success.

Acknowledgments

We thank the whole field team, and especially Agnes Türk, Andrea Wittenzellner, Carles Durà, Cécile Vansteenberghe, Friederike Böhm and Giulia Bambini for data collection and Peter Loës and Peter Skripsky for nest box and feeder maintenance. Further, we a grateful to Sylvia Kuhn and Alexander Girg for microsatellite genotyping, and Mihai Valcu for constructive comments on the analyses. We thank the Bavarian regional office for forestry (LWF) for permission to work in Westerholz.

References

Alberts SC. 2019. Social influences on survival and reproduction: Insights from a long-term study of wild baboons. J Anim Ecol. 88(1):47–66.

Aplin LM, Farine DR, Morand-Ferron J, Sheldon BC. 2012. Social networks predict patch discovery in a wild population of songbirds. Proc R Soc London B Biol Sci. 279(1745):4199–4205.

Aplin LM, Farine DR, Morand-Ferron J, Cole EF, Cockburn A, Sheldon BC. 2013. Individual personalities predict social behaviour in wild networks of great tits (Parus major). Ecol Lett. 16(11):1365–1372.

Aplin LM, Firth JA, Farine DR, Voelkl B, Crates RA, Culina A, Garroway CJ, Hinde CA, Kidd LR, Psorakis I. 2015. Consistent individual differences in the social phenotypes of wild great tits, Parus major. Anim Behav. 108:117–127.

Bates D, Maechler M, Bolker B, Walker S. 2015. lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1–7. 2014.

Beck KB, Farine DR, Kempenaers B. 2020. Winter associations predict social and extra-pair mating patterns in a wild songbird. Proc R Soc B. 287(1921):20192606.

Black JM, Hulme M. 1996. Partnerships in birds: The study of monogamy: The study of monogamy. Oxford University Press, UK.

Blaszczyk MB. 2018. Consistency in social network position over changing environments in a seasonally breeding primate. Behav Ecol Sociobiol. 72(1):11.

Brouwer L, Griffith SC. 2019. Extra-pair paternity in birds. Mol Ecol. 28(22):4864–4882.

Cairns SJ, Schwager SJ. 1987. A comparison of association indices. Anim Behav. 35(5):1454–1469.

Cantor M, Maldonado-Chaparro A, Beck K, Carter G, He P, Hillemann F, Klarevas-Irby J, Lang S, Ogino M, Papageorgiou D. 2019. Animal social networks: revealing the causes and implications of social structure in ecology and evolution. EcoEvoRxiv.

Chuang HC, Webster MS, Holmes RT. 1999. Extrapair paternity and local synchrony in the Black-throated Blue Warbler. Auk.:726–736.

Cleasby IR, Nakagawa S. 2012. The influence of male age on within-pair and extra-pair paternity in passerines. Ibis. 154(2):318–324.

Croft DP, Darden SK, Wey TW. 2016. Current directions in animal social networks. Curr Opin Behav Sci. 12:52–58.

Csardi G, Nepusz T. 2006. The igraph software package for complex network research, InterJournal, Complex Systems 1695. 2006. http://igraph.org.

Delhey K, Johnsen A, Peters A, Andersson S, Kempenaers B. 2003. Paternity analysis reveals opposing selection pressures on crown coloration in the blue tit (Parus caeruleus). Proc R Soc London B Biol Sci. 270(1528):2057–2063.

Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carré G, Marquéz JRG, Gruber B, Lafourcade B, Leitão PJ. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography. 36(1):27–46.

Farine DR. 2013. Animal social network inference and permutations for ecologists in R using asnipe. Methods Ecol Evol. 4(12):1187–1194.

Farine DR. 2017. A guide to null models for animal social network analysis. Methods Ecol Evol. 8(10):1309–1320.

Farine DR, Aplin LM, Sheldon BC, Hoppitt W. 2015. Interspecific social networks promote information transmission in wild songbirds. Proc R Soc B Biol Sci. 282(1803):20142804.

Farine DR, Sheldon BC. 2015. Selection for territory acquisition is modulated by social network structure in a wild songbird. J Evol Biol. 28(3):547–556.

Farine DR, Whitehead H. 2015. Constructing, conducting and interpreting animal social network analysis. J Anim Ecol. 84(5):1144–1163.

Firth JA, Cole EF, Ioannou CC, Quinn JL, Aplin LM, Culina A, McMahon K, Sheldon BC. 2018. Personality shapes pair bonding in a wild bird social system. Nat Ecol Evol. 2(11):1696–1699.

Fisher DN, Rodríguez-Muñoz R, Tregenza T. 2016. Comparing pre-and post-copulatory mate competition using social network analysis in wild crickets. Behav Ecol. 27(3):912–919.

Formica VA, McGlothlin JW, Wood CW, Augat ME, Butterfield RE, Barnard ME, Brodie III ED. 2011. Phenotypic assortment mediates the effect of social selection in a wild beetle population. Evolution. 65(10):2771–2781.

Formica VA, Wood CW, Larsen WB, Butterfield RE, Augat ME, Hougen HY, BRODIE III ED. 2012. Fitness consequences of social network position in a wild population of forked fungus beetles (Bolitotherus cornutus). J Evol Biol. 25(1):130–137.

Freeman LC, Roeder D, Mulholland RR. 1979. Centrality in social networks: II. Experimental results. Soc Networks. 2(2):119–141.

Le Galliard J-F, Fitze PS, Ferrière R, Clobert J. 2005. Sex ratio bias, male aggression, and population collapse in lizards. Proc Natl Acad Sci. 102(50):18231–18236.

Gelman A. 2008. Scaling regression inputs by dividing by two standard deviations. Stat Med. 27(15):2865–2873.

Gelman A, Su Y-S. 2018. arm: Data Analysis Using Regression and Multilevel/Hierarchical Models. R package version 1.10-1. https://CRAN.R-project.org/package=arm.

Gilsenan C, Valcu M, Kempenaers B. 2020. Timing of arrival in the breeding area is repeatable and affects reproductive success in a non-migratory population of blue tits. J Anim Ecol.

Godfrey SS, Bull CM, James R, Murray K. 2009. Network structure and parasite transmission in a group living lizard, the gidgee skink, Egernia stokesii. Behav Ecol Sociobiol. 63(7):1045–1056.

Grant PR, Grant BR. 2019. Adult sex ratio influences mate choice in Darwin's finches. Proc Natl Acad Sci. 116(25):12373–12382.

Griffith SC, Owens IPF, Thuman KA. 2002. Extra pair paternity in birds: a review of interspecific variation and adaptive function. Mol Ecol. 11(11):2195–2212.

Griggio M, Hoi H. 2011. An experiment on the function of the long-term pair bond period in the socially monogamous bearded reedling. Anim Behav. 82(6):1329–1335.

Hamede RK, Bashford J, McCallum H, Jones M. 2009. Contact networks in a wild Tasmanian devil (Sarcophilus harrisii) population: using social network analysis to reveal seasonal variability in social behaviour and its implications for transmission of devil facial tumour disease. Ecol Lett. 12(11):1147–1157.

He P, Maldonado-Chaparro AA, Farine DR. 2019. The role of habitat configuration in shaping social structure: a gap in studies of animal social complexity. Behav Ecol Sociobiol. 73(1):1–14.

Hoppitt WJE, Farine DR. 2018. Association indices for quantifying social relationships: how to deal with missing observations of individuals or groups. Anim Behav. 136:227–238.

Ihle M, Kempenaers B, Forstmeier W. 2015. Fitness benefits of mate choice for compatibility in a socially monogamous species. PLoS Biol. 13(9):e1002248.

Jirotkul M. 1999. Operational sex ratio influences female preference and male–male competition in guppies. Anim Behav. 58(2):287–294.

Jirotkul M. 2000. Male trait distribution determined alternative mating tactics in guppies. J Fish Biol. 56(6):1427–1434.

Kalinowski ST, Taper ML, Marshall TC. 2007. Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. Mol Ecol. 16(5):1099–1106.

Kempenaers B, Verheyen GR, Van den Broeck M, Burke T, Van Broeckhoven C, Dhondt A. 1992. Extra-pair paternity results from female preference for high-quality males in the blue tit. Nature. 357(6378):494–496.

Kulahci IG, Quinn JL. 2019. Dynamic relationships between information transmission and social connections. Trends Ecol Evol. 34(6):545-554.

Loës P, Skripsky P, Kempenaers B. 2019a. Github repository RFID-MS. doi:10.5281/zenodo.3516586.

Loës P, Skripsky P, Kempenaers B. 2019b. Github repository MOMO. doi:10.5281/zenodo.3516588.

Maldonado-Chaparro AA, Montiglio P, Forstmeier W, Kempenaers B, Farine DR. 2018. Linking the fine-scale social environment to mating decisions: a future direction for the study of extra-pair paternity. Biol Rev. 93(3):1558–1577.

McDonald GC, James R, Krause J, Pizzari T. 2013. Sexual networks: measuring sexual selection in structured, polyandrous populations. Philos Trans R Soc B Biol Sci. 368(1613):20120356.

McDonald GC, Pizzari T. 2018. Structure of sexual networks determines the operation of sexual selection. Proc Natl Acad Sci. 115(1):E53–E61.

Niemelä PT, Tiso S, Dingemanse NJ. 2019. Density-dependent costs and benefits of male mating success in a wild insect. bioRxiv.:733832. doi:10.1101/733832.

Van Oers K, Drent PJ, Dingemanse NJ, Kempenaers B. 2008. Personality is associated with extrapair paternity in great tits, Parus major. Anim Behav. 76(3):555–563.

Oh KP, Badyaev A V. 2010. Structure of social networks in a passerine bird: consequences for sexual selection and the evolution of mating strategies. Am Nat. 176(3):E80–E89.

Perrins CM. 1979. British tits. HarperCollins.

Psorakis I, Roberts SJ, Rezek I, Sheldon BC. 2012. Inferring social network structure in ecological systems from spatio-temporal data streams. J R Soc Interface. 9(76):3055–3066.

Rodway MS. 2007. Timing of pairing in waterfowl I: Reviewing the data and extending the theory. Waterbirds. 30(4):488–505.

Ryder TB, Parker PG, Blake JG, Loiselle BA. 2009. It takes two to tango: reproductive skew and social correlates of male mating success in a lek-breeding bird. Proc R Soc B Biol Sci. 276(1666):2377–2384.

Sabol AC, Lambert CT, Keane B, Solomon NG, Dantzer B. 2020. How does individual variation in sociality influence fitness in prairie voles? Anim Behav. 163:39–49.

Schlicht E, Kempenaers B. 2013. Effects of social and extra-pair mating on sexual selection in blue tits (cyanistes caeruleus). Evolution. 67(5):1420–1434.

Schlicht L, Girg A, Loës P, Valcu M, Kempenaers B. 2012. Male extrapair nestlings fledge first. Anim Behav. 83(6):1335–1343.

Schlicht L, Valcu M, Kempenaers B. 2015. Spatial patterns of extra-pair paternity: beyond paternity gains and losses. J Anim Ecol. 84(2):518–531.

Sih A, Chang AT, Wey TW. 2014. Effects of behavioural type, social skill and the social environment on male mating success in water striders. Anim Behav. 94:9–17.

Spoon TR, Millam JR, Owings DH. 2006. The importance of mate behavioural compatibility in parenting and reproductive success by cockatiels, Nymphicus hollandicus. Anim Behav. 71(2):315–326.

Stanton MA, Mann J. 2012. Early social networks predict survival in wild bottlenose dolphins. PLoS One. 7(10):e47508.

Stutchbury BJ, Morton ES. 1995. The effect of breeding synchrony on extra-pair mating systems in songbirds. Behaviour. 132(9):675–690.

Svensson L. 1992. Identification guide to European passerines. L. Svensson.

Team RC. 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Teitelbaum CS, Converse SJ, Mueller T. 2017. Birds choose long-term partners years before breeding. Anim Behav. 134:147–154.

Thusius KJ, Dunn PO, Peterson KA, Whittingham LA. 2001. Extrapair paternity is influenced by breeding synchrony and density in the common yellowthroat. Behav Ecol. 12(5):633–639.

Valcu M, Schlicht L. 2013. Package ‘expp.’

Webber QMR, Vander Wal E. 2019. Trends and perspectives on the use of animal social network analysis in behavioural ecology: a bibliometric approach. Anim Behav. 149:77–87.

Westneat DF, Sherman PW. 1997. Density and extra-pair fertilizations in birds: a comparative analysis. Behav Ecol Sociobiol. 41(4):205–215.

Wey TW, Chang AT, Fogarty S, Sih A. 2015. Personalities and presence of hyperaggressive males influence male mating exclusivity and effective mating in stream water striders. Behav Ecol Sociobiol. 69(1):27–37.

Williams AE, Worsley-Tonks KEL, Ezenwa VO. 2017. Drivers and consequences of variation in individual social connectivity. Anim Behav. 133:1–9.

Ziv EB, Ilany A, Demartsev V, Barocas A, Geffen E, Koren L. 2016. Individual, social, and sexual niche traits affect copulation success in a polygynandrous mating system. Behav Ecol Sociobiol. 70(6):901–912.

Supplementary material

Additional information on the paternity analysis

Table S1. Microsatellite loci for blue tits. Primer sequences include information on fluorescence labels used. *C* refers to the primer concentration in multiplex primer mix. Size range and number of alleles refer to 2018 data (*n*=1696; Phtr3 from 2017, *n*=1905).

Locus	**Accession no.**	**Primer sequences (5' - 3')**	***C* (µM)**	**Multiplex Mix**	**Size range (bp)**	**number of alleles**
ADCYAP1_bm	FJ464427	VIC-GATGTGAGTAACCAGCCACT ATAACACAGGAGCGGTGA	0,2 µM	2	160 - 172	10
ClkpolyQ	AY338423-28	6FAM-TTTTCTCAAGGTCAGCAGCTTGT CTGTAGGAACTGTTGYGGKTGCTG	0,36 µM	4	266 - 283	7
Mcµ4	U82388	PET-ATAAGATGACTAAGGTCTCTGGTG TAGCAATTGTCTATCATGGTTTG	1,1 µM	2	156 - 194	19
PAT MP 2-43	AM056063	6FAM- ACAGGTAGTCAGAAATGGAAAG GTATCCAGAGTCTTTGCTGATG	0,24 µM	4	125 - 155	8
Pca3	AJ279805	PET-GGTGTTTGTGAGCCGGGG TGTTACAACCAAAGCGGTCATTTG	0,8 µM	1	154 - 234	43
Pca4	AJ279806	NED-AATGTCTTACAGGCAAAGTCCCCA AACTTGAAGCTTCTGGCCTGAATG	0,42 µM	4	149 - 201	18
Pca7	AJ279809	6FAM-TGAGCATCGTAGCCCAGCAG GGTTCAGGACACCTGCACAATG	0,25 µM	1	105 - 141	18
Pca8	AJ279810	NED-ACTTCTGAAACAAAGATGAAATCA TGCCATCAGTGTCAAACCTG	0,48 µM	1	255 - 401	73
Pca9	AJ279811	VIC-ACCCACTGTCCAGAGCAGGG AGGACTGCAGCAGTTTGTGGG	0,3 µM	3	111 - 135	13
Phtr3 [1]	AM056070	NED-ATTTGCATCCAGTCTTCAGTAATT CTCAAAGAAGTGCATAGAGATTTCAT	1,4 µM	2 [1]	118 - 148 [1]	16 [1]
PK11	AF041465	PET-CTTTAAGAATTCAAATACAGAGTAGG GTTTTCTCCTTTCTACACTGAGG	0,54 µM	4	63 - 97	14
PK12	AF041466	VIC-CCTCCTGCAGTTGCCTCCCG CGTGGCCATGTTTATAGCCTGGCACTAAGAAC	1,14 µM	4	168 - 226	27
PmaTAGAn71 [1]	AY260537	NED-TCAGCCTCCAAGGAAAACAG GCATAAGCAACACCATGCAG	0,3 µM	2 [1]	190 - 310 [1]	29 [1]
POCC1	U59113	6FAM- TTCTGTGCTGCAATCACACA GCTTCCAGCACCACTTCAAT	0,8 µM	3	219 - 255	25
POCC6	U59117	VIC-TCACCCTCAAAAACACACACA ACTTCTCTCTGAAAAGGGGAGC	0,25 µM	1	195 - 253	28
P2/P8	AF006659-62	6FAM-CTCCCAAGGA TGAGRAAYTG TCTGCATCGC TAAATCCTTT	0,3 µM	2	319, 383	2

[1] Phtr3 was replaced by PmaTAGAn71 from 2018 onwards.

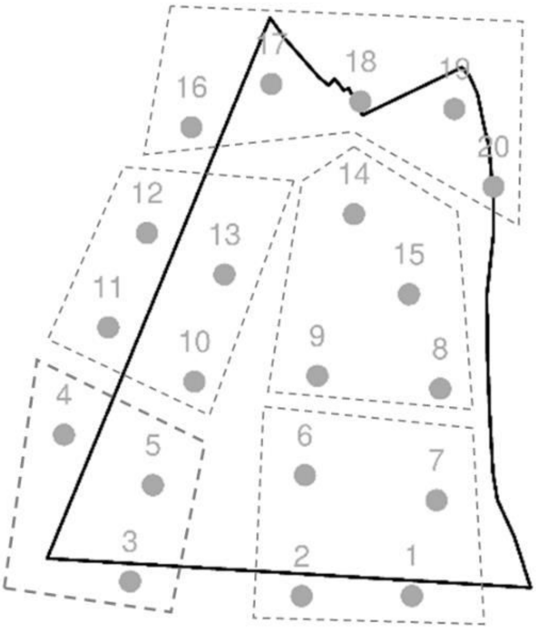


Figure S1. Sketch of our study site. The black outline represents the boundary of the forest patch including all breeding nest boxes and the dashed grey outline represents the spatial clusters. The locations of all 20 bird feeders are represented by grey nodes and label above indicating the feeder identity.

Post-hoc analyses

Table S2. Results of the models examining the effect of the number of opposite-sex associates, the average association strength, the sex ratio, the betweenness centrality, age (yearling vs adult) and the arrival time on the likelihood to acquire a mate in males (N = 118). Significant *P* values are shown in bold and the *P* values for the four network metrics that were inferred from 1000 random permutations are shown in italic. *P* values derived from the unrestricted null model are indicated by a triangle (Δ) and values derived from the location-specific null model with an asterisk (*).

	Males		
Fixed effect	**Estimate ± SE**	**z**	***P***
Intercept	-0.54 ± 0.22	-2.50	
Number of associates	-0.37 ± 0.50	-0.74	*0.45* $^{\Delta}$ *0.40 **
Average association strength	0.28 ± 0.48	0.58	*0.54* $^{\Delta}$ *0.53 **
Sex ratio	-0.20 ± 0.47	-0.43	*0.67* $^{\Delta}$ *0.64 **
Betweenness centrality	**1.43** **± 0.62**	**2.31**	***0.03*** $^{\Delta}$ ***0.02 ****
Age (adult)	**-1.00** **± 0.47**	**-2.13**	**0.03**
Arrival time	**-1.49** **± 0.49**	**-3.04**	**0.002**

Table S3. Summary statistics of the number of female associates for adult and yearling male blue tits. Significant difference was examined performing a Wilcoxon rank sum test. *P* values are inferred from 1000 random permutations.

	Adults			**Yearlings**				
	Range	**Mean**	**sd**	**Range**	**Mean**	**sd**	**W**	**P**
Number of female associates	1-125	70	29	36-142	81	27	1639	0.11

Table S4. Results of the model examining the effect of the number of female associates during winter on 1) the number of neighbours and 2) the proportion of familiar females in the close breeding neighbourhood (1st and 2nd order neighbours). *P* values are inferred from 1000 random permutations. *P* values derived from the unrestricted null model are indicated by a triangle (Δ) and values derived from the location-specific null model with an asterisk (*).

	Number of neighbours			**Proportion of familiar females**		
	Estimate ± SE	**z**	***P***	**Estimate ± SE**	**z**	***P***
Intercept	2.59 ± 0.03	84.74		0.99 ± 0.07	14.25	
Number female associates	0.09 ± 0.06	1.42	0.19^{Δ} 0.77*	**1.20 ± 0.14**	**8.42**	**<0.001**$^{\Delta}$ **<0.001***

Chapter 3

Analysis of within-individual variation in extra-pair paternity in blue tits (*Cyanistes caeruleus*) shows low repeatability and little effect of changes in neighbourhood

Kristina B. Beck, Mihai Valcu, Bart Kempenaers

Many studies investigated variation in the frequency of extra-pair paternity (EPP) among individuals. However, our understanding of within-individual variation in EPP remains limited. Here, we comprehensively investigate variation in extra-pair paternity at the within-individual level in a population of blue tits (*Cyanistes caeruleus*). Our study is based on parentage data comprising >10000 genotyped offspring across 11 breeding seasons. First, we examined the repeatability of the occurrence of EPP, the number of extra-pair offspring, the number of extra-pair partners and the occurrence of paternity loss using data from males and females that bred in multiple years. Second, we tested whether within-individual changes in EPP between breeding seasons relate to between-year changes in the local social environment. Repeatabilities were generally low, but significant for the occurrence and number of extra-pair young in females and for whether a male sired extra-pair young or not. We found no evidence that the presence of the former social partner, changes in the proportion of familiar individuals or in phenotypic traits of the neighbors influenced changes in levels of EPP in females. However, in adult males, a decrease in the average body size of male neighbors was associated with higher extra-pair siring success. If confirmed, this result suggests that the competitive ability of a male relative to its neighbors influences his extra-pair mating success. We suggest that alternative hypotheses including the idea that within-individual changes in EPP are due to "chance events" rather than to changes in an individual's social breeding environment deserve more consideration.

Accepted for publication in Behavioral Ecology:

Beck KB, Valcu M, Kempenaers B. 2020. Analysis of within-individual variation in extra-pair paternity in blue tits (Cyanistes caeruleus) shows low repeatability and little effect of changes in neighborhood. Behav Ecol. DOI:araa069.

Introduction

Animals often show within-population variation in mating behavior. This variation can be caused by several underlying mechanisms: from genetically determined strategies (e.g., Tsubaki 2003; Küpper et al. 2016), via age-dependent mating tactics (e.g., Richard et al. 2005; Apio et al. 2007) to individual flexibility in response to the (social) environment (e.g., Leary et al. 2008; Mulrey et al. 2015).

A well-studied example of such variation is the occurrence of extra-pair paternity in birds. Although the majority of species are socially monogamous, copulations outside the social pair bond are widespread and cause varying levels of extra-pair paternity (Griffith et al. 2002; Westneat and Stewart 2003; Brouwer and Griffith 2019). Extra-pair copulations will typically benefit males because they can sire additional offspring, but the adaptive value of extra-pair behavior for females remains controversial (Forstmeier et al. 2014; Whittingham and Dunn 2016; Plaza et al. 2019). To understand the evolution of extra-pair paternity and its consequences for sexual selection (Webster et al. 1995; Schlicht and Kempenaers 2013), we need to find out why males vary in extra-pair siring success and why females vary in how many of their eggs are sired by their social mate.

In general, extra-pair behavior and its outcome can be considered individual-specific traits. This would be the case (1) if males and females differ in their propensity to be promiscuous (e.g. if extra-pair behavior is heritable; Reid et al. 2010; Forstmeier et al. 2011; Germain et al. 2018), (2) if some males are better at competing for extra-pair copulations (e.g. because they are larger, Weatherhead and Boag 1995; Schlicht et al. 2015a) or at siring extra-pair offspring (e.g. because they produce more or more competitive sperm, Moller and Briskie 1995; González-Solís and Becker 2002; Knief et al. 2017), or (3) if females consistently choose particular (high-quality or highly attractive) males for extra-pair copulations (Hasselquist et al. 1996; Whittingham and Dunn 2016). Within-individual consistency in levels of extra-pair paternity can also arise if (4) individuals consistently breed in an environmental context that increases opportunities for extra-pair behavior (Schlicht et al. 2015a; Biagolini-Jr et al. 2017).

Within-individual consistency of extra-pair paternity has been examined by considering multiple measures of the trait for a set of individuals (e.g. across several years) and calculating the repeatability of the trait, defined as the proportion of the total variance that is due to between-individual variation (Lessells and Boag 1987; Bell et al. 2009). The consistency of extra-pair paternity traits can provide information about the potential strength of sexual selection and past studies often examined the repeatability of female extra-pair behavior as an indirect estimate of heritability (Boake 1989). Studies on a variety of songbirds reported the repeatability in the number of extra-pair young produced or sired (e.g., Dietrich et al. 2004: $R_{Females}$=0.30, R_{Males}=0.29; Reid et al., 2010: $R_{Females}$=0.13; Whittingham et al., 2006: $R_{Females}$=0.83), the number of extra-pair sires (e.g., Whittingham et al., 2006: $R_{Females}$=0.73) and the occurrence of extra-pair paternity (Charmantier and Blondel, 2003: no evidence for repeatability in females and males; Møller and Tegelström, 1997: $R_{Females}$=0.72). Although measures of extra-pair paternity are repeatable to some extent, the estimates vary considerably and the underlying causes remain unclear.

Some studies report a low or modest repeatability of extra-pair paternity, suggesting that much of the variation is due to changing circumstances that relate to opportunities to engage in extra-pair copulations or to success in siring extra-pair offspring. First, individual characteristics might change over time. For instance, many studies have shown that young (yearling) males have lower extra-pair siring success compared to older (adult) males (Cleasby and Nakagawa 2012; Hsu et al. 2017; Michálková et al. 2019). Second, the environmental context relevant for extra-pair behavior can change considerably for an individual between breeding attempts. For example, levels of extra-pair paternity may vary with aspects of the current (social) environment such as breeding synchrony (Stutchbury and Morton 1995; Saino et al. 1999; Thusius et al. 2001), breeding density (Westneat et al. 1990; Dunn et al. 1994; Araya-Ajoy et al. 2015), the density of the vegetation (Biagolini-Jr et al. 2017), the presence of predators (Santema et al. 2019), or whether an individual breeds with the same or a different social partner (within-pair repeatability; Dietrich et al., 2004). However, most studies that examined effects of the local environment on extra-pair paternity considered among-individual variation within a given breeding season (for our study population, see e.g. Schlicht et al. 2015a; Beck et al. 2020) instead of within-individual variation across seasons.

Here, we comprehensively investigate within-individual variation in patterns of extra-pair paternity across successive breeding attempts in a population of blue tits (*Cyanistes caeruleus*) comprising 11 breeding seasons. First, we examined to what extent the occurrence of extra-pair paternity is a repeatable, individual-specific trait for males and females. Second, we investigated whether within-individual changes in measures of extra-pair paternity between years can be explained by between-year changes in the local breeding environment of a focal individual. This approach allows disentangling effects of individual-specific, “intrinsic” traits from those due to the local breeding environment and may thus help to understand variation in extra-pair paternity. For example, extra-pair paternity levels may be highly repeatable because individuals breed consistently in an environment favoring extra-pair copulations (i.e., a high repeatability in the breeding environment). In such case, we expect that between-year changes in the local environment will explain the observed within-individual variation in extra-pair paternity. If there is no effect of the local environment, it is more likely that the occurrence or frequency of extra-pair paternity reflects one or more individual-specific “intrinsic” traits. Conversely, if levels of extra-pair paternity show low repeatability and changes in the local environment explain the observed within-individual variation, extra-pair paternity is a highly context-dependent trait.

We considered three relevant contexts in which the breeding environment of a focal individual can change between years, whereby we specifically focus on the social context: territory size, the identity of the social partner and the local neighborhood (for an overview of all variables included for males and females, their interpretation and our predictions see Table 1 and Fig. S1). Extra-pair behavior is inherently an interaction between multiple individuals (i.e. the male or female, its social partner and the potential extra-pair mates) but how the social environment affects patterns of extra-pair paternity has rarely been examined (Petrie and Kempenaers 1998; Westneat and Stewart 2003; Maldonado-Chaparro et al. 2018).

The quality of the social partner might be an important aspect influencing the decision of a focal individual to engage in extra-pair mating. For instance, a weak pair bond resulting from behavioral incompatibility between the partners (Ihle et al. 2015) or genetic quality and/or compatibility (Foerster et al. 2003) could influence extra-pair behavior. Furthermore, the tendency of an individual to engage in extra-pair behavior might also influence the extra-pair behavior of its partner (Maldonado-Chaparro et al. 2018). Thus, we also examined whether the occurrence of extra-pair paternity is more consistent between years when the focal individual breeds with the same partner. Furthermore, past studies reported that divorced blue tits might still have extra-pair young with their previous partner (Valcu and Kempenaers 2008; Gilsenan et al. 2017). Thus, for individuals paired with a different social partner, we assessed whether changes in levels of extra-pair paternity depended on the presence of the former partner in the neighborhood.

Changes in extra-pair paternity between years may also be explained by changes in the phenotypic composition of the breeding neighbors. For example, in blue tits, adult (compared to yearling) and larger males are more successful in siring extra-pair young (Kempenaers et al. 1997; Schlicht et al. 2015a). Because most extra-pair young are sired by first- or second-order neighbors (Schlicht et al. 2015a), the number or proportion of large, adult male neighbors may influence the likelihood that a pair has extra-pair young in their nest, or for a focal male to sire extra-pair young in a neighboring nest (but see Roth et al. 2019). Similarly, there is competition among females (Kempenaers 1994, Midamegbe et al. 2011). A neighborhood containing a higher proportion of adult and larger females (i.e. potentially dominant or stronger females) may influence the likelihood that a focal female can obtain extra-pair copulations with a neighboring male. Further, individuals breeding in the same area over multiple years might be familiar with some of the neighbors from previous breeding seasons. Familiarity might influence the decision to engage in extra-pair behavior or it might increase the chances to obtain extra-pair copulations, for example if it leads to reduced territorial conflicts and allows more extra-territorial visits, thereby facilitating meeting potential extra-pair partners (Beletsky and Orians 1989; Grabowska-Zhang et al. 2011; Beck et al. 2020). Thus, we examine whether a higher proportion of familiar females and males and the presence of former extra-pair partners influence changes in patterns of extra-pair paternity.

Materials and Methods

Study species and population

Blue tits are small, hole-nesting songbirds that breed only once per year (except for some replacement clutches) and that engage frequently in extra-pair mating (about half of the broods contain at least one extra-pair young and 10-15% of all offspring are sired by extra-pair males; Kempenaers et al. 1992; Kempenaers et al. 1997; Delhey et al. 2003). Roughly half of the individuals breed in multiple years with the same social partner (Valcu and Kempenaers 2008; Gilsenan et al. 2017).

For this study, we use data on extra-pair paternity from a population that breeds in a mixed-deciduous, oak-dominated forest close to Landsberg am Lech, Germany (“Westerholz”, 48°08’N 10°53’E, c. 40 ha; see also Schlicht et al. 2012). In 2007, we put up 277 wooden, small-holed (diameter 26mm) nestboxes at the site and studied the breeding behavior of the blue tits nesting in the boxes (60-176 pairs per year). Nestboxes were distributed evenly across the site and placed approximately 40 m apart. Working permits were obtained from the Bavarian government and the Bavarian regional office for forestry (LWF).

Assessment of extra-pair paternity

We took blood samples (circa 10µl) from all nestlings (at the age of 14 days) and breeding adults (which we caught inside the nestbox or with mistnets either during the breeding season or in the preceding winter) and we collected all unhatched eggs and dead nestlings for genotyping. Some unhatched eggs could not be genotyped and some nestlings disappeared from the nest and were not sampled (in 23% of nests at least one egg was not genotyped). We used 14 microsatellite markers and one sex chromosome linked marker (ADCbm; ClkpolyQ; Mcµ4; PAT MP 2-43; Pca3, Pca4, Pca7, Pca8, Pca9; Phtr3; PK11, PK12; POCC1, POCC6; and the sex chromosome linked P2/P8). Microsatellite amplifications were performed in multiplexed PCRs (each 10µl multiplex PCR contained 20 – 80ng DNA) and primer mixes containing two to five primer pairs. Overall, we genotyped 10227 out of 11624 laid eggs (88%; between-year range: 80 – 97%) and compared the genotypes of parents and their offspring using the software CERVUS (Kalinowski et al. 2007). For each breeding season, we assigned to each male how many extra-pair young he sired and for each female how many extra-pair sired eggs her clutch contained. For both sexes, we also determined the number of extra-pair partners. Although the majority of the fertilized eggs were genotyped, the observed patterns of extra-pair paternity may not be identical with the actual patterns.

Measurements of changes in the local environment

For each focal individual (females and males separately), we examined the following changes in the local breeding environment over subsequent years (Table 1, Fig. S1).

1. Territory size. We estimated the size of the breeding territory (in m^2) using the r package “expp” (Valcu and Schlicht 2013; Schlicht et al. 2015a). The package assigns each point in the study area to the nearest breeding pair, thereby creating distinct territories using Thiessen polygons (Valcu and Kempenaers 2010; Schlicht et al. 2014; see Fig. S1). We then calculated changes in territory size by dividing the size in year x + 1 by the size in year x (ratio). We also calculated the difference in absolute territory size. We report the results using the proportional change in territory size. However, we repeated all analyses including the absolute change in territory size (see Table S1-3).

2. Social partner. We examined whether or not the focal individual bred with a new partner in year x + 1 (binary variable: yes or no) and further assessed whether a former social partner was still breeding nearby in the 1st order neighborhood (i.e. all neighbors whose territories adjoin the focal individuals’ territory borders) or not and tested whether this had an effect on the likelihood of having extra-pair paternity. Further, we calculated the change in body size of the social male by calculating the difference in tarsus length between the year x + 1 social male and the year x social male (analysis of female extra-pair paternity, see Table 1).

3. The local neighborhood. We calculated the number of neighbors using the r package “expp” (see above). Based on the estimated territory distribution, we defined 1st order (direct) neighbors as all territories sharing the focal pair’s territory border, and 2nd order neighbors as territories where one territory was in between. We calculated changes in the number of 1st order neighbors by dividing the measure in year x + 1 by the measure in year x (see Table 1, Fig. S1). In the main text, we report the results of analyses using this ratio. However, we repeated all analyses using the absolute change in the number of 1st order neighbors (Table S1-3). We also examined changes in the phenotypic composition of the neighborhood by calculating the average age and tarsus length of the direct neighbors (males or females). We assigned age as a binary variable (yearling = 1; adult = 2). The change was then calculated as the difference between year x + 1 and year x. Finally, we examined the change in the proportion of familiar female and male neighbors. We defined two birds as being familiar to each other when they had bred together (former partner after divorce), were previous extra-pair partners or had

been 1st order neighbors in previous years. For each focal individual we then quantified for each year the proportion of familiar males and females in the local neighborhood, and whether a former social or extra-pair partner was present. We calculated changes as the difference in the proportion of familiar birds between year x + 1 and year x.

Investigating changes in extra-pair paternity between years in relation to changes in the breeding environment might also shed light on the general, but little-understood effect that older males are more successful in siring extra-pair young (Cleasby and Nakagawa 2012; Schlicht et al. 2015a; Hsu et al. 2017). When yearlings turn adult there might be specific changes in the environment causing this effect. For example, as yearlings, by definition none of the neighbors are familiar and no previous breeding partner can be around. To investigate such age-specific changes, we ran two separate analyses: one for males that turned from yearling to adult and one including only adult males.

For all analyses, we only considered 1st order neighbors, because (a) individuals typically meet near territory borders, (b) most extra-territorial nestbox visits are with direct neighbors (Schlicht et al. 2015b), and (c) the probability that a female and a male have extra-pair young together strongly decreases with increasing breeding distance (see Schlicht et al., 2015b; in our dataset 61% of the EP partners are 1st order neighbors, 23% are 2nd order neighbors). Repeating the analyses including 2nd order neighbors did not qualitatively change any of the conclusions (results not shown).

Table 1. Overview of the variables reflecting the local environmental context in which extra-pair paternity occurs and predictions about how they can explain between-season changes in the expression of extra-pair paternity.

Explanatory variable	**Definition** *	**Background**	**Predictions**	
			Female	**Male**
Δ Territory size	$year_{x+1}$ / $year_x$	Individuals possessing larger territories may be less likely to engage in EPCs because the larger distance might limit the encounter probability with potential extra-pair mates [1,2,3], but see [4].	An increase in territory size is associated with less EPP	
Δ Number of neighbors	$year_{x+1}$ / $year_x$	A higher local breeding density (i.e., a higher number of neighbors) should increase opportunities for EPCs, because more potential extra-pair partners are in close proximity [1,2,4].	An increase in the number of neighbors will lead to more EPP	
Δ Tarsus length of social partner	$year_{x+1}$ - $year_x$	Larger males are more likely to gain EPP [5], and less likely to lose paternity [6], but see [7].	Females paired with a larger social partner in $year_{x+1}$ will have less EPP, as larger males might be better at mate guarding or are of higher quality	-
Consistency of social partner	Same or different social partner in $year_{x+1}$	Remaining with the same mate over multiple years can be seen as a sign of pair compatibility [8], which might reduce extra-pair behavior.	Individuals that keep the same social partner might have less EPP in $year_{x+1}$	
Δ Familiar neighbors	$year_{x+1}$ - $year_x$	Familiarity among neighbors can facilitate extra-territorial visits through reduced territorial aggression [10,11] and familiar individuals (including former extra-pair or social mate) might be more likely to visit each other.	Females with more familiar male or female neighbors will have more EPP in $year_{x+1}$	Males with more familiar male or female neighbors will have more EPP in $year_{x+1}$
Δ Proportion of yearling male neighbors	$year_{x+1}$ - $year_x$	Adult males are more likely to gain EPP [5]. More adult males in the neighborhood might reduce the chances for a male to gain EPP and increase the probability that the female has EPY.	If the proportion of yearling males increases, females will have less EPP	If the proportion of yearling males increases, the focal males will have more EPP
Δ Average tarsus length of male neighbors	$year_{x+1}$ - $year_x$	Larger males are more likely to gain EPP [5]. Larger males in the neighborhood might reduce the chances for a male to gain EPP and increase the probability that the female has EPY.	If the average size of neighboring males increases, females will have more EPP.	If the average size of neighboring males decreases, males will have more EPP (less competitive environment).

Δ Proportion of yearling female neighbors	year_{x+1} - year_x	Adult females may be more aggressive towards intruding neighbor females than yearling females. More adult females in the neighborhood might reduce the chances for a female to obtain EPCs.	If the proportion of yearling females increases, females will have more EPP	-
Δ Average tarsus length of female neighbors	year_{x+1} - year_x	Larger females may be more successful in displacing intruding neighbor females than smaller females. More large females in the neighborhood might reduce the chances for a female to obtain EPCs.	If the average size of neighboring females increases, females will have less EPP.	-
Previous social partner	Previous social partner present in neighborhood in year_{x+1} or not	Blue tits engage in EPCs with previous social partners [12].	Individuals that have a previous social partner in their close neighborhood might have more EPP.	
Previous extra-pair partner	Previous extra-pair partner present in neighborhood in year_{x+1} or not	Blue tits may engage in EPCs with previous extra-pair partners.	Individuals that have a previous extra-pair partner in their close neighborhood might have more EPP.	

* Δ refers to the change between breeding seasons, calculated either as proportional change (year_{x+1} / year_x) in the trait or as the difference (year $_{x+1}$ – year $_x$) in the trait.

References: [1] Westneat & Sherman, (1997); [2] Thusius et al., (2001); [3] Westneat & Mays, (2005); [4] Schlicht, Valcu & Kempenaers, (2015a); [5] Akçay & Roughgarden, (2007); [6] Kempenaers et al., (1992); [7] Strohbach et al., (1998); [8] Ihle, Kempenaers & Forstmeier, (2015); [9] Blomqvist et al., (2002); [10] Beletsky & Orians, (1989); [11] Grabowska-Zhang, Wilkin & Sheldon, (2011); [12] Gilsenan, Valcu & Kempenaers, (2017).

Data selection and statistical analysis

For all statistical analysis we used the software R 3.5.1 (R Development Core Team, 2018).

Repeatability of extra-pair paternity

We used data from all individuals that bred in our study area in at least two years and for which information on extra-pair paternity was available ($N_{\text{Males}} = 221$, $N_{\text{Females}} = 233$). For males and females separately, we calculated the repeatability of (a) the number of extra-pair partners, (b) the total number of extra-pair young obtained by an individual and (c) the occurrence of extra-pair paternity (yes/no) within a given breeding season. For males, we additionally examined the repeatability in paternity loss, i.e. in (d) the proportion of young in the male's nest that were sired by another male (number of extra-pair young/total number of young) and in (e) the occurrence of paternity loss (yes/no). We calculated repeatability for different measures of extra-pair paternity, because they have different biological meanings. For instance, high repeatability in the occurrence of extra-pair paternity may indicate that some females and males are more likely to engage in extra-pair behavior than others. The number of extra-pair young sired by males refers directly to gains in reproductive success, whereas the number of extra-pair young in a clutch represents both female behavior and her social mate's reproductive loss. The number of extra-pair young may be influenced by the relative number and timing of within- and extra-pair copulations, but also by post-copulatory mechanisms, and hence may depend more on female identity than on male identity.

We fitted a generalized linear mixed-effect model (GLMM) using the rpt function of the R package "rptR" (Stoffel et al. 2017) with a Poisson distribution for the models using the dependent variables (a) and (b), proportion data for (d) and binary data for the models using variable (c) and (e). As random intercept we included individual identity. We repeated the models including additionally either the box identity or the pair identity as random intercept to control for variation explained by the location (nestbox) or the pair. We calculated the repeatability coefficient R, its 95% confidence interval, and the associated p-value using 1000 bootstrapping runs. We report all repeatability estimates only on the original scale approximation as estimates did not differ considerably compared to the link-scale approximation (Nakagawa and Schielzeth 2010; Stoffel et al. 2017). For females, we repeated the analyses on a subset of individuals for which all eggs had been genotyped (N_{Female} = 83) to exclude a bias in the repeatability estimates due to incomplete sampling. Additionally, we calculated adjusted repeatabilities for females by including clutch size as a fixed effect and individual identity as random intercept. We included clutch size to control for the fact that extra-pair young are usually found among the first-laid eggs (Magrath et al. 2009), and we would thus expect a lower proportion of extra-pair young with increasing clutch size. Furthermore, clutch size gives an upper limit to the number of extra-pair offspring. For males, we calculated adjusted repeatabilities by adding territory location (central or edge territory) as fixed effect, assuming that males breeding on the edge of the study area were more likely to have sired young in unsampled nests. As random intercept we included individual identity. We also included male age as a fixed effect, because adults are more likely to sire extra-pair young than yearlings (Schlicht et al. 2015).

Effects of changes in the breeding environment

To relate between-year changes in extra-pair paternity to changes in the breeding environment, we only included individuals that were breeding in consecutive years and for which all relevant information of the breeding environment (Table 1) was available for both years (N_{Males} = 203, $N_{Females}$ = 190). We tested our general hypothesis that between-year changes in the local breeding environment can explain changes in the levels of extra-pair paternity in females and males by examining the response variables (a) change in the number of extra-pair partners, (b) change in the total number of extra-pair young and (c) change in status (i.e., individuals that had no extra-pair young in year x but did so in year x + 1 or vice versa, compared to individuals that did or did not have extra-pair offspring in both years). We did not examine whether between-year changes in the local breeding environment can explain changes in paternity loss in males as paternity loss likely depends on the female perspective rather than changes within the males' local neighborhood.

For the variables "number of extra-pair partners" and "number of extra-pair young" we calculated for each individual the difference between year x + 1 and year x and used this as the dependent variable in a linear mixed-effect model (LMM; package "lme4", Bates et al., 2014). For females, we included twelve fixed effects describing changes in their breeding environment (see Table 1). We calculated correlation coefficients between all fixed effects to check for collinearity (Dormann et al. 2013). As none of the parameters strongly correlated (all $r < 0.5$; see Table S4, S5 in the supplementary material) we included all into our models. As random effects we included individual identity and year. For males, we constructed two models for each response variable: one including only individuals that turned from yearling to adult (N = 172) and one only including adult individuals (N = 49). We included nine fixed effects describing changes in the males' breeding environment (see Table 1) and verified potential correlations as described above (all $r < 0.5$). As random effects we included individual identity and year in the models for adult males, but only year in the model for "yearling to adult" because each individual only appeared once in that dataset.

For the dependent variable "change in EPP status (yes/no)" we fitted generalized linear mixed-effect models (GLMM; package "lme4", Bates et al., 2014) with a binomial error structure and a logit-link function. For both sexes we included the same fixed effects as described for the previous models. However, in this case, we used absolute values, because we examined whether a change in any of the environmental variables can explain a change in extra-pair paternity status, regardless of the direction of that change (i.e. an increase or a decrease).

All model results include adjusted approximations of the p-values based on multiple comparisons of predictors using the "glht" function of the "multcomp" package (Hothorn et al. 2008).

Results

Repeatability of extra-pair paternity

For females, the repeatability of the occurrence and the number of extra-pair young in her clutch was small, but significant, and increased when only completely genotyped clutches were included (Table 2). Accounting for the effect of clutch size did not affect the results (Table 2). The number of extra-pair sires was not significantly repeatable, even when only completely genotyped clutches were considered (Table 2).

For males, the between-year repeatability of the different measures of extra-pair paternity was low (Table 2). The occurrence of extra-pair paternity, i.e. whether a male sired extra-pair offspring or not, was significantly repeatable, while the number of extra-pair young sired, the number of extra-pair partners and paternity loss were not (Table 2). Repeatability values did not change when controlling for territory location or age (Table 2).

Repeatability estimates were somewhat higher in females than in males, but the confidence intervals overlapped for all metrics (Table 2). Hence, these differences may not be biologically meaningful.

For both sexes, repeatability values for location (nestbox) and the specific partner (pair identity) were close to zero (Table S6 and S7).

Table 2. Repeatability of extra-pair paternity (total number of extra-pair young, number of extra-pair mates and the occurrence of extra-pair paternity) for male and female blue tits and the repeatability of paternity loss in males (i.e., the proportion of young lost and the occurrence of paternity loss). Shown are the repeatability coefficients (R), their range, their 95% confidence intervals (CI) and the associated P-values. R_{adj} refers to models controlling for the fixed effects territory location (central vs edge), male age (yearling vs adult) or clutch size. For females, results on the repeatability of EPP are once shown for all data and once only including completely genotyped clutches. Significant p values are indicated in bold.

	R	Range	95%CI	P	Fixed effect	R_{adj}	Range	95%CI	P
Males									
Number of EPY	0.03	0.00 - 0.11	0.00 - 0.06	0.12	Location	0.03	0.00 - 0.10	0.00 - 0.05	0.12
					Age	0.06	0.00 - 0.21	0.00 - 0.13	**0.04**
Number of EP mates	0.07	0.00 - 0.24	0.00 - 0.14	0.08	Location	0.07	0.00 - 0.22	0.00 - 0.14	0.08
					Age	0.10	0.00 - 0.32	0.00 - 0.19	**0.03**

EPP occurrence	0.08	0.00 - 0.23	0.00 – 0.14	**0.02**	Location	0.08	0.00 - 0.20	0.00 - 0.14	**0.02**
					Age	0.10	0.00 - 0.23	0.00 - 0.15	**0.01**
Proportion of young lost	0.00	0.00 - 0.04	0.00 – 0.01	1.00	Location	0.00	0.00 - 0.03	0.00 - 0.01	1.00
					Age	0.00	0.00 - 0.23	0.00 - 0.01	1.00
Paternity loss	0.01	0.00 - 0.13	0.00 – 0.07	0.34	Location	0.01	0.00 - 0.14	0.00 - 0.08	0.34
					Age	0.02	0.00 - 0.23	0.00 - 0.08	0.31
Females									
Number of EPY									
All	0.12	0.00 - 0.35	0.00 - 0.19	**0.003**	Clutch size	0.10	0.00 - 0.26	0.00 - 0.18	**0.004**
complete	0.33	0.00 - 0.84	0.06 - 0.61	**<0.001**	Clutch size	0.33	0.00 - 0.78	0.05 - 0.57	**<0.001**
Number of EP mates									
All	0.00	0.00 - 0.15	0.00 - 0.06	1.00	Clutch size	0.00	0.00 - 0.12	0.00 - 0.06	1.00
complete	0.09	0.00 - 0.31	0.00 - 0.24	0.11	Clutch size	0.10	0.00 - 0.31	0.00 - 0.22	0.11
EPP occurrence									
All	0.10	0.00 - 0.22	0.00 – 0.15	**0.01**	Clutch size	0.09	0.00 - 0.19	0.00 – 0.14	**0.01**
complete	0.25	0.00 - 0.55	0.03 - 0.38	**0.003**	Clutch size	0.22	0.00 - 0.75	0.02 - 0.39	**0.003**

Effects of changes in the breeding environment

For males, we found considerable variation in the between-year changes in the number of extra-pair partners (from - 4 to + 5; mean = 0.2 ± 1.0 sd) and in the number of extra-pair young sired (from - 8 to + 11; mean = 0.5 ± 2.3 sd). However, these changes or the change in status were generally not predicted by changes in the local environment (Tables 3 and 4, Fig. 1), neither for males that turned from yearling to adult, nor for adult males that bred in multiple years. Only one effect was significant: a decrease in the average body size of male neighbors was associated with an increase in the total number of extra-pair young sired (LMM estimate ± se: - 2.10 ± 0.72, $p = 0.03$).

For females, between-year changes in the number of extra-pair partners varied between - 2 to + 3 (mean = - 0.04 ± 0.8 sd) and changes in the number of extra-pair young varied between - 6 and + 5 (mean = - 0.04 ± 1.5 sd). We found no evidence that changes in the local environment between years explained changes in levels of extra-pair paternity (Table 5, Fig. 2).

Table 3. Effects of changes in the local social environment on between-year changes in levels of extra-pair paternity for yearling male blue tits that become adult (N = 172). Extra-pair paternity is measured as the change in the number of females with whom a male sired extra-pair offspring (EP females), the number of young a male sired (EPY) and whether a male changed its' EPP status (i.e., changed or remained the same). See methods for details on the models.

	Δ EP females			**Δ EPY**			**Change in EPP status**		
	Estimate ± SE	**t**	**P**	**Estimate ± SE**	**t**	**P**	**Estimate ± SE**	**t**	**P**
Intercept	0.56 ± 0.27			1.12 ± 0.58			- 0.20 ± 0.72		
Number of neighbors	0.01 ± 0.20	0.04	1.00	-0.15 ± 0.44	-0.35	0.99	-0.18 ± 0.51	-0.35	0.99
Territory size	-0.18 ± 0.10	-1.89	0.37	-0.16 ± 0.21	-0.76	0.99	-0.43 ± 0.26	-1.67	0.54
Consistent social partner	-0.09 ± 0.10	-0.85	0.98	0.02 ± 0.22	0.10	1.00	-0.26 ± 0.26	-0.97	0.96
Proportion yearling male neighbors	-0.02 ± 0.22	-0.07	1.00	-0.43 ± 0.49	-0.88	0.97	0.44 ± 0.80	0.55	0.99
Average male neighbor tarsus length	-0.17 ± 0.24	-0.72	0.99	-0.53 ± 0.52	-1.01	0.94	-1.09 ± 0.97	-1.13	0.90
Proportion familiar males	0.40 ± 0.38	1.06	0.93	0.62 ± 0.81	0.77	0.99	1.26 ± 0.89	1.42	0.73
Proportion familiar females	-0.14 ± 0.37	-0.36	0.99	-0.25 ± 0.81	-0.31	0.99	-0.28 ± 0.90	-0.31	0.99
Previous social partner present	0.02 ± 0.30	0.07	1.00	0.003 ± 0.66	0.01	1.00	0.18 ± 0.71	0.25	0.99
Previous extra-pair partner present	Not applicable as a previous extra-pair partner was only present in one case								

Table 4. Effects of changes in the local environment on between-year changes in levels of extra-pair paternity for adult male blue tits (N = 49). Extra-pair paternity is measured as the change in the number of females with whom a male sired extra-pair offspring (EP females), the number of young a male sired (EPY) and whether a male changed its' EPP status (i.e., changed or remained the same). See methods for details on the models. Significant p values are indicated in bold.

	Δ EP females			**Δ EPY**			**Change in EPP status**		
	Estimate ± SE	**t**	**P**	**Estimate ± SE**	**t**	**P**	**Estimate ± SE**	**t**	**P**
Intercept	0.45 ± 0.27			1.41 ± 0.73			- 0.03 ± 0.82		
Number of neighbors	-0.36 ± 0.23	-1.56	0.65	-1.07 ± 0.61	-1.74	0.52	-0.67 ± 0.59	-1.14	0.92
Territory size	-0.09 ± 0.08	-1.10	0.93	-0.14 ± 0.23	-0.61	0.99	0.37 ± 0.32	1.16	0.91
Consistent social partner	-0.01 ± 0.10	-0.13	1.00	0.25 ± 0.26	0.93	0.98	0.10 ± 0.25	0.40	0.99
Proportion yearling male neighbors	0.59 ± 0.25	2.31	0.17	0.98 ± 0.72	1.36	0.80	- 0.77 ± 0.92	-0.84	0.99
Average male neighbor tarsus length	-0.58 ± 0.27	-2.15	0.24	-2.10 ± 0.72	-2.90	**0.03**	0.12 ± 0.99	0.12	1.00
Proportion familiar males	0.62 ± 0.36	1.73	0.52	1.32 ± 0.97	1.36	0.80	0.15 ± 1.06	0.14	1.00
Proportion familiar females	0.51 ± 0.30	1.71	0.54	0.67 ± 0.80	0.84	0.99	0.57 ± 1.02	0.55	0.99
Previous social partner present	-0.35 ± 0.24	-1.45	0.73	-0.87 ± 0.65	-1.33	0.82	0.30 ± 0.55	0.55	0.99
Previous extra-pair partner present	-0.56 ± 0.34	-1.68	0.56	-1.62 ± 0.90	-1.80	0.47	-1.97 ± 1.15	-1.71	0.54

Table 5. Effects of changes in the local environment on between-year changes in levels of extra-pair paternity for female blue tits (N = 190). Extra-pair paternity is measured as the number of males that sired extra-pair offspring in the female's clutch (EP males), the number of extra-pair young in the clutch (EPY) and whether a female changed its' EPP status (i.e., changed or remained the same). See methods for details on the models.

	Δ EP males			**Δ EPY**			**Change in EPP status**		
	Estimate ± SE	**t**	**P**	**Estimate ± SE**	**t**	**P**	**Estimate ± SE**	**t**	**P**
Intercept	- 0.08 ± 0.12			0.001 ± 0.23			- 0.99 ± 0.56		
Number of neighbors	- 0.004 ± 0.09	- 0.05	1.00	- 0.06 ± 0.17	- 0.36	0.99	-0.40 ± 0.26	-1.55	0.77
Territory size	0.10 ± 0.05	2.06	0.36	0.13 ± 0.10	1.34	0.89	0.17 ± 0.21	0.79	0.99
Consistent social partner	0.20 ± 0.11	1.83	0.54	0.11 ± 0.22	0.50	0.99	0.87 ± 0.39	2.24	0.26
Social partner body size	0.14 ± 0.08	1.83	0.54	- 0.03 ± 0.15	- 0.20	1.00	0.22 ± 0.39	0.56	0.99
Proportion familiar males	0.002 ± 0.18	0.01	1.00	0.35 ± 0.35	0.99	0.99	0.57 ± 0.64	0.89	0.99
Proportion familiar females	0.06 ± 0.21	0.29	1.00	-0.18 ± 0.41	-0.43	1.00	0.61 ± 0.70	0.87	0.99
Average male neighbor body size	0.07 ± 0.15	0.49	0.99	0.24 ± 0.29	0.83	0.99	1.18 ± 0.72	1.65	0.70
Proportion yearling male neighbors	0.12 ± 0.17	0.70	0.99	0.05 ± 0.33	0.15	0.99	-0.49 ± 0.73	-0.68	0.99
Average female neighbor body size	-0.31 ± 0.16	-1.91	0.48	-0.71 ± 0.32	-2.25	0.25	0.28 ± 0.80	0.35	0.99
Proportion yearling female neighbors	0.01 ± 0.16	0.05	1.00	-0.21 ± 0.32	-0.64	0.99	0.26 ± 0.68	0.39	0.99
Previous social partner present	0.003 ± 0.15	0.02	1.00	-0.10 ± 0.29	-0.33	1.00	0.22 ± 0.45	0.48	0.99
Previous extra-pair partner present	-0.53 ± 0.20	-2.74	0.07	-0.83 ± 0.38	-2.19	0.28	-0.10 ± 0.59	-0.16	1.00

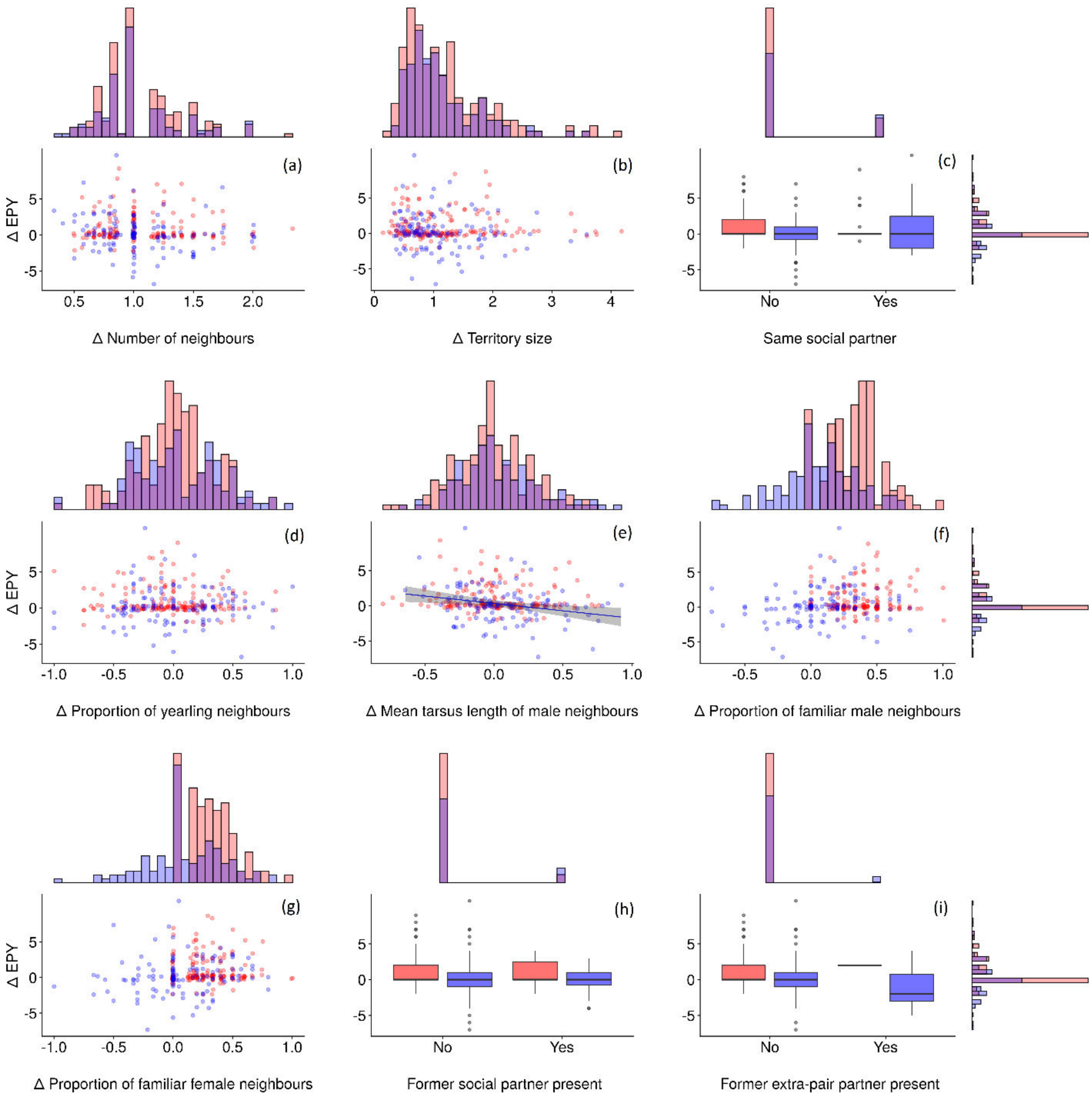


Figure 1. Between-year changes (Δ) in the number of extra-pair young a male blue tit sired in relation to changes in the local breeding environment. (a) Change in the number of neighbors (range$_{\text{YEARLING TO ADULT}}$=0.50-2.30 , mean$_{\text{YEARLING TO ADULT}}$=1.08; range$_{\text{ONLY ADULT}}$=0.33-2.00 , mean$_{\text{ONLY ADULT}}$=1.05); (b) change in territory size (range$_{\text{YEARLING TO ADULT}}$=0.15-4.18, mean$_{\text{YEARLING TO ADULT}}$=1.16; range$_{\text{ONLY ADULT}}$=0.34-3.59 , mean$_{\text{ONLY ADULT}}$=1.08; estimated based on Dirichlet tiles); (c) change of social partner (yes/no); (d) change in the proportion of yearling male neighbors (range$_{\text{YEARLING TO ADULT}}$=-1.00-0.86, mean$_{\text{YEARLING TO ADULT}}$=-0.02; range$_{\text{ONLY ADULT}}$=-1.00-1.00 , mean$_{\text{ONLY ADULT}}$=0.01); (e) change in the mean tarsus length of male neighbors (range$_{\text{YEARLING TO ADULT}}$=-0.80-0.76, mean$_{\text{YEARLING TO ADULT}}$=0.02; range$_{\text{ONLY ADULT}}$=-0.64-0.93 , mean$_{\text{ONLY ADULT}}$=0.06); (f) change in the proportion of familiar male neighbors (range$_{\text{YEARLING TO ADULT}}$=0.00-1.00, mean$_{\text{YEARLING TO ADULT}}$=0.35; range$_{\text{ONLY ADULT}}$=-0.75-0.75 , mean$_{\text{ONLY ADULT}}$=0.09); (g) change in the proportion of familiar female neighbors (range$_{\text{YEARLING TO ADULT}}$=0.00-1.00 , mean$_{\text{YEARLING TO ADULT}}$=0.27; range$_{\text{ONLY ADULT}}$=-1.00-0.80 , mean$_{\text{ONLY ADULT}}$=0.07); (h) whether the former social partner was still present in the neighborhood (yes/no); (i) whether a former extra-pair partner was still present in the neighborhood (yes/no). Individuals that turned from yearling to adult (N = 172) are shown in red, adult males (N = 49) are shown in blue. In (c), (h) and (i) boxplots show the minimum values, lower quartile, median, upper quartile, maximum values and outliers ((c): Yearling to adult: No=150 cases,

Yes=22; only adult: No=98, Yes=26; (h): Yearling to adult: No=162, Yes=10; only adult: No=106, Yes=18) ; (i): Yearling to adult: No=171, Yes=1; only adult: No=116, Yes=8). We found a significant relationship between the mean tarsus length of male neighbors and changes in the number of EPY gained for adult males which is why we added in (e) a linear regression line (in blue) and 95% confidence intervals from the LMM described in the main text (in grey). See methods for variable and model definitions and Table 3, 4 for results of statistical analyses.

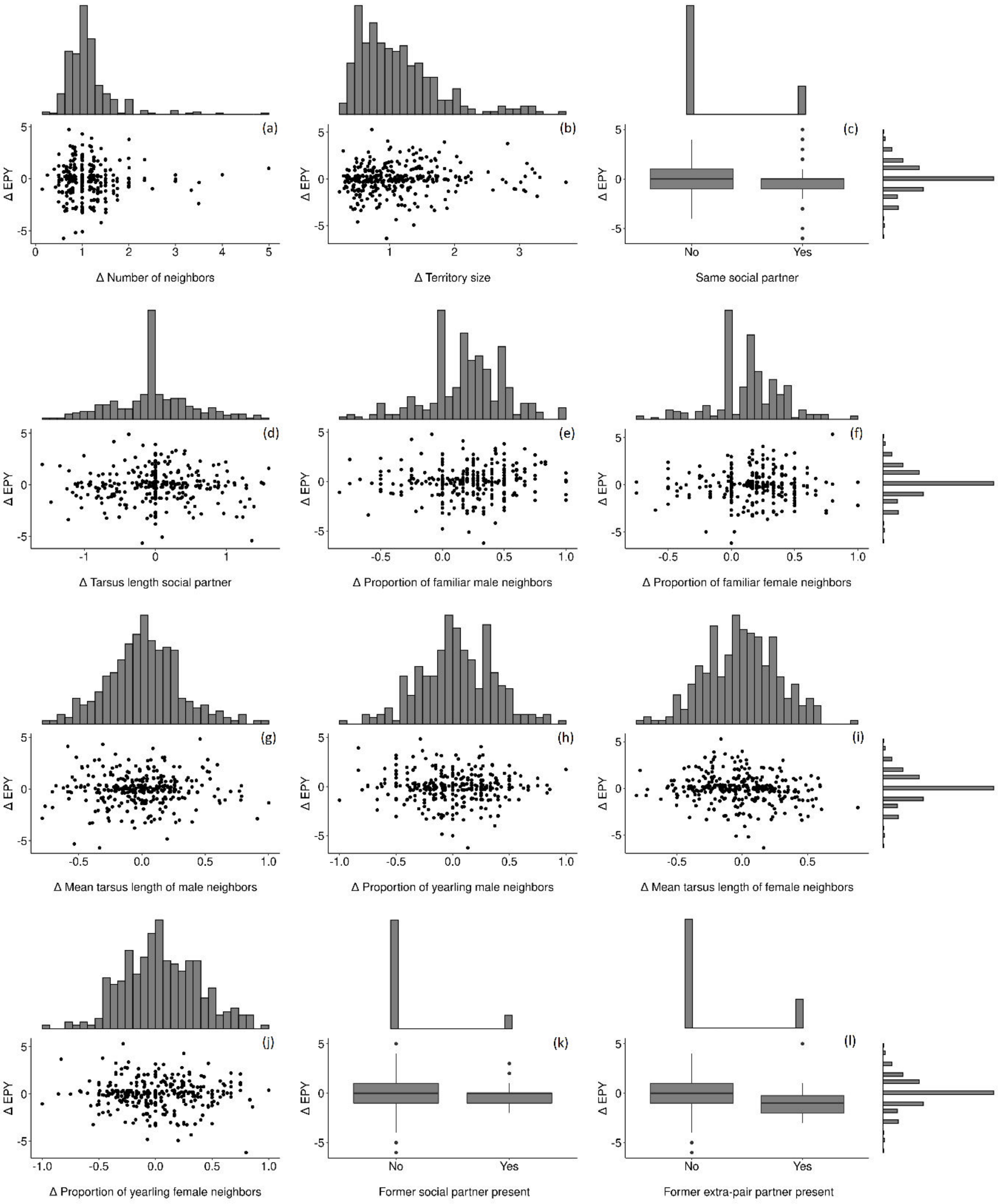


Figure 2. Between-year changes (Δ) in the number of extra-pair young in a female blue tit's clutch in relation to changes in the local breeding environment (N = 190 females). (a) Change in the number of neighbors (range=0.14-5.00 , mean=1.13); (b) change in territory size (estimated based on Dirichlet tiles; range=0.23-3.72, mean=1.12); (c) change of social partner (yes/no); (d) change in tarsus length of the social partner (range=-1.59-1.60 , mean=0.03); (e) change in the proportion of familiar male neighbors (range=-0.83-1.00 , mean=0.20); (f) change in the proportion of familiar female neighbors (range=-0.75-1.00 , mean=0.16); (g) change in the mean tarsus length of male neighbors (range=-0.79-1.00 , mean=-0.002); (h) change in the proportion of yearling male neighbors (range=-1.00-1.00 , mean=-0.002); (i) change in the mean tarsus length of female neighbors (range=-0.81-0.88 , mean=-

0.02); (j) change in the proportion of yearling female neighbors (range=-1.00-1.00 , mean=-0.02); (k) whether the former social partner was still present in the neighborhood (yes/no); (l) whether a former extra-pair partner was still present in the neighborhood (yes/no). In (c), (k) and (l) box plots show the minimum values, lower quartile, median, upper quartile, maximum values and outliers ((c): No=248 cases, Yes=65; (k): No=278, Yes=35; (l): No=295, Yes=18). See methods for variable definitions and Table 5 and S3 for the results of statistical analyses.

Discussion

Many studies aimed to determine the underlying causes of the observed individual variation in the expression of extra-pair paternity (Schlicht et al. 2015a; Baldassarre et al. 2016; Johnsen et al. 2017; Edwards et al. 2018). However, our understanding of this variation remains limited. We studied changes in levels of extra-pair paternity for the same individuals that bred in different years. Using a long-term dataset from a blue tit population, we investigated (1) to what extent extra-pair paternity patterns are repeatable for an individual and (2) whether between-year changes in the local breeding environment can explain within-individual changes in measures of extra-pair paternity. Overall, our results show relatively low, but significant repeatability of extra-pair paternity patterns and little effect of changes in the local environment. Although we cannot exclude that other, unmeasured individual or environmental changes play a role, variation in levels of extra-pair paternity may also be due to chance events, at least to some extent.

Repeatability of extra-pair paternity

Extra-pair matings have the potential to increase the intensity of sexual selection if males with specific phenotypic traits are more successful in acquiring extra-pair matings (Møller and Birkhead 1994; Webster et al. 1995). Alternatively, extra-pair paternity can have no impact on the strength of sexual selection if for instance all males have an equal likelihood to gain extra-pair young (Schlicht and Kempenaers 2011), or it may even decrease the strength of sexual selection if extra-pair sires are often males that failed to acquire a social mate (Lebigre et al. 2012).

Estimates of repeatability can be used to evaluate the consistency of a trait and to provide an upper limit for its heritability and hence for the potential for (sexual) selection. Several studies have estimated the repeatability of different behaviors ranging from exploratory behavior to mate preferences and foraging (average of 759 repeatability estimates across different behaviors and species: R=0.37; Bell et al. 2009). Repeatability estimates of extra-pair paternity vary considerably (see above), with some reports of high estimates such as in female tree swallows (*Tachycineta bicolor*) for the proportion of extra-pair young in the brood (R=0.83) and the number of extra-pair sires (R=0.73), suggesting that these behaviors may be heritable and can undergo selection (Whittingham et al. 2006). The repeatability of patterns of extra-pair paternity in blue tits was generally low for both sexes, but significant for the occurrence and the number of extra-pair young in females and for the occurrence of extra-pair paternity in males, despite considerable between-year changes in the local breeding context (see data distributions in Fig. 1 and 2, Table 2). The repeatability of extra-pair paternity did not increase when individuals retained the same social partner between years and we also found no evidence that extra-pair paternity levels were location-specific (no effect of nestbox identity).

The low repeatabilities reported in our study may partly be due to measurement errors caused by incomplete sampling, because repeatability estimates of female extra-pair paternity levels increased somewhat when only completely genotyped clutches were included (Table 2). Our results suggest that females are to some extent consistent in the likelihood to have extra-pair offspring and in the number of extra-pair young they produce. The number of extra-pair sires was not repeatable and may rather depend on aspects of the breeding neighborhood (e.g. the number of mates available), the timing of extra-pair copulations or the phenotypes of the extra-pair male(s), including variation in sperm quality and quantity. In some other species, repeatability estimates were moderate to high (see above), further suggesting that female extra-pair paternity is an individual-specific trait. The underlying cause of the significant repeatability in female extra-pair paternity and potential targets of selection could be for instance individual differences in the tendency to engage in extra-pair copulations (Forstmeier 2007) or individual differences in the frequency of within-pair copulations. Studies on the heritability of female extra-pair behavior are rare. In song sparrows (*Melospiza melodia*), the proportion of extra-pair young in a clutch showed an estimated heritability of 0.12 (Reid et al. 2010). In zebra finches (*Taeniopygia guttata*), the responsiveness to extra-pair courtships was also heritable ($h^2 = 0.11$; Forstmeier et al. 2011). However, more research will be needed to show that female extra-pair paternity or the underlying behavioral traits are heritable.

In males, consistency in extra-pair paternity loss or gain can indicate that specific individual characteristics increase the probability to successfully engage in extra-pair copulations or to successfully defend paternity, which in turn may result in sexual selection. This would for instance be the case if females prefer to copulate with males of a specific phenotype (Weatherhead and Boag 1995; Yezerinac and Weatherhead 1997; Whittingham and Dunn 2016). Male blue tits showed significant repeatability only in whether they obtained extra-pair offspring, but not in the number of extra-pair partners or in the number of extra-pair young gained. This indicates that certain male phenotypes may consistently be more likely to sire extra-pair young, while the number of offspring sired and with how many extra-pair partners may depend more on the composition of the breeding environment (e.g. the availability of mates) or on post-copulatory mechanisms (i.e. sperm competition). Our findings and previous studies reported low repeatabilities for extra-pair paternity in males (see Introduction), suggesting that extra-pair paternity is not simply an individual-specific trait. Repeatability estimates in males might also be lower due to incomplete sampling. This is hard to avoid in natural populations, because males may have sired extra-pair young in broods that were not or not completely genotyped (e.g. abandoned clutches, broods in natural cavities in- or outside the study area). To reduce this effect, we repeated the analyses controlling for territory location (i.e., edge or central territory), assuming that males breeding on the edge of the study site are more likely to sire young in unsampled broods. However, this did not change the repeatability estimates qualitatively (Table 2).

Taken together, the observed low repeatabilities of measures of extra-pair paternity in both sexes suggest that extra-pair paternity may not cause strong sexual selection. A previous study on blue tits showed that the contribution of extra-pair paternity to variance in overall male reproductive success was small but significant (Schlicht and Kempenaers 2013). As expected, estimates of the potential for sexual selection were higher for males than for females, but opportunities for sexual selection may still be limited. The authors concluded that variation in reproductive success may largely be caused by stochastic processes, and was unrelated to phenotypic traits, which is in line with our findings.

Studies on zebra finches in aviaries showed that the number of extra-pair courtships (i.e., mating effort) performed by males and the responsiveness of females to extra-pair courtships are highly repeatable, heritable traits that contribute to the occurrence of extra-pair copulations and the resulting levels of extra-pair paternity (Forstmeier 2004; Forstmeier 2007; Forstmeier et al. 2011). Thus, an alternative or additional explanation for the low repeatability reported in our study is related to the fact that most studies – including ours – only measure the outcome of extra-pair behavior in terms of paternity. In natural systems, we still do not know to which extent variation in extra-pair paternity patterns reflects variation in extra-pair behavior of individuals and in the number of extra-pair copulations they obtained. Many extra-pair copulations may not lead to fertilizations (Hunter et al. 1992) and hence remain undetected (Girndt et al. 2018). Extra-pair paternity emerges from a series of behavioral and physiological processes involving multiple individuals. Thus, for an extra-pair copulation to successfully fertilize an egg, other factors such as the number and timing of within-pair copulations, ejaculate size, and the relative competitiveness of sperm from different males will also play a role. These factors are hard if not impossible to control for, but likely influence the observed levels of paternity and contribute to the “unexplained variation”. In most natural situations, accurately recording extra-pair (and within-pair) copulations is not feasible (but see Hunter et al. 1992). However, individual repeatability in extra-pair behavior can be investigated either in colony breeders (e.g., Hunter et al. 1992) or in a captive environment (e.g., Forstmeier 2004).

Effects of changes in the local breeding environment

Most studies investigating effects of the local environment on extra-pair paternity considered among-individual variation within a given breeding season instead of within-individual variation across seasons. Such approach does not allow to disentangle whether variation in extra-pair paternity is caused by environmental or individual-specific differences. Here, we find that changes in the breeding environment between years had little effect on individual-level changes in the occurrence or frequency of extra-pair paternity. We considered the effect of two potentially important aspects of the social context in which extra-pair behavior occurs. First, we investigated the characteristics of the local neighborhood, that is, the phenotypic composition, in terms of male traits known to explain extra-pair paternity patterns in blue tits within a given season (age and body size, Schlicht et al., 2015b), in terms of female traits potentially reflecting dominance or competitive ability (age and body size) and in terms of the familiarity of the focal individuals with their neighbors (proportion of familiar neighbors).

For adult males, a decrease in average body size of their male neighbors was associated with a higher number of extra-pair offspring sired (Table 4). In blue tits, extra-pair males are typically larger than within-pair males (Kempenaers et al. 1997), and hence smaller males in the neighborhood might have increased the chances for a male to sire extra-pair offspring. If this result is robust, it suggests that extra-pair mating success may depend on the competitiveness of a male relative to its neighbors (male-male competition). In females, variation in the competitiveness of the breeding neighborhood did not explain between-year changes in extra-pair paternity (Table 5). Similarly, in great tits, the phenotypic composition of the neighborhood (in this case age and exploration behavior of both sexes) was not related to patterns of extra-pair paternity within years (Roth et al. 2019). Although familiarity among neighbors could potentially also enhance the probability of extra-pair copulations, we found no evidence for such effects.

Second, we investigated whether between-year changes in extra-pair paternity could be explained by the presence of the social partner from the previous breeding season. We considered the effect of having the same or a different social partner, or of having the former social partner still present in the local neighborhood. Neither of these factors explained changes in patterns of extra-pair paternity in males or in females. Similarly, a study on patterns of extra-pair paternity in two other blue tit populations in France (Charmantier and Blondel 2003) reported no effect of mate fidelity (i.e. breeding with the same or a different social partner). Furthermore, if mate fidelity plays a role, we would expect a higher repeatability of extra-pair paternity for pairs, as reported in coal tits (*Parus ater*); repeatability in the number of extra-pair young produced was high for pairs staying together but decreased in cases of mate change (Dietrich et al. 2004). In our blue tit population, however, repeatability did not increase when social pairs were considered instead of individuals.

Other unmeasured individual and/or environmental aspects might explain variation in extra-pair paternity. For instance, extra-pair siring success in male blue tits has been related to plumage coloration or song characteristics (Delhey et al. 2006; Poesel et al. 2006; Poesel et al. 2011). Thus, considering changes in the expression of these traits within the close neighborhood may better explain changes in extra-pair paternity. Further, these individual traits can change over the course of a lifetime. For instance, American redstarts (*Setophaga ruticilla*) were most colorful in their second breeding season (Marini et al. 2015; Reudink et al. 2015), and in blue tits, crown coloration (Delhey and Kempenaers 2006) and song characteristics differ with age (Poesel et al. 2006). Investigating within-individual changes in such traits may potentially explain changes in extra-pair success and could also shed light on the little understood effect of male age on extra-pair paternity. Finally, environmental factors such as weather conditions (Bouwman and Komdeur 2006; Grant and Grant 2019) or food availability (Václav et al. 2003) may cause changes in social structure (prior or during breeding) or in the costs of engaging in extra-pair copulations and consequently may alter patterns of extra-pair paternity.

Extra-pair paternity is inherently a social process involving several individuals. Thus, the probability to engage in extra-pair copulations may be predicted better by recent interactions between individuals (i.e. between social pairs and potential extra-pair partners) rather than by events from the previous breeding season or by individual-specific phenotypic traits. For instance, blue tits frequently interact in larger flocks during winter. These associations seem to play an important role in the formation of social pairs (Smith 1984; Culina 2014; Gilsenan et al. 2017), in extra-pair associations (Beck et al. 2020) and in the composition of breeding neighborhoods (Firth and Sheldon 2016). Furthermore, it might be interesting to study the number and timing of interactions between close neighbors after settlement at the breeding box (i.e. when nest building had started) and during the fertile period of the female (Schlicht et al. 2015b). Such data would allow to examine the intensity of mate guarding and effects of local breeding synchrony (i.e. the overlap in fertile period of females in the close neighborhood) in relation to patterns of extra-pair paternity.

Lastly, we examined whether adult males sired more extra-pair offspring than yearlings because they experienced a different (social) environment. Yearling males by definition breed for the first time, implying that they have no familiar neighbors from previous breeding seasons and no former partner(s) that can still breed nearby. However, we found no evidence for an effect of changes in the number of familiar neighbors from previous breeding seasons or in other aspects of the local environment on extra-pair success, either for males that bred first as yearling and then as adult, or for adult males that bred in multiple years (Table 3, 4). A recent study on captive house sparrows showed that although older males outperformed yearling males in siring extra-pair offspring, yearling and adult males did not differ in their success in obtaining extra-pair copulations (Girndt et al. 2018). However, adult males delivered almost three times more sperm to the female’s egg than young males (as estimated by counting sperm on the perivitelline membrane; Girndt et al. 2019), suggesting that post-copulatory mechanisms (sperm competition) may play a role rather than differences in local environment or male attractiveness.

Conclusions and future directions

This study shows that extra-pair paternity in blue tits is somewhat repeatable, perhaps more so for females than for males. Individual-level changes in patterns of extra-pair paternity between years were largely independent of changes in the local, social neighborhood, including changes in territory size (local breeding density), the identity of the social partner and the composition of the neighborhood. Males however were more likely to sire extra-pair young when their neighbors were smaller, an effect that – if true – suggests that the relative competitive ability of males is important. Alternatively, changes in other, unmeasured aspects of the local environment, such as associations or interactions between individuals prior to breeding, and individual qualities such as plumage color or song characteristics, may be important determinants of extra-pair paternity. Although the readiness to engage in extra-pair behavior may be an individual-specific trait, extra-pair paternity is the ultimate outcome of behavioral events and physiological processes involving several individuals. Therefore, variation in extra-pair paternity may also depend to some extent on coincidental opportunities, such as “chance meetings” between two individuals that are willing to copulate and can do so without disturbance, or to other “chance events” such as the exact timing of within- and extra-pair copulations and the amount of sperm transferred.

Acknowledgments

We are grateful to Agnes Türk, Andrea Wittenzellner and the many people who contributed to data collection in the field and to Sylvia Kuhn and Alexander Girg for microsatellite genotyping. We thank Marc Naguib and two anonymous reviewers for constructive comments on the manuscript. KB is a PhD student in the International Max Planck Research School for Organismal Biology. We thank the Bavarian regional office for forestry (LWF) for permission to work in Westerholz.

Data accessibility

Analyses reported in this article can be reproduced using the data provided by Beck et al. (2020).

References

Akçay E, Roughgarden J. 2007. Extra-pair paternity in birds: review of the genetic benefits. Evol Ecol Res. 9:855.

Apio A, Plath M, Tiedemann R, Wronski T. 2007. Age-dependent mating tactics in male bushbuck (Tragelaphus scriptus). Behaviour. 144:585–610.

Araya-Ajoy YG, Dingemanse NJ, Kempenaers B. 2015. Timing of extrapair fertilizations: within-pair fertilization trade-offs or pair synchrony spillovers? Behav Ecol. 27(2):377-384.

Baldassarre DT, Greig EI, Webster MS. 2016. The couple that sings together stays together: duetting, aggression and extra-pair paternity in a promiscuous bird species. Biol Lett. 12:20151025.

Bates D, Maechler M, Bolker B, Walker S. 2014. lme4: Linear mixed-effects models using Eigen and S4. R Packag version. 1:1–23.

Beck KB, Farine DR, Kempenaers B. 2020. Winter associations predict social and extra-pair mating patterns in a wild songbird. Proc R Soc London Ser B Biol Sci. 287(1921).

Beck KB, Valcu M, Kempenaers B. 2020. Data from: Analysis of within-individual variation in extra-pair paternity in blue tits (*Cyanistes caeruleus*) shows low repeatability and little effect of changes in neighborhood. Behav Ecol. https://doi.org/10.5061/dryad.nzs7h44p5.

Beletsky LD, Orians GH. 1989. Familiar neighbors enhance breeding success in birds. Proc Natl Acad Sci. 86:7933–7936.

Bell AM, Hankison SJ, Laskowski KL. 2009. The repeatability of behaviour: a meta-analysis. Anim Behav. 77:771–783.

Biagolini-Jr C, Westneat DF, Francisco MR. 2017. Does habitat structural complexity influence the frequency of extra-pair paternity in birds? Behav Ecol Sociobiol. 71:101.

Blomqvist D, Andersson M, Küpper C, Cuthill IC, Kis J, Lanctot RB, Sandercock BK, Székely T, Wallander J, Kempenaers B. 2002. Genetic similarity between mates and extra-pair parentage in three species of shorebirds. Nature. 419:613.

Boake CRB. 1989. Repeatability: its role in evolutionary studies of mating behavior. Evol Ecol. 3:173–182.

Bouwman KM, Komdeur J. 2006. Weather conditions affect levels of extra-pair paternity in the reed bunting Emberiza schoeniclus. J Avian Biol. 37:238–244.

Brouwer L, Griffith SC. 2019. Extra-pair paternity in birds. Mol Ecol. 28:4864–4882.

Charmantier A, Blondel J. 2003. A contrast in extra-pair paternity levels on mainland and island populations of Mediterranean blue tits. Ethology. 109:351–363.

Cleasby IR, Nakagawa S. 2012. The influence of male age on within-pair and extra-pair paternity in passerines. Ibis. 154:318–324.

Culina A. 2014. With or without you: pair fidelity and divorce in monogamous birds.

Delhey K, Johnsen A, Peters A, Andersson S, Kempenaers B. 2003. Paternity analysis reveals opposing selection pressures on crown coloration in the blue tit (Parus caeruleus). Proc R Soc London B Biol Sci. 270:2057–2063.

Delhey K, Kempenaers B. 2006. Age differences in blue tit Parus caeruleus plumage colour: within-individual changes or colour-biased survival? J Avian Biol. 37:339–348.

Delhey K, Peters A, Johnsen A, Kempenaers B. 2006. Fertilization success and UV ornamentation in blue tits Cyanistes caeruleus: correlational and experimental evidence. Behav Ecol. 18:399–409.

Dietrich V, Schmoll T, Winkel W, Epplen JT, Lubjuhn T. 2004. Pair identity—an important factor concerning variation in extra-pair paternity in the coal tit (Parus ater). Behaviour. 141:817–835.

Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carré G, Marquéz JRG, Gruber B, Lafourcade B, Leitão PJ. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography. 36:27–46.

Dunn PO, Whittingham LA, Lifjeld JT, Robertson RJ, Boag PT. 1994. Effects of breeding density, synchrony, and experience on extrapair paternity in tree swallows. Behav Ecol. 5:123–129.

Edwards HA, Dugdale HL, Richardson DS, Komdeur J, Burke T. 2018. Extra-pair parentage and personality in a cooperatively breeding bird. Behav Ecol Sociobiol. 72(3):37.

Firth JA, Sheldon BC. 2016. Social carry-over effects underpin trans-seasonally linked structure in a wild bird population. Ecol Lett. 19:1324–1332.

Foerster K, Delhey K, Johnsen A, Lifjeld JT, Kempenaers B. 2003. Females increase offspring heterozygosity and fitness through extra-pair matings. Nature. 425:714.

Forstmeier W. 2004. Female resistance to male seduction in zebra finches. Anim Behav. 68:1005–1015.

Forstmeier W. 2007. Do individual females differ intrinsically in their propensity to engage in extra-pair copulations? PLoS One. 2:e952.

Forstmeier W, Martin K, Bolund E, Schielzeth H, Kempenaers B. 2011. Female extrapair mating behavior can evolve via indirect selection on males. Proc Natl Acad Sci. 108:10608–10613.

Forstmeier W, Nakagawa S, Griffith SC, Kempenaers B. 2014. Female extra-pair mating: adaptation or genetic constraint? Trends Ecol Evol. 29:456–464.

Germain RR, Wolak ME, Reid JM. 2018. Individual repeatability and heritability of divorce in a wild population. Biol Lett. 14:20180061.

Gilsenan C, Valcu M, Kempenaers B. 2017. Difference in arrival date at the breeding site between former pair members predicts divorce in blue tits. Anim Behav. 133:57–72.

Girndt A, Chng CWT, Burke T, Schroeder J. 2018. Male age is associated with extra-pair paternity, but not with extra-pair mating behaviour. Sci Rep. 8:8378.

Girndt A, Cockburn G, Sánchez-Tójar A, Hertel M, Burke T, Schroeder J. 2019. Male age and its association with reproductive traits in captive and wild house sparrows. J Evol Biol. 32:1432–1443.

González-Solís J, Becker PH. 2002. Mounting frequency and number of cloacal contacts increase with age in common terns Sterna hirundo. J Avian Biol. 33:306–310.

Grabowska-Zhang AM, Wilkin TA, Sheldon BC. 2011. Effects of neighbor familiarity on reproductive success in the great tit (Parus major). Behav Ecol. 23:322–333.

Grant PR, Grant BR. 2019. Adult sex ratio influences mate choice in Darwin’s finches. Proc Natl Acad Sci. 116:12373–12382.

Griffith SC, Owens IPF, Thuman KA. 2002. Extra pair paternity in birds: a review of interspecific variation and adaptive function. Mol Ecol. 11:2195–2212.

Hasselquist D, Bensch S, von Schantz T. 1996. Correlation between male song repertoire, extra-pair paternity and offspring survival in the great reed warbler. Nature. 381:229–232.

Hothorn T, Bretz F, Westfall P. 2008. Simultaneous inference in general parametric models. Biometrical J. 50:346–363.

Hsu Y, Simons MJP, Schroeder J, Girndt A, Winney IS, Burke T, Nakagawa S. 2017. Age-dependent trajectories differ between within-pair and extra-pair paternity success. J Evol Biol. 30:951–959.

Hunter FM, Burke T, Watts S emsp 14 E. 1992. Frequent copulation as a method of paternity assurance in the northern fulmar. Anim Behav. 44:149–156.

Ihle M, Kempenaers B, Forstmeier W. 2015. Fitness benefits of mate choice for compatibility in a socially monogamous species. PLoS Biol. 13:e1002248.

Johnsen A, Pauliny A, Lifjeld JT, Blomqvist D. 2017. Is telomere length associated with mate choice in a songbird with a high rate of extra-pair paternity? PLoS One. 12:e0182446.

Kalinowski ST, Taper ML, Marshall TC. 2007. Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. Mol Ecol. 16:1099–1106.

Kempenaers B, Verheyen GR, Van den Broeck M, Burke T, Van Broeckhoven C, Dhondt A. 1992. Extra-pair paternity results from female preference for high-quality males in the blue tit. Nature. 357:494–496.

Kempenaers B. 1994. Polygyny in the blue tit: unbalanced sex ratio and female aggression restrict mate choice. Anim Behav. 47:943-957.

Kempenaers B, Verheyen GR, Dhondt AA. 1997. Extrapair paternity in the blue tit (Parus caeruleus): female choice, male charateristics, and offspring quality. Behav Ecol. 8:481–492.

Knief U, Forstmeier W, Pei Y, Ihle M, Wang D, Martin K, Opatová P, Albrechtová J, Wittig M, Franke A. 2017. A sex-chromosome inversion causes strong overdominance for sperm traits that affect siring success. Nat Ecol Evol. 1:1177.

Küpper C, Stocks M, Risse JE, dos Remedios N, Farrell LL, McRae SB, Morgan TC, Karlionova N, Pinchuk P, Verkuil YI. 2016. A supergene determines highly divergent male reproductive morphs in the ruff. Nat Genet. 48:79.

Leary CJ, Garcia AM, Knapp R. 2008. Density-dependent mating tactic expression is linked to stress hormone in Woodhouse’s toad. Behav Ecol. 19:1103–1110.

Lebigre C, Arcese P, Sardell RJ, Keller LF, Reid JM. 2012. Extra-pair paternity and the variance in male fitness in song sparrows (Melospiza melodia). Evol Int J Org Evol. 66:3111–3129.

Lessells CM, Boag PT. 1987. Unrepeatable repeatabilities: a common mistake. Auk.:116–121.

Magrath MJL, Vedder O, Van der Velde M, Komdeur J. 2009. Maternal effects contribute to the superior performance of extra-pair offspring. Curr Biol. 19:792–797.

Maldonado-Chaparro AA, Montiglio P, Forstmeier W, Kempenaers B, Farine DR. 2018. Linking the fine-scale social environment to mating decisions: a future direction for the study of extra-pair paternity. Biol Rev. 93:1558–1577.

Marini KLD, McKellar AE, Ratcliffe LM, Marra PP, Reudink MW. 2015. Age-related change in carotenoid-based plumage of the American Redstart (Setophaga ruticilla). J Ornithol. 156:783–793.

Michálková R, Tomášek O, Adámková M, Kreisinger J, Albrecht T. 2019. Extra-pair paternity patterns in European barn swallows Hirundo rustica are best explained by male and female age rather than male ornamentation. Behav Ecol Sociobiol. 73:119.

Midamegbe A, Grégoire A, Perret P, Doutrelant C. 2011. Female-female aggressiveness is influenced by female coloration in blue tits. Anim Behav. 82:245-253.

Møller, AP, Birkhead, TR. 1994. The evolution of plumage brightness in birds is related to extrapair paternity. Evolution. 48:1089-1100.

Møller AP, Briskie J V. 1995. Extra-pair paternity, sperm competition and the evolution of testis size in birds. Behav Ecol Sociobiol. 36:357–365.

Møller AP, Tegelström H. 1997. Extra-pair paternity and tail ornamentation in the barn swallow Hirundo rustica. Behav Ecol Sociobiol. 41:353–360.

Mulrey TEP, Eggert A-K, Sakaluk SK. 2015. Switching tactics: phenotypic plasticity in the alternative mate-finding tactics of burying beetles. Anim Behav. 108:175–182.

Nakagawa S, Schielzeth H. 2010. Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. Biol Rev. 85:935–956.

Petrie M, Kempenaers B. 1998. Extra-pair paternity in birds: explaining variation between species and populations. Trends Ecol Evol. 13:52–58.

Plaza M, Cantarero A, Gil D, Moreno J. 2019. Experimentally flight-impaired females show higher levels of extra-pair paternity in the pied flycatcher Ficedula hypoleuca. Biol Lett. 15:20190360.

Poesel A, Gibbs HL, Nelson DA. 2011. Extrapair fertilizations and the potential for sexual selection in a socially monogamous songbird. Auk. 128:770–776.

Poesel A, Kunc HP, Foerster K, Johnsen A, Kempenaers B. 2006. Early birds are sexy: male age, dawn song and extrapair paternity in blue tits, Cyanistes (formerly Parus) caeruleus. Anim Behav. 72:531–538.

Reid JM, Arcese P, Sardell RJ, Keller LF. 2010. Heritability of female extra-pair paternity rate in song sparrows (Melospiza melodia). Proc R Soc London B Biol Sci.:rspb20101704.

Reudink MW, McKellar AE, Marini KLD, McArthur SL, Marra PP, Ratcliffe LM. 2015. Inter-annual variation in American redstart (Setophaga ruticilla) plumage colour is associated with rainfall and temperature during moult: an 11-year study. Oecologia. 178:161–173.

Richard M, Lecomte J, De Fraipont M, Clobert J. 2005. Age-specific mating strategies and reproductive senescence. Mol Ecol. 14:3147–3155.

Roth AM, Firth JA, Patrick SC, Cole EF, Sheldon BC. 2019. Partner’s age, not social environment, predicts extrapair paternity in wild great tits (Parus major). Behav Ecol. 30:1782–1793.

Saino N, Primmer CR, Ellegren H, Møller AP. 1999. Breeding synchrony and paternity in the barn swallow (Hirundo rustica). Behav Ecol Sociobiol. 45:211–218.

Santema P, Valcu M, Clinchy M, Zanette LY, Kempenaers B. 2019. Effects of predator call playbacks on reproductive success and extrapair paternity in blue tits. Anim Behav. 155:97–109.

Schlicht E, Kempenaers B. 2011. Extra-pair paternity and sexual selection. In: From genes to animal behavior. Springer. p. 35–65.

Schlicht E, Kempenaers B. 2013. Effects of social and extra-pair mating on sexual selection in blue tits (cyanistes caeruleus). Evolution. 67:1420–1434.

Schlicht L, Girg A, Loës P, Valcu M, Kempenaers B. 2012. Male extrapair nestlings fledge first. Anim Behav. 83:1335–1343.

Schlicht L, Valcu M, Kempenaers B. 2014. Thiessen polygons as a model for animal territory estimation. Ibis. 156:215–219.

Schlicht L, Valcu M, Kempenaers B. 2015a. Spatial patterns of extra-pair paternity: beyond paternity gains and losses. J Anim Ecol. 84:518–531.

Schlicht L, Valcu M, Kempenaers B. 2015b. Male extraterritorial behavior predicts extrapair paternity pattern in blue tits, Cyanistes caeruleus. Behav Ecol. 26:1404–1413.

Smith SM. 1984. Flock switching in chickadees: why be a winter floater? Am Nat. 123:81–98.

Stoffel MA, Nakagawa S, Schielzeth H. 2017. rptR: Repeatability estimation and variance decomposition by generalized linear mixed-effects models. Methods Ecol Evol. 8:1639–1644.

Strohbach S, Curio E, Bathen A, Epplen J, Lubjuhn T. 1998. Extrapair paternity in the great tit (Parus major): a test of the “good genes” hypothesis. Behav Ecol. 9:388–396.

Stutchbury BJ, Morton ES. 1995. The effect of breeding synchrony on extra-pair mating systems in songbirds. Behaviour. 132:675–690.

Team RC. 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Thusius KJ, Dunn PO, Peterson KA, Whittingham LA. 2001. Extrapair paternity is influenced by breeding synchrony and density in the common yellowthroat. Behav Ecol. 12:633–639.

Tsubaki Y. 2003. The genetic polymorphism linked to mate-securing strategies in the male damselfly Mnais costalis Selys (Odonata: Calopterygidae). Popul Ecol. 45:263–266.

Václav R, Hoi H, Blomqvist D. 2003. Food supplementation affects extrapair paternity in house sparrows (Passer domesticus). Behav Ecol. 14:730–735.

Valcu M, Kempenaers B. 2008. Causes and consequences of breeding dispersal and divorce in a blue tit, Cyanistes caeruleus, population. Anim Behav. 75:1949–1963.

Valcu M, Kempenaers B. 2010. Spatial autocorrelation: an overlooked concept in behavioral ecology. Behav Ecol. 21:902–905.

Valcu M, Schlicht L. 2013. Package ‘expp’. See http://CRAN.R-project.org/package=expp.

Weatherhead PJ, Boag PT. 1995. Pair and extra-pair mating success relative to male quality in red-winged blackbirds. Behav Ecol Sociobiol. 37:81–91.

Webster MS, Pruett-Jones S, Westneat DF, Arnold SJ. 1995. Measuring the effects of pairing success, extra-pair copulations and mate quality on the opportunity for sexual selection. Evolution. 49:1147–1157.

Westneat DF, Mays HL. 2005. Tests of spatial and temporal factors influencing extra-pair paternity in red-winged blackbirds. Mol Ecol. 14:2155–2167.

Westneat DF, Sherman PW. 1997. Density and extra-pair fertilizations in birds: a comparative analysis. Behav Ecol Sociobiol. 41:205–215.

Westneat DF, Sherman PW, Morton ML. 1990. The ecology and evolution of extra-pair copulations in birds. Curr Ornithol. 7:331–369.

Westneat DF, Stewart IRK. 2003. Extra-pair paternity in birds: causes, correlates, and conflict. Annu Rev Ecol Evol Syst. 34:365–396.

Whittingham LA, Dunn PO. 2016. Experimental evidence that brighter males sire more extra-pair young in tree swallows. Mol Ecol. 25:3706–3715.

Whittingham LA, Dunn PO, Stapleton MK. 2006. Repeatability of extra-pair mating in tree swallows. Mol Ecol. 15:841–849.

Yezerinac SM, Weatherhead PJ. 1997. Extra–pair mating, male plumage coloration and sexual selection in yellow warblers (Dendroica petechia). Proc R Soc London B Biol Sci. 264:527–532.

Supplementary material

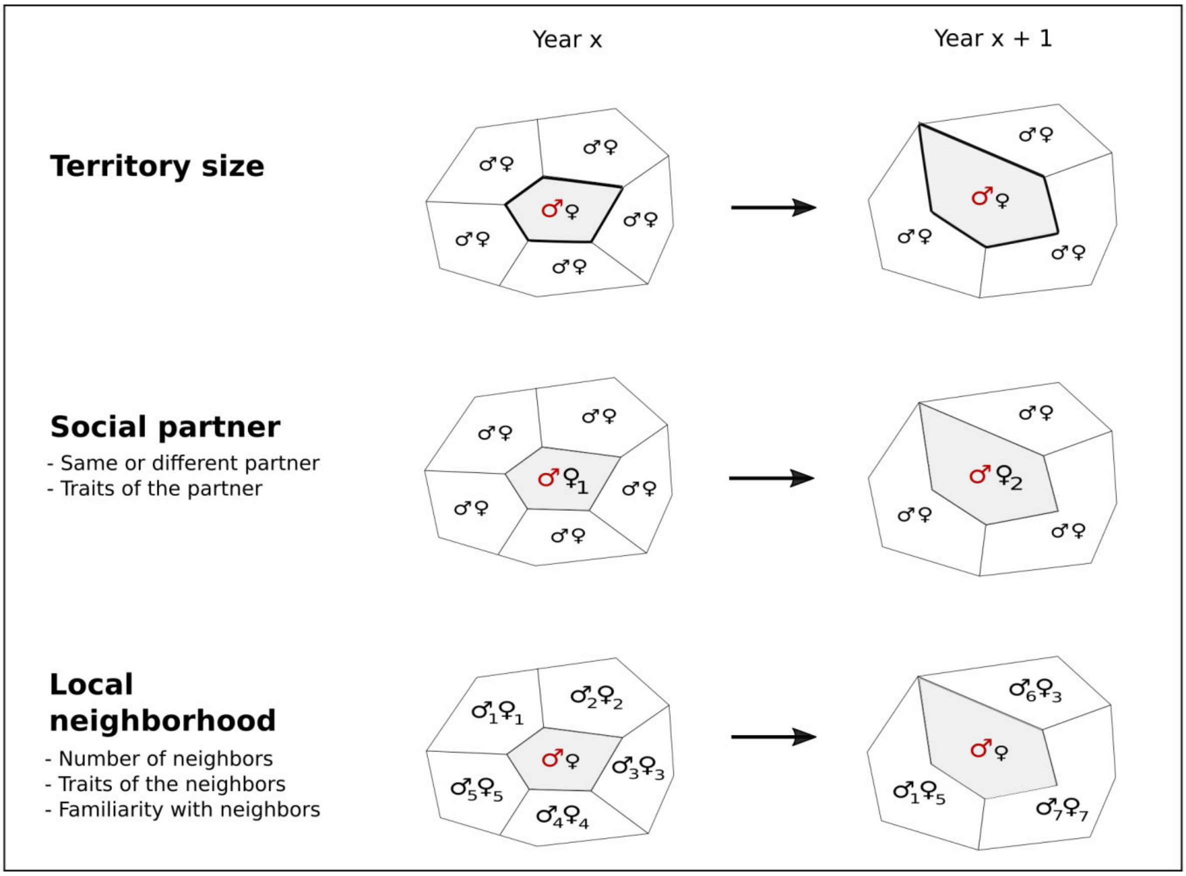


Figure S1. Schematic illustration of the different environmental contexts in which extra-pair paternity occurs that can change for an individual from one breeding season to the next (year x to year x+1). The focal individual (here a male) is represented in red, neighbors and the social partner in black. Breeding territories are represented by polygons. The corresponding context which might change between years is marked in bold. See also Table 1.

Table S1. Effects of changes in the local environment on between-year changes in levels of extra-pair paternity for yearling male blue tits that become adult (N=172). Extra-pair paternity is measured as the change in the number of females with whom a male sired extra-pair offspring (EP females), the number of young a male sired (EPY) and whether a male changed its' EPP status (i.e., changed or remained the same). The change in territory size and the number of neighbors was here calculated as difference and not as proportion and both variables were standardized. See methods for details on the models.

	Δ EP females			**Δ EPY**			**Change in EPP status**		
	Estimate ± SE	**t**	**p**	**Estimate ± SE**	**t**	**p**	**Estimate ± SE**	**t**	**p**
Intercept	0.36 ± 0.15			0.78 ± 0.32			- 0.67 ± 0.55		
Number of neighbours	0.01 ± 0.07	0.13	1.00	-0.03 ±0.15	-0.16	0.99	-0.38 ±0.29	-1.31	0.81
Territory size	-0.13 ± 0.07	-1.84	0.41	-0.07 ±0.16	-0.46	0.99	0.12 ±0.26	0.45	0.99
Consistent social partner	-0.09 ± 0.10	-0.83	0.98	0.03 ±0.22	0.14	1.00	-0.23 ±0.26	-0.86	0.98
Proportion yearling male neighbours	-0.004 ± 0.22	-0.02	1.00	-0.42 ±0.49	-0.87	0.98	0.30 ±0.79	0.39	0.99
Average male neighbour tarsus length	-0.20 ± 0.24	-0.82	0.98	-0.53 ±0.52	-1.02	0.94	-1.07 ±0.98	-1.09	0.92
Proportion familiar males	0.40 ± 0.38	1.07	0.92	0.60 ±0.81	0.73	0.99	0.96 ±0.87	1.10	0.91
Proportion familiar females	-0.12 ±0.37	-0.32	0.99	-0.25 ±0.81	-0.31	0.99	-0.18 ±0.91	-0.20	0.99
Previous social partner present	-0.02 ± 0.31	-0.07	1.00	-0.02 ±0.66	-0.03	1.00	0.27 ±0.71	0.38	0.99

Table S2. Effects of changes in the local environment on between-year changes in levels of extra-pair paternity for adult male blue tits (N=49). Extra-pair paternity is measured as the change in the number of females with whom a male sired extra-pair offspring (EP females), the number of young a male sired (EPY) and whether a male changed its' EPP status (i.e., changed or remained the same). The change in territory size and the number of neighbors was here calculated as difference and not as proportion and both variables were standardized. See methods for details on the models.

	Δ EP females			**Δ EPY**			**Change in EPP status**		
	Estimate ± SE	**t**	**p**	**Estimate ± SE**	**t**	**p**	**Estimate ± SE**	**t**	**p**
Intercept	0.07 ± 0.11			0.27 ± 0.32			- 0.71 ± 0.58		
Number of neighbours	-0.13 ± 0.08	-1.54	0.68	-0.48 ±0.23	-2.13	0.25	0.33 ±0.35	0.94	0.97
Territory size	-0.10 ± 0.09	-1.20	0.89	-0.13 ±0.23	-0.57	0.99	0.17 ±0.32	0.53	0.99
Consistent social partner	-0.04 ± 0.10	-0.36	0.99	0.19 ±0.26	0.71	0.99	0.11 ±0.25	0.45	0.99
Proportion yearling male neighbours	0.48 ± 0.26	1.87	0.41	0.74 ±0.72	1.03	0.95	-0.96 ±1.00	-0.96	0.97
Average male neighbour tarsus length	-0.49 ± 0.27	-1.81	0.46	-1.86 ±0.72	-2.58	0.08	0.53 ±1.00	0.53	0.99
Proportion familiar males	0.50 ± 0.36	1.41	0.77	1.05 ±0.96	1.09	0.93	0.60 ±1.15	0.52	0.99
Proportion familiar females	0.55 ± 0.30	1.82	0.46	0.71 ±0.80	0.88	0.98	-0.08 ±1.08	-0.08	1.00
Previous social partner present	-0.34 ± 0.25	-1.37	0.80	-0.81 ±0.66	-1.23	0.87	0.43 ±0.58	0.73	0.99
Previous extra-pair partner present	-0.55 ± 0.34	-1.64	0.59	-1.56 ±0.90	-1.73	0.53	-1.82 ±1.17	-1.56	0.66

Table S3. Effects of changes in the local environment on between-year changes in levels of extra-pair paternity for female blue tits (N=190). Extra-pair paternity is measured as the change in the number of males with whom a female sired extra-pair offspring (EP males), the number of young within the females clutch (EPY) and whether a female changed its' EPP status (i.e., changed or remained the same). The change in territory size and the number of neighbors was here calculated as difference and not as proportion and both variables were standardized. See methods for details on the models.

	Δ EP males			**Δ EPY**			**Change in EPP status**		
	Estimate ± SE	**t**	**P**	**Estimate ± SE**	**t**	**P**	**Estimate ± SE**	**t**	**P**
Intercept	- 0.08 ± 0.06			- 0.06 ± 0.13			- 1.42 ± 0.50		
Number of neighbours	0.02 ±0.03	0.69	0.99	0.003 ±0.05	0.06	1.00	-0.09 ± 0.12	-0.77	0.99
Territory size	0.08 ±0.05	1.60	0.72	0.08 ±0.10	0.86	0.99	0.23 ± 0.23	1.03	0.98
Consistent social partner	0.20 ±0.11	1.79	0.57	0.10 ±0.22	0.44	0.99	0.84 ± 0.39	2.17	0.30
Social partner body size	0.14 ±0.08	1.85	0.52	-0.03 ±0.15	-0.17	1.00	0.25 ± 0.39	0.64	0.99
Proportion familiar males	-0.001 ±0.18	-0.003	1.00	0.35 ±0.36	0.99	0.99	0.68 ± 0.64	1.07	0.98
Proportion familiar females	0.06 ±0.21	0.30	0.99	-0.18 ±0.41	-0.44	0.99	0.66 ± 0.70	0.95	0.99
Average male neighbour body size	0.09 ±0.15	0.61	0.99	0.26 ±0.29	0.88	0.99	1.09 ± 0.72	1.52	0.79
Proportion yearling male neighbours	0.10 ±0.17	0.60	0.99	0.03 ±0.33	0.10	1.00	-0.50 ± 0.72	-0.70	0.99
Average female neighbor body size	-0.32 ± 0.16	-1.98	0.42	-0.73 ± 0.32	-2.30	0.22	0.34 ± 0.80	0.42	0.99
Proportion yearling female neighbors	-0.001 ± 0.17	-0.01	1.00	-0.23 ± 0.32	-0.72	0.99	0.30 ± 0.67	0.45	0.99
Previous social partner present	0.004 ±0.15	0.03	1.00	-0.09 ±0.29	-0.32	0.99	0.17 ± 0.45	0.38	0.99
Previous extra-pair partner present	-0.55 ±0.20	-2.80	0.06	-0.85 ±0.38	-2.22	0.26	-0.09 ± 0.59	-0.15	1.00

Table S4. Table showing the correlation coefficients of all fixed effects included in the female model (excluding the categorical variables). In addition, we calculated the variance inflation factor (VIF) for all fixed effects in each model (including the categorical variables). The VIF was well below the threshold in all cases (ranging from 1.04 – 1.80; Dormann et al. 2013).

	Number of neighbors	Social partner body size	Territory size	Proportion familiar males	Proportion familiar females	Average male neighbor tarsus length	Proportion yearling male neighbors	Proportion yearling female neighbors
Social partner body size	-0.010							
Territory size	0.297	0.074						
Proportion familiar males	-0.046	0.056	0.020					
Proportion familiar females	-0.089	-0.046	-0.003	0.418				
Proportion yearling male neighbors	0.038	-0.018	-0.155	-0.419	-0.104			
Average male neighbor tarsus length	-0.041	-0.072	-0.066	-0.057	-0.007	-0.016		
Proportion yearling female neighbors	0.008	-0.021	-0.272	-0.055	-0.340	0.101	0.405	
Average female neighbor body size	0.018	0.090	-0.105	-0.039	-0.154	0.090	0.070	0.098

Table S5. Table showing the correlation coefficients of all fixed effects included in the models on yearling males turning adult and only adults (in italic), excluding the categorical variables. In addition, we calculated the variance inflation factor (VIF) for all fixed effects for each model (including the categorical variables). The VIF was well below the threshold in all cases (Range in males turning from yearling to adult: 1.02 – 1.39; only adults: 1.04 – 1.79; Dormann et al. 2013).

	Number of neighbors	Territory size	Proportion familiar males	Proportion familiar females	Proportion yearling male neighbors
Territory size	0.159				
	0.154				
Proportion familiar males	-0.052	0.172			
	-0.135	*-0.025*			
Proportion familiar females	-0.034	0.071	0.431		
	-0.151	*0.109*	*0.439*		
Proportion yearling male neighbors	0.123	-0.125	-0.341	-0.158	
	0.054	*-0.129*	*-0.409*	*-0.131*	
Average male neighbor tarsus length	-0.112	-0.001	0.077	0.057	-0.059
	-0.139	*-0.074*	*-0.101*	*-0.073*	*0.006*

Table S6. Repeatability of extra-pair paternity (total number of extra-pair young, number of extra-pair mates and the occurrence of extra-pair paternity) for male and female blue tits and the repeatability of paternity loss in males (i.e., the number of young lost and the occurrence of paternity loss). Shown are the repeatability coefficients (R), their 95% confidence intervals (CI) and the associated P-values for the two random intercepts „individual identity“ and „box identity“.

	Individual			**Box**		
	R	**95%CI**	**P**	**R**	**95%CI**	**P**
Males						
Number of EPY	0.03	0.00 - 0.06	0.12	0.00	0.00 – 0.02	1.00
Number of EP mates	0.06	0.00 - 0.15	0.14	0.03	0.00 – 0.10	0.27
EPP occurrence	0.07	0.00 – 0.13	0.07	0.02	0.00 – 0.09	0.31
Proportion of young lost	0.00	0.00 – 0.02	0.50	0.01	0.00 – 0.03	0.10
Paternity loss	0.00	0.00 – 0.06	1.00	0.04	0.00 – 0.10	0.13
Females						
Number of EPY	0.12	0 - 0.21	**0.003**	0.04	0.00 - 0.11	0.12
Number of EP mates	0.00	0 - 0.05	0.50	0.00	0.00 - 0.05	1.00
EPP occurrence	0.10	0 – 0.15	**0.01**	0.00	0.00 – 0.04	1.00

Table S7. Repeatability of extra-pair paternity (total number of extra-pair young, number of extra-pair mates, the occurrence of extra-pair paternity) for male and female blue tits and the repeatability of paternity loss in males (i.e., the number of young lost and the occurrence of paternity loss). Shown are the repeatability coefficients (R), their 95% confidence intervals (CI) and the associated P-values for the two random intercept „individual identity“ and „pair identity“.

	Individual			**Pair**		
	R	**95%CI**	**P**	**R**	**95%CI**	**P**
Males						
Number of EPY	0.01	0.00 - 0.02	0.40	0.02	0.00 – 0.20	0.34
Number of EP mates	0.04	0.00 - 0.11	0.22	0.09	0.00 – 0.32	0.18
EPP occurrence	0.06	0.00 - 0.11	0.09	0.00	0.00 – 0.04	1.00
Proportion of young lost	0.01	0.00 - 0.08	0.34	0.00	0.00 – 0.04	1.00
Paternity loss	0.00	0.00 - 0.05	1.00	0.00	0.00 – 0.21	0.50
Females						
Number of EPY	0.12	0.00 - 0.20	**0.003**	0.04	0.00 - 0.11	0.12
Number of EP mates	0.00	0.00 - 0.06	0.50	0.00	0.00 - 0.12	1.00
EPP occurrence	0.10	0.00 – 0.15	**0.01**	0.00	0.00 – 0.03	1.00

References

Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carré G, Marquéz JRG, Gruber B, Lafourcade B, Leitão PJ. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography (Cop). 36:27–46.

Chapter 4

Cooperative neighbourhood benefits are not a major driver of extra-pair paternity in blue tits

Kristina B. Beck, Peter Santema, Lotte Schlicht, Bart Kempenaers

Why females of socially monogamous species engage in extra-pair copulations is a long-standing question in behavioural ecology. It has recently been proposed that females may benefit if extra-pair copulations incentivize males to extend focus from their own brood towards the entire neighbourhood in which they may have sired extra-pair young. This would generate a more cooperative neighbourhood which would benefit the extra-pair female, as well as other individuals breeding in such an environment. Using twelve years of data from a population of blue tits (*Cyanistes caeruleus*), we examined whether having extra-pair young or breeding in a neighbourhood with a higher prevalence of extra-pair paternity was associated with improved breeding success or survival. Nests that contained extra-pair young or nests in a neighbourhood with more extra-pair paternity were not more likely to produce fledglings, did not have higher fledging success and did not produce nestlings in better condition. We also found no effects on survival of offspring and males, although there was some indication that females breeding in a neighbourhood with more extra-pair paternity were more likely to survive. Although we measured behaviour indirectly through its outcome on paternity, our findings suggest that it is unlikely that female extra-pair behaviour in blue tits arises through "cooperative neighbourhood" benefits.

Unpublished manuscript

Introduction

Most of the studied socially monogamous bird species engage in sexual behaviour outside the pair-bond, often resulting in extra-pair paternity (EPP) (Petrie and Kempenaers 1998; Griffith et al. 2002; Westneat and Stewart 2003; Brouwer and Griffith 2019). The advantage of extra-pair copulations (EPCs) for males is clear as they can increase their fitness by gaining additional offspring without providing additional care. However, it remains controversial whether and how females benefit from extra-pair copulations. Extra-pair copulations do not increase the number of offspring produced and may involve costs such as sexually transmitted diseases, reduced paternal care and physical punishment by the social male (Poiani and Wilks 2000; Arnqvist and Kirkpatrick 2005; Sardell et al. 2012; Forstmeier et al. 2014; Hsu et al. 2014; Plaza et al. 2019). However, in several species females actively solicit extra-pair copulations (Kempenaers et al. 1992; Birkhead and Møller 1993; Sheldon 1994; Forstmeier 2007), suggesting that either females acquire benefits from this behaviour, or that the behaviour has evolved as a side-effect of selection on male promiscuity (Forstmeier et al. 2011; but see Wang et al. 2019).

Several benefits of female extra-pair behaviour have been proposed. Among those, indirect, genetic benefits received much attention in the past (Jennions and Petrie 2000; Akçay and Roughgarden 2007). Genetic benefits can only occur if extra-pair copulations lead to extra-pair paternity (Akçay and Roughgarden 2007; Mays et al. 2008). They include the production of more attractive offspring ("sexy sons"), higher quality offspring (through good genes or higher genetic diversity) or more genetically diverse offspring ("bet-hedging"; reviewed in Westneat et al. 1990; Kempenaers and Dhondt 1993; Jennions and Petrie 2000; Griffith et al. 2002). However, most studies found no or weak evidence for indirect benefits (Akçay and Roughgarden 2007) or even showed fitness costs of extra-pair paternity (Sardell et al. 2012; Forstmeier et al. 2014; Hsu et al. 2014).

In contrast, direct benefits of extra-pair copulations can arise from the behaviour itself, i.e. they do not necessarily require that the copulations lead to fertilizations (Petrie and Kempenaers 1998), and they can come in a variety of forms at different stages of reproduction. For example, females can ensure fertilization of their eggs (Sheldon 1994), they can benefit from increased predator mobbing by the extra-pair male (Gray 1997a), or from a higher tolerance while foraging in the extra-pair male's territory (Gray 1997a), or they can receive additional parental care from the extra-pair male (Townsend et al. 2010). Receiving such direct benefits should increase female fitness by improving reproductive success (Gray 1997b).

Recently, Eliassen and Jørgensen (2014) proposed an additional direct benefit. Based on a theoretical model, they suggest that potential paternity gains from extra-pair copulations with neighbouring females could incentivize males to extend their focus from a single brood towards the entire neighbourhood ('cooperative neighbourhood hypothesis'). Thus, besides providing parental care at their own nest, extra-pair males should engage in activities such as vigilance and predator mobbing that benefit the entire neighbourhood, and they may also become more tolerant towards neighbours foraging in their territory. Consequently, selection might favour females that engage in extra-pair copulations with neighbouring males, because it creates a safer and more productive breeding environment. Importantly, in such a scenario not only the female that performs the behaviour would benefit, but the entire neighbourhood.

The 'cooperative neighbourhood hypothesis' is consistent with several common observations. For instance, extra-pair sires are typically close neighbours (Komdeur 2001; Schlicht et al. 2015), levels of extra-pair paternity often correlate with breeding density (Westneat and Sherman 1997; Schlicht et al. 2015) and help by extra-pair males has been observed in some species (in blue tits: Kempenaers 1993; in american crows (*Corvus brachyrhynchos*): Townsend et al. 2010). However, the ultimate consequence of receiving direct benefits from extra-pair copulations – whether through additional care for the extra-pair female's brood or through a more cooperative neighbourhood – is that broods or social parents with extra-pair young or located in a neighbourhood with a higher prevalence of extra-pair behaviour should do better in terms of survival. Yet, few empirical studies have assessed such direct fitness benefits of female extra-pair behaviour (Gray 1997b; Gray 1997a; Sheldon and Mangel 2014; Mennerat et al. 2018).

Here, we examined in a population of blue tits (*Cyanistes caeruleus*) whether reproductive success and adult survival is related to (a) the occurrence of extra-pair young in the brood or (b) to being located in a neighbourhood with a higher prevalence of extra-pair paternity. We did not investigate extra-pair copulations directly, because it is not feasible to obtain a comprehensive dataset for this population. Instead, we used the resulting extra-pair paternity as a proxy for extra-pair behaviour. During the breeding season (March – June), blue tits form socially monogamous pairs and extra-pair paternity is common (about half of the broods contain at least one extra-pair young and 10-15 % of all offspring are sired by extra-pair males; Kempenaers et al. 1992; Kempenaers 1997; Delhey et al. 2003). Blue tits fulfil several of the predictions of the 'cooperative neighbourhood hypothesis', as outlined in Eliassen and Jørgensen (2014). For instance, extra-pair partners are mostly close neighbours (Schlicht et al. 2015), levels of extra-pair paternity depend on the breeding density (Schlicht et al. 2015) and help by an extra-pair male in feeding and predator defence has been recorded anecdotally (Kempenaers 1993). Thus, the blue tit seems a suitable study species to test the 'cooperative neighbourhood hypothesis'.

We used data from twelve breeding seasons to examine whether brood success and parental survival were related to patterns of extra-pair paternity. Specifically, we tested the following predictions. (i) Broods with extra-pair young or broods in neighbourhoods with higher levels of extra-pair paternity should be less likely to fail completely. Reduced brood failure might arise because of a reduced risk of brood predation when extra-pair males help mobbing predators of nestlings (e.g. woodpeckers), or because of a reduced risk of parental predation – a known cause of brood failure in blue tits (Santema and Kempenaers 2018). (ii) Broods with extra-pair young or broods in neighbourhoods with higher levels of extra-pair paternity should have fledglings of higher body mass and a higher fledging success. These effects are expected if extra-pair males directly contribute to offspring care or if they allow parents to invest more in offspring care, e.g. by creating a safer neighbourhood. In combination with extra-pair males mobbing predators after fledging, this potentially could lead to higher local recruitment. (iii) Social parents from broods with extra-pair young or social parents from neighbourhoods with high levels of extra-pair paternity should have a higher probability of survival to the next breeding season. Higher survival is predicted when extra-pair males alert others to danger (reduced likelihood of predation) or when extra-pair males invest in the focal brood (reduced likelihood of predation or exhaustion, because of extra help with offspring care).

Methods

Study system

Between 2007 and 2018, we studied a population of blue tits breeding in nest boxes in a mixed-deciduous woodland near Landsberg am Lech, Germany ("Westerholz", 48°08′26′′N 10°53′29′′E, ca. 40ha; for more details see Schlicht et al. 2012). The site contains 277 wooden, small-holed (diameter 26 mm) nest boxes. During each breeding season, nest boxes were checked at least once per week (from mid-March onwards) to monitor nest-building activity and clutch size and boxes were checked daily to determine laying onset (date of first egg), and the date(s) of hatching and fledging.

Adult blue tits were either trapped inside the nest box during the nestling provisioning phase (nestling age: 8–12 days) or throughout the winter with either mist-nets (since 2014) or by catching roosting individuals inside the nest box during the night. Each bird was equipped with a metal ring and 1–3 colour rings. When nestlings were 14 days old, we banded and weighed them. From all adults and nestlings we took a small (5–10µl) blood sample for paternity analysis and sexing. We also collected any unhatched eggs and dead young when the oldest nestling was 5 days old for later parentage analysis.

Data on extra-pair paternity

We extracted DNA from all blood samples and – when possible – from embryo or nestling tissue. For genotyping, we used 14 microsatellite markers (ADCbm; ClkpolyQ; Mcµ4; PAT MP 2-43; Pca3, Pca4, Pca7, Pca8, Pca9; Phtr3 (until 2017); PK11, PK12; PmaTAGAn71 (from 2018 onwards); POCC1, and POCC6. Microsatellite amplifications were performed in multiplexed PCRs with primer mixes containing two to five primer pairs (Table S1). Each 10µl multiplex PCR contained 20–80ng DNA (see the supplementary material for PCR cycling conditions). We compared the genotypes of parents and their offspring using the software CERVUS (Kalinowski et al. 2007). This allowed us to determine whether a brood contained extra-pair young and which males sired extra-pair young. Our data underestimate the number of males and females that engaged in extra-pair copulations, for two reasons. (i) We only detected extra-pair events if they led to extra-pair paternity. This is unavoidable, because it is not feasible to observe all copulations. (ii) In 24% of the nests at least one egg was not genotyped, leading to an underestimation of the proportion of nests containing extra-pair young. To assess the importance of this limitation, we repeated all analyses including only data of completely genotyped nests.

Statistical analysis

We included data from twelve breeding seasons (2007-2018) and investigated whether the occurrence of extra-pair young in the nest and the proportion of nests with extra-pair young in the close neighbourhood are related to (i) the probability of complete brood failure (no hatchlings fledged, yes/no) and – for nests that did not fail – (ii) the proportion of hatchlings that fledged, (iii) whether the nest produced a local recruit, i.e. whether at least one fledgling was detected breeding in the population in subsequent years and (iv) the average nestling mass at the age of 14 days. We examined the close breeding neighbourhood using the package “expp” (Valcu and Schlicht, 2013) in R (version 3.6.1; R Development Core Team 2019). The package uses Thiessen polygons to assign territories to breeding pairs (Valcu and Schlicht, 2013; for an empirical study using this package see Schlicht et al. 2015). In short, each point in the study area is assigned to the nearest breeding pair, thereby creating distinct territories. Based on this information, we defined the close breeding neighbourhood as all territories sharing the focal pair’s territory border (1st order) and those where one territory was in between (2nd order). We did not include higher-order neighbours, because most of the extra-pair young (86%) are sired by neighbouring males from the 1st and 2nd order.

We used generalized linear mixed models (GLMMs) with a binomial error structure (logit-link function) for the models (i)-(iii) and a linear mixed model (LMM) for the analysis on average nestling mass (iv) using the R package “lme4” (Bates et al. 2015). For all models, we included as the explanatory variable whether the focal nest contained extra-pair young (yes/no) and the proportion of nests containing extra-pair young within the close neighbourhood (1st and 2nd order neighbours). For the model on local recruitment (iii) we further included the number of fledglings, the average nestling mass and the average nestling sex ratio as explanatory variables. For the model on average nestling mass (iv) we included the number of hatchlings as additional explanatory variable. As random effects we included year and the identity of the social female and the social male for models (i) and (ii), and year and nest identity for models (iii) and (iv).

We also examined whether either the presence of extra-pair young in the nest or the proportion of neighbouring nests with extra-pair young are related to adult local survival. For females and males separately, we constructed GLMMs with a binomial error structure and a logit-link function including whether an adult was observed breeding in a subsequent year or not (yes/no) as dependent variable. As explanatory variables we included whether their brood contained extra-pair young (yes/no), the proportion of nests with extra-pair young in the close neighbourhood and the individual's age. We included age as a continuous variable and excluded birds identified as adults when first caught, as we could not determine the real age of those individuals (final sample size: $N_{Females} = 529$, $N_{Males} = 457$). Due to sample size limitations, we grouped all individuals older than 4 years into one category (females: 12 five-year olds, 6 six-year olds, 1 seven-year old and 1 eight-year old; males: 10 five-year olds, 3 six-year olds and 1 seven-year old). We used orthogonal polynomials (up to second degree) to take into account potential non-linear relationships between local survival and age. We then compared the full model with the model only including the linear term of the fixed effect age and selected the model with the lowest Akaike's Information Criterion, AIC (Hurvich and Tsai 1989). As random effects, we included year and individual identity. For females, the full model had a lower AIC value ($\Delta AIC = 4.11$) compared to the model that only included the linear age term, so we present the results of the model including both a linear and quadratic term for age. For males, $\Delta AIC < 1$, so we only present models including the linear age term. Note that including or excluding the quadratic term for age did not qualitatively change the results.

For all models, we also examined how much of the variance they explained. Following Nakagawa et al. (2017), we report the marginal R^2-values (variance explained by the fixed effects) and the conditional R^2-values (variance explained by fixed and random effects). In addition, we present for all results adjusted approximations of the *P* values using the "glht" function of the "multcomp" package (Hothorn et al. 2008).

Given that the effects of a more cooperative neighbourhood might be stronger within the direct (1st order) neighbourhood, we repeated all analyses excluding the 2nd order neighbours. Further, to exclude a potential bias due to incomplete sampling (see paternity analysis), we repeated all analyses including only focal nests where all young were genotyped. However, the variables on the number of neighbouring nests with extra-pair young still included all nests, because neighbourhoods for which all nests were completely genotyped were rare. Lastly, we repeated all analyses excluding broods located at the edge of our study site as we might have underestimated the number of neighbours for those territories.

Results

Each year on average 43% of all nests contained extra-pair young (range 35-53%) and the proportion of nests with extra-pair young in the close breeding neighbourhood ranged from 0 to 0.83 (mean = 0.42).

Out of 1169 nests, 192 (16.4%) failed completely. The probability that a brood failed was independent of whether it contained extra-pair young but decreased with an increasing prevalence of extra-pair paternity in the neighbourhood (Table 1). The fixed effects explained less than 1% of the variation (marginal $R^2 < 0.01$), whereas the random effects (i.e. year and female and male identity) explained more than 20% of the variation (conditional $R^2 = 0.22$). When adjusting for multiple testing the effect was not statistically significant anymore (Table 1).

Partial brood failure occurred in 409 of the remaining 977 nests (41.9 %). The presence of extra-pair young in the focal brood or the proportion of nests that contained extra-pair young in the neighbourhood did not predict fledging success (Fig. 1, Table 1, marginal $R^2 < 0.01$). The random effects (i.e. year and female and male identity) explained about 37% of the variation (conditional $R^2 = 0.37$).

The brood average mass of 14-day old nestlings ranged from 6.7 g to 12.5 g (mean = 10.3g, N = 977 broods). Average nestling mass decreased with increasing brood size (Fig. S1, Table 1), but the presence of extra-pair young in the nest or the proportion of nests with extra-pair young in the neighbourhood did not influence average nestling mass (Fig. 1, Table 1). In total, the fixed effects explained 14% of the variation (marginal $R^2 = 0.14$) and the random effects (i.e. year and nest identity) about 26% (conditional $R^2 = 0.40$).

Table 1. Results of generalized linear mixed-effect models (GLMM) and linear mixed-effect models (LMM) examining the effect of the presence of extra-pair young in a brood and the proportion of nests in the close neighbourhood (1st and 2nd order) containing extra-pair young on aspects of reproductive success.

Dependent variable	**Explanatory variable**	**Estimate ± SE**	**Test statistic**	***P***	***P adjusted***
Brood failure (GLMM)	Intercept	- 1.40 ± 0.40	- 3.47	<0.001	
	Proportion of nests with EPY	**- 1.38 ± 0.69**	**- 1.99**	**0.047**	**0.09**
	EPY in focal nest (yes)	- 0.06 ± 0.17	- 0.35	0.73	0.93
Fledging success (GLMM)	Intercept	3.16 ± 0.31	10.30	<0.001	
	Proportion of nests with EPY	- 0.61 ± 0.42	- 1.46	0.15	0.27
	EPY in focal nest (yes)	0.01 ± 0.11	0.09	0.93	0.99
Mean weight (LMM)	Intercept	11.93 ± 0.21	55.84	<0.001	
	Proportion of nests with EPY	0.12 ± 0.21	0.60	0.55	0.91
	EPY in focal nest (yes)	- 0.06 ± 0.05	- 1.08	0.28	0.63
	Number of hatchlings	**- 0.18 ± 0.01**	**- 14.12**	**<0.001**	**<0.001**

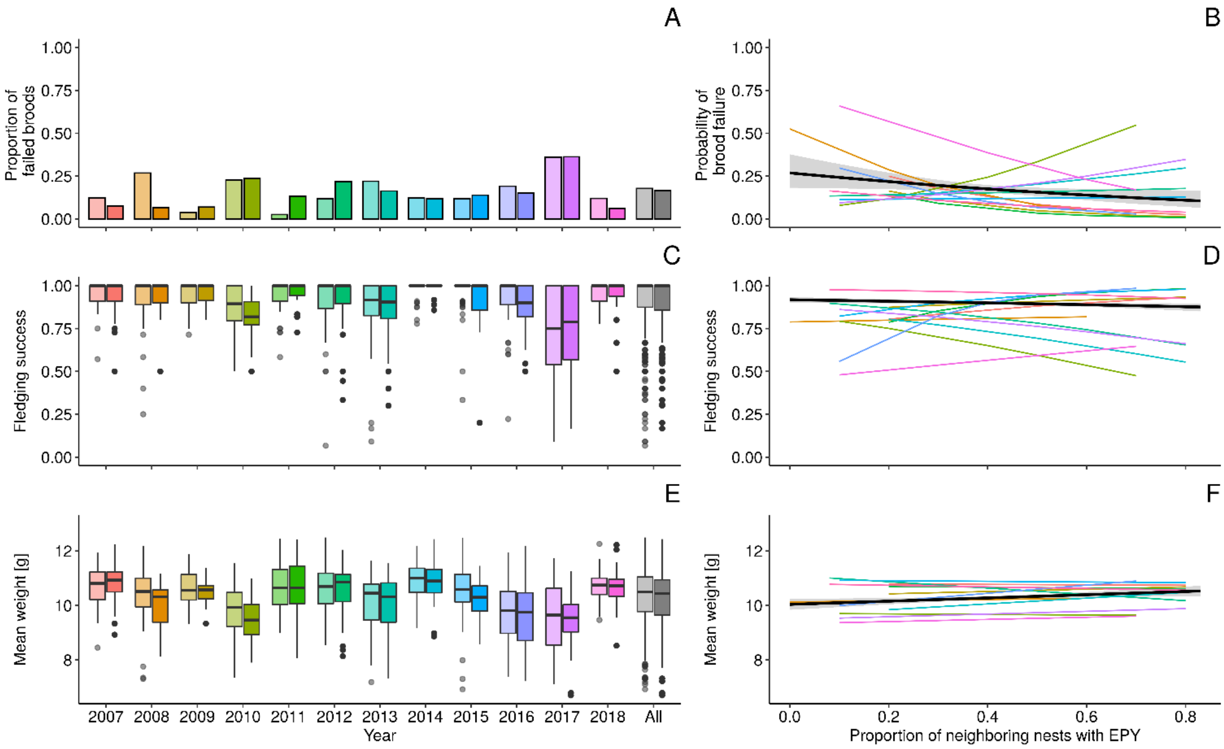


Figure 1. Relationship between measures of brood success and the occurrence of extra-pair young (EPY). **A,C,E**: Yearly comparisons of measures of brood success for nests without EPY (less saturated colour) and with EPY (saturated colour). Colours represent the different years and the data from all years combined are shown in grey. **A**: The proportion of failed broods, i.e. clutches that produced no fledglings. **C**: Fledging success, i.e. the proportion of hatchlings that fledged, excluding broods that failed completely. Boxplots show the minimum values, lower quartile, median, upper quartile, maximum values and outliers. **E**: Mean nestling mass at day 14. Shown are boxplots. **B,D,F:** Predicted relationship between measures of brood success and the proportion of nests with EPY in the neighbourhood (1st + 2nd order; range = 0-0.83). Shown are the effects from generalized linear models (**B**,**D**) and linear models (**F**) for each year separately (represented in different colours) while keeping all other independent variables constant at their mean values. The overall effect from all years combined is shown as a black line and the 95% confidence intervals as grey ribbon. See main text for model details.

Of the 8365 nestlings that fledged, 588 individuals (7%) from 384 nests were detected breeding in our study site in subsequent years. Nests with more and heavier fledglings were more likely to produce a local recruit (Fig. S2, S3, Table 2), but we found no effect of the presence of extra-pair young in the nest or of the proportion of nests with extra-pair young in the neighbourhood on the likelihood that a nest produced at least one local recruit (Fig. 2, Table 2). The fixed effects explained about 8% of the variation (marginal R^2 = 0.08) and the random effects (i.e. year and nest identity) about 19% (conditional R^2 = 0.27).

We recorded 529 females of which 206 (38.9%) bred again at least once and 457 males of which 221 (48.4%) bred again at least once. In males, local survival did not depend on the presence of extra-pair young in the nest or in the neighbourhood or on individual age (Fig. 2, Table 2). In females, the probability to survive was independent of whether the own brood contained extra-pair young but increased with an increasing prevalence of extra-pair paternity in the close neighbourhood. The quadratic term for female age was negative and significant, indicating an initial increase in the likelihood to survive followed by a decrease (Table 2). However, when adjusting for multiple testing both effect were not statistically significant anymore (Table 2). In both models, the random effects explained about 4% of the variation (conditional R^2: females = 0.04, males = 0.04, marginal R^2: females = 1, males < 1).

Repeating the analyses considering only nests within the direct neighbourhood (1st order), nests with completely genotyped clutches or excluding edge territories did not change the conclusions for the analyses on fledging success, average nestling mass, local recruitment and male survival (Tables S3-S10). However, the effect of the proportion of nests with extra-pair young in the neighbourhood on the probability of brood failure was no longer present (Table S2, S4, S9). When only considering completely genotyped nests, females were more likely to survive when they had bred in a neighbourhood (1st and 2nd order) containing a higher proportion of nests with extra-pair young (Estimate ± SE: 2.07 ± 0.82, $P = 0.01$; Table S8) and the effect remained borderline significant when adjusting P values for multiple testing ($P_{adjusted} = 0.045$; Table S8). In all other models, this effect was absent (Table S3, S10).

Table 2. Results of generalized linear mixed-effect models examining the effect of the occurrence of extra-pair young in a brood and the proportion of neighbouring nests (1st and 2nd order) containing extra-pair young on the probability of survival of either fledglings or adults.

Dependent variable	**Explanatory variable**	**Estimate ± SE**	**z**	***P***	***P adjusted***
Local recruitment*	Intercept	- 5.95 ± 1.34	- 4.45	<0.001	
	Proportion of nests with EPY	0.52 ± 0.59	0.88	0.38	0.91
	EPY in focal nest (yes)	0.06 ± 0.15	0.40	0.69	1.00
	Number of fledglings	**0.21 ± 0.04**	**5.39**	**<0.001**	**<0.001**
	Mean nestling body mass	**0.34 ± 0.09**	**3.79**	**<0.001**	**<0.001**
	Brood sex ratio	0.08 ± 0.42	- 0.19	0.98	1.00
Adult survival (females)	Intercept	- 0.73 ± 0.30	-2.46	0.01	
	Proportion of nests with EPY	**1.13 ± 0.57**	**1.99**	**0.046**	**0.17**
	EPY in focal nest (yes)	0.12 ± 0.14	0.85	0.39	0.87
	Age	0.13 ± 2.14	0.06	0.95	0.99
	Age^2	**-5.19 ± 2.13**	**-2.44**	**0.02**	**0.06**
Adult survival (males)	Intercept	0.46 ± 0.30	1.53	0.13	
	Proportion of nests with EPY	-0.63 ± 0.56	-1.12	0.26	0.60
	EPY in focal nest (yes)	-0.14 ± 0.15	-0.99	0.32	0.69
	Age	-0.11 ± 0.08	-1.43	0.15	0.39

* At least one fledging surviving until the next breeding season

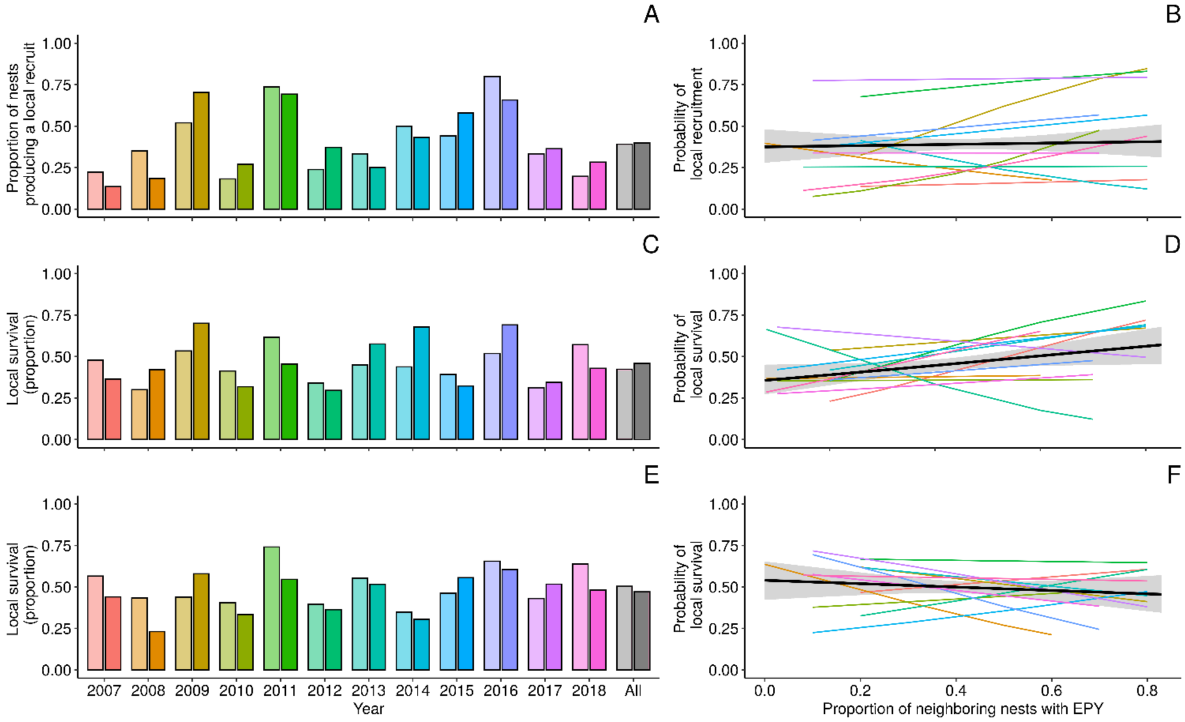


Figure 2. Relationship between fledgling and adult local survival and the occurrence of extra-pair young (EPY). **A,C,E**: Yearly comparisons of measures of local survival for nests without EPY (less saturated colour) and with EPY (saturated colour). Colours represent the different years and the data from all years combined are shown in grey. **A**: Yearly comparisons of the proportion of nests producing a local recruit and the occurrence of EPY. **C,E**: Yearly comparisons of adult local survival for females (**C**) and males (**E**). **B,D,F:** Predicted relationship between measures of local survival and the proportion of nests with EPY in the neighbourhood (1st + 2nd order; range = 0-0.83). Shown are the effects from generalized linear models for each year separately (represented in different colours) while keeping all other independent variables constant at their mean values. The overall effect from all years combined is shown as a black line and the 95% confidence intervals as grey ribbon. See main text for model details.

Discussion

Despite decades of research, the adaptive value of female extra-pair behaviour remains subject to ongoing debate. A recent theoretical model suggested that females may benefit from extra-pair copulations if this leads to a more cooperative neighbourhood (Eliassen and Jørgensen 2014). In this study, we examined whether reproductive success and parental survival are related to the occurrence of extra-pair young in the nest or in the neighbourhood. Analysing more than 1100 breeding attempts across 12 years, we found little evidence that the likelihood of producing fledglings, the proportion of fledglings produced, or their body mass were related to the occurrence of extra-pair paternity, both within the own nest or the neighbourhood. Also, there were no effects of the occurrence of extra-pair paternity on fledgling or male local survival, but females breeding in a neighbourhood with a high prevalence of extra-pair paternity seemed to be somewhat more likely to survive until the next breeding season.

Previous work reported several ways in which females may receive direct benefits from extra-pair copulations. For instance, in red-winged blackbirds (*Agelaius phoeniceus*) males are more tolerant towards the females they copulated with (Gray 1997a) and in american crows and (anecdotally) in blue tits, males were reported to provide parental care at the nest where they sired extra-pair young (Kempenaers 1993; Townsend et al. 2010). Such direct benefits should lead to higher fitness of the extra-pair female's brood. For example, female red-winged blackbirds that had extra-pair young hatched a greater proportion of eggs and fledged a greater proportion of young (Gray 1997b) and in blue tits complete brood failure was less common in nests with extra-pair young (Mennerat et al. 2018). If extra-pair males redirect from care solely provided at their own nest towards neighborhood activities such as predator mobbing or higher vigilance, not only the extra-pair female's offspring but nests located in such cooperative neighbourhood should do better in terms of survival. In our study, we found overall no support that nests containing extra-pair young or nests located in a neighbourhood with a higher proportion of extra-pair paternity had a higher fledging success, heavier offspring or were more likely to locally recruit (Fig.1, 2 Table 1, 2). Nests located in a neighbourhood with a lower proportion of nests containing extra-pair young were somewhat more likely to fail (Table 1). However, this effect disappeared when adjusting the *P* value for multiple testing (Table 1), when considering only the direct neighbours (Table S2) or when analysing a reduced dataset (i.e. only completely genotyped nests or excluding edge territories, Table S4, S9). Thus, we suggest that this result is likely a type I error.

Extra-pair paternity can also increase adult survival if extra-pair males directly provide care to the extra-pair female's brood (e.g. decreasing exhaustion of the social parents) or if extra-pair males engage in cooperative neighbourhood activities such as vigilance or anti-predator behaviour (decreasing predation risk). In the latter, both the focal parents and breeding pairs located in the close neighbourhood should benefit. We found no evidence that males breeding in a neighbourhood with a higher prevalence of extra-pair paternity or having extra-pair young in their own brood benefit in terms of increased survival (Table 2). In females, individuals located in a neighbourhood with a higher proportion of nests containing extra-pair young had an increased probability to locally survive (Table 2). The effect was absent when adjusting the *P* value for multiple testing (Table 2), when considering only the direct neighbours (Table S3) or when excluding edge territories (Table S10). But, the effect was present when analysing only completely genotyped nests, even after adjusting the *P* value (Table S8). As the observed effect was borderline significant and not present in all models we would interpret these findings with caution. If the results hold, they would suggest that females, but not males, survive better when breeding in a potentially more cooperative environment. This could occur, for instance, if a cooperative neighbourhood generally enhances survival, while the extra male investment in cooperative behaviour simultaneously reduces male survival.

A limitation of our study (and of other studies that investigate direct benefits of extra-pair copulations) is that we used patterns of extra-pair paternity as a proxy for extra-pair copulations, even though the acquisition of direct benefits does not require to result in fertilizations. Extra-pair copulations do not necessarily result in extra-pair paternity, and an unknown number of nests is thus assigned as containing no extra-pair young even though the female engaged in extra-pair copulations. The extent to which extra-pair paternity in the brood reflects extra-pair behaviour of the female is still poorly understood. Hence, using study systems where all or most extra-pair copulations can be observed would improve our understanding of female extra-pair behaviour and may come to different conclusions about direct benefits. Further, we did not examine the behaviour of extra-pair males during the breeding season. Although blue tits fulfill many of the predictions of the theoretical model proposed by Eliassen and Jørgensen (2014), not much is known about their cooperative behaviour during breeding. Help during predator mobbing by an extra-pair male was observed anecdotally in blue tits (Kempenaers 1993), but such behaviour is probably rare.

Taken together, our findings provide little evidence that breeding success and adult survival are related to either the presence of extra-pair young in the brood or to the proportion of nests with extra-pair young within the neighbourhood. Thus, we find little support that female extra-pair behaviour is driven by cooperative neighbourhood benefits. In blue tits, extra-pair copulations may provide genetic benefits (Foerster et al. 2003; but see Charmantier et al. 2004) or insurance against male infertility (Santema et al., *provisional acceptance*) rather than direct benefits. Alternatively, the entire population might be a “cooperative neighbourhood” and the small-scale variation in extra-pair paternity might not be relevant. Future studies examining extra-pair behaviour and interactions between extra-pair partners during breeding and comparable studies on other species or populations would be needed to assess the generality of our findings.

Acknowledgments

We are grateful to Agnes Türk, Andrea Wittenzellner and the many people who contributed to data collection in the field, to Sylvia Kuhn and Alexander Girg for microsatellite genotyping, to Mihai Valcu for establishing and maintaining the database, and to Emmi Schlicht for constructive comments on the analyses. We thank the Bavarian regional office for forestry (LWF) for permission to work in Westerholz.

References

Akçay E, Roughgarden J. 2007. Extra-pair paternity in birds: review of the genetic benefits. Evol Ecol Res. 9:855.

Arnqvist G, Kirkpatrick M. 2005. The evolution of infidelity in socially monogamous passerines: the strength of direct and indirect selection on extrapair copulation behavior in females. Am Nat. 165:S26–S37.

Bates D, Maechler M, Bolker B, Walker S. 2015. lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1–7. 2014.

Birkhead T, Møller A. 1993. Female control of paternity. Trends Ecol Evol. 8:100–104.

Brouwer L, Griffith SC. 2019. Extra-pair paternity in birds. Mol Ecol. 28:4864–4882.

Charmantier A, Blondel J, Perret P, Lambrechts MM. 2004. Do extra-pair paternities provide genetic benefits for female blue tits Parus caeruleus? J Avian Biol. 35:524–532.

Delhey K, Johnsen A, Peters A, Andersson S, Kempenaers B. 2003. Paternity analysis reveals opposing selection pressures on crown coloration in the blue tit (Parus caeruleus). Proc R Soc London B Biol Sci. 270:2057–2063.

Eliassen S, Jørgensen C. 2014. Extra-pair mating and evolution of cooperative neighbourhoods. PLoS One. 9:e99878.

Foerster K, Delhey K, Johnsen A, Lifjeld JT, Kempenaers B. 2003. Females increase offspring heterozygosity and fitness through extra-pair matings. Nature. 425:714-717.

Forstmeier W. 2007. Do individual females differ intrinsically in their propensity to engage in extra-pair copulations? PLoS One. 2:e952.

Forstmeier W, Martin K, Bolund E, Schielzeth H, Kempenaers B. 2011. Female extrapair mating behavior can evolve via indirect selection on males. Proc Natl Acad Sci. 108:10608–10613.

Forstmeier W, Nakagawa S, Griffith SC, Kempenaers B. 2014. Female extra-pair mating: adaptation or genetic constraint? Trends Ecol Evol. 29:456–464.

Gray EM. 1997a. Female red-winged blackbirds accrue material benefits from copulating with extra-pair males. Anim Behav. 53:625–639.

Gray EM. 1997b. Do female red-winged blackbirds benefit genetically from seeking extra-pair copulations? Anim Behav. 53:605–623.

Griffith SC, Owens IPF, Thuman KA. 2002. Extra pair paternity in birds: a review of interspecific variation and adaptive function. Mol Ecol. 11:2195–2212.

Hothorn T, Bretz F, Westfall P. 2008. Simultaneous inference in general parametric models. Biometrical J. 50:346–363.

Hsu Y, Schroeder J, Winney I, Burke T, Nakagawa S. 2014. Costly infidelity: Low lifetime fitness of extra-pair offspring in a passerine bird. Evolution. 68:2873–2884.

Hurvich CM, Tsai C-L. 1989. Regression and time series model selection in small samples. Biometrika. 76:297–307.

Jennions MD, Petrie M. 2000. Why do females mate multiply? A review of the genetic benefits. Biol Rev. 75:21–64.

Kalinowski ST, Taper ML, Marshall TC. 2007. Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. Mol Ecol. 16:1099–1106.

Kempenaers B. 1993. A case of polyandry in the blue tit: female extra-pair behaviour results in extra male help. Ornis Scand. 24:246–249.

Kempenaers B. 1997. Does reproductive synchrony limit male opportunities or enhance female choice for extra-pair paternity? Behaviour. 134:551–562.

Kempenaers B, Dhondt A. 1993. Why do females engage in extra-pair copulations? A review of hypotheses and their predictions. Belgian J Zool. 123:93–103.

Kempenaers B, Verheyen GR, Van den Broeck M, Burke T, Van Broeckhoven C, Dhondt A. 1992. Extra-pair paternity results from female preference for high-quality males in the blue tit. Nature. 357:494–496.

Komdeur J. 2001. Mate guarding in the Seychelles warbler is energetically costly and adjusted to paternity risk. Proc R Soc London B Biol Sci. 268:2103–2111.

Mays HL, Albrecht T, Liu M, Hill GE. 2008. Female choice for genetic complementarity in birds: a review. Genetica. 134:147–158.

Mennerat A, Charmantier A, Jørgensen C, Eliassen S. 2018. Correlates of complete brood failure in blue tits: could extra-pair mating provide unexplored benefits to females? J Avian Biol. 49.

Nakagawa S, Johnson PC, Schielzeth, H. 2017. The coefficient of determination R 2 and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. J R Soc Interface. 14.

Petrie M, Kempenaers B. 1998. Extra-pair paternity in birds: explaining variation between species and populations. Trends Ecol Evol. 13:52–58.

Plaza M, Cantarero A, Gil D, Moreno J. 2019. Experimentally flight-impaired females show higher levels of extra-pair paternity in the pied flycatcher Ficedula hypoleuca. Biol Lett. 15.

Poiani A, Wilks C. 2000. Sexually transmitted diseases: A possible cost of promiscuity in birds? Auk. 117:1061–1065.

Santema P, Kempenaers B. 2018. Complete brood failure in an altricial bird is almost always associated with the sudden and permanent disappearance of a parent. J Anim Ecol. 87:1239–1250.

Santema P, Teltscher K, Kempenaers B. Extra-pair copulations can insure female blue tits against male infertility. J Avian Biol., 51.

Sardell RJ, Arcese P, Keller LF, Reid JM. 2012. Are there indirect fitness benefits of female extra-pair reproduction? Lifetime reproductive success of within-pair and extra-pair offspring. Am Nat. 179:779–793.

Schlicht L, Girg A, Loës P, Valcu M, Kempenaers B. 2012. Male extrapair nestlings fledge first. Anim Behav. 83:1335–1343.

Schlicht L, Valcu M, Kempenaers B. 2015. Spatial patterns of extra-pair paternity: beyond paternity gains and losses. J Anim Ecol. 84:518–531.

Sheldon BC. 1994a. Sperm competition in the chaffinch: the role of the female. Anim Behav. 47:163–173.

Sheldon BC. 1994b. Male phenotype, fertility, and the pursuit of extra-pair copulations by female birds. Proc R Soc Lond B. 257:25–30.

Sheldon BC, Mangel M. 2014. Behavioural ecology: Love thy neighbour. Nature. 512:381–382.

Townsend AK, Clark AB, McGowan KJ. 2010. The direct benefits and genetic costs of extrapair paternity in the cooperatively breeding American crow. Am Nat. 175:1–9.

Valcu M, Schlicht L. 2013. expp: Spatial analysis of extra-pair paternity. R package version 1.2.4. Available from: http://CRAN.R-project.org/package=expp.

Wang D, Forstmeier W, Martin K, Wilson A, Kempenaers B. 2020. The role of genetic constraints and social environment in explaining female extra-pair mating. Evolution. 74:544–558.

Westneat DF, Sherman PW. 1997. Density and extra-pair fertilizations in birds: a comparative analysis. Behav Ecol Sociobiol. 41:205–215.

Westneat DF, Sherman PW, Morton ML. 1990. The ecology and evolution of extra-pair copulations in birds. Curr Ornithol. 7:331–369.

Westneat DF, Stewart IRK. 2003. Extra-pair paternity in birds: causes, correlates, and conflict. Annu Rev Ecol Evol Syst. 34:365–396.

Supplementary material

PCR cycling conditions

Cycling conditions for mix 1: 5 min initial denaturation at 95˚C; 15 cycles of 30 s denaturation at 94˚C, 90 s touch down annealing at 60˚C decreasing by 0.3°C per cycle, and 1 min extension at 72˚C; 11 cycles of 30 s denaturation at 94˚C, 90 s annealing at 53˚C, and 1 min extension at 72˚C; followed by a 30 min completing final extension at 60˚C. Cycling conditions for mix 2: 5 min initial denaturation at 95˚C; 27 cycles of 30 s denaturation at 94˚C, 90 s annealing at 56°C, and 1 min extension at 72˚C; followed by a 30 min completing final extension at 60˚C. Cycling conditions for mix 3: 5 min initial denaturation at 95˚C; 14 cycles of 30 s denaturation at 94˚C, 90 s annealing at 56°C, and 1 min extension at 72˚C; 11 cycles of 30 s denaturation at 94˚C, 90 s annealing at 57°C, and 1 min extension at 72˚C; followed by a 30 min completing final extension at 60˚C. Cycling conditions for mix 4: 5 min initial denaturation at 95˚C; 23 cycles of 30 s denaturation at 94˚C, 90 s annealing at 58°C, and 1 min extension at 72˚C; followed by a 30 min completing final extension at 60˚C.

Additional figures

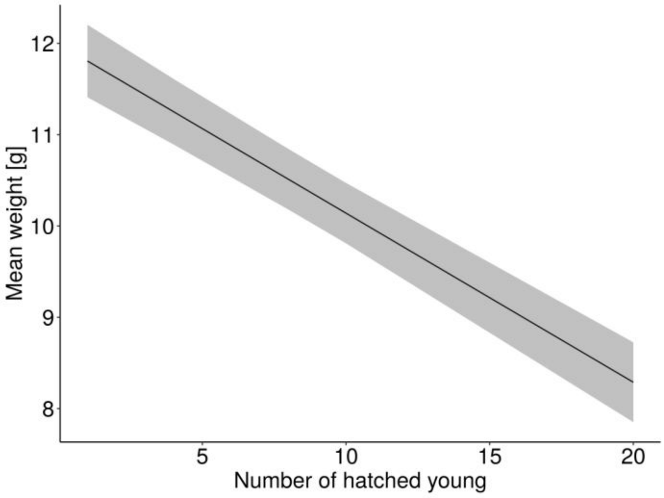


Figure S1. The relationship between the number of young that hatched within a nest and the mean nestling weight (all other independent variables are kept constant at their mean values). The grey ribbon shows the 95% confidence interval from a generalized linear mixed model (see main text).

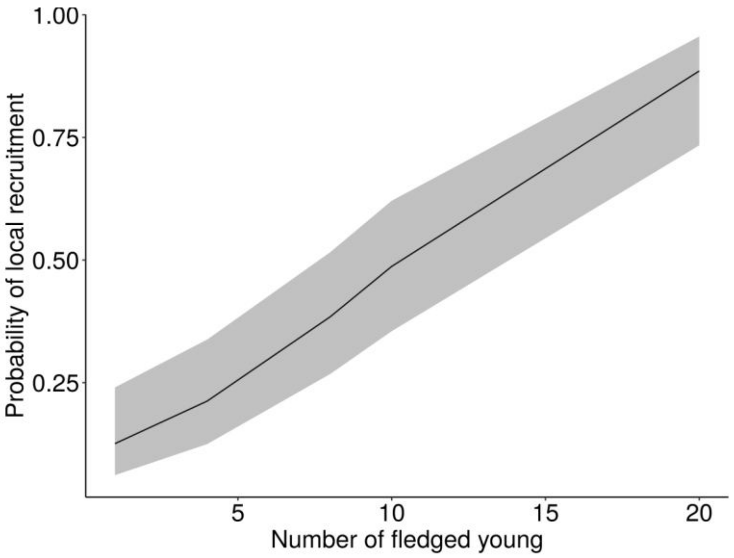


Figure S2. The predicted probability of a nest to produce at least one local recruit in relation to the number of fledged young (all other independent variables are kept constant at their mean values). The grey ribbon shows the 95% confidence interval from a generalized linear mixed model (see main text).

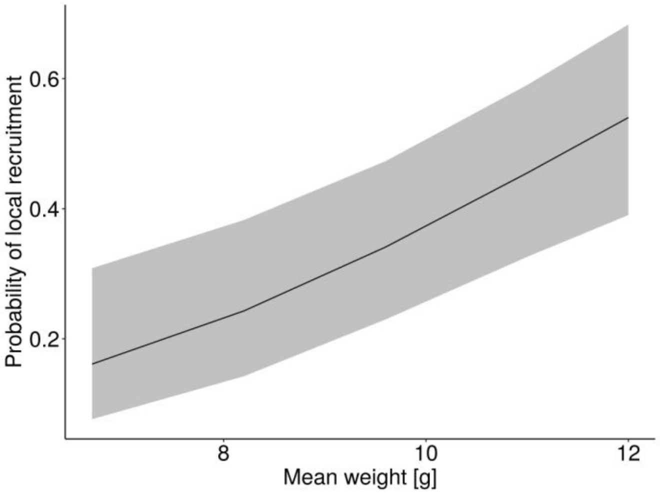


Figure S3. The predicted probability of a nest to produce at least one local recruit in relation to the mean nestling weight (all other independent variables are kept constant at their mean values). The grey ribbon shows the 95% confidence interval from a generalized linear mixed model (see main text).

Additional tables

Table S1. Microsatellite loci for blue tits. Primer sequences include information on fluorescence labels used. *C* refers to the primer concentration in multiplex primer mix. Size range and number of alleles refer to 2018 data (*n*=1696; Phtr3 from 2017, *n*=1905).

Locus	**Accession no.**	**Primer sequences (5' - 3')**	***C* (µM)**	**Multiplex Mix**	**Size range (bp)**	**number of alleles**
ADCYAP1_bm	FJ464427	VIC-GATGTGAGTAACCAGCCACT ATAACACAGGAGCGGTGA	0,2 µM	2	160 - 172	10
ClkpolyQ	AY338423-28	6FAM-TTTTCTCAAGGTCAGCAGCTTGT CTGTAGGAACTGTTGYGGKTGCTG	0,36 µM	4	266 - 283	7
Mcµ4	U82388	PET-ATAAGATGACTAAGGTCTCTGGTG TAGCAATTGTCTATCATGGTTTG	1,1 µM	2	156 - 194	19
PAT MP 2-43	AM056063	6FAM- ACAGGTAGTCAGAAATGGAAAG GTATCCAGAGTCTTTGCTGATG	0,24 µM	4	125 - 155	8
Pca3	AJ279805	PET-GGTGTTTGTGAGCCGGGG TGTTACAACCAAAGCGGTCATTTG	0,8 µM	1	154 - 234	43
Pca4	AJ279806	NED-AATGTCTTACAGGCAAAGTCCCCA AACTTGAAGCTTCTGGCCTGAATG	0,42 µM	4	149 - 201	18
Pca7	AJ279809	6FAM-TGAGCATCGTAGCCCAGCAG GGTTCAGGACACCTGCACAATG	0,25 µM	1	105 - 141	18
Pca8	AJ279810	NED-ACTTCTGAAACAAAGATGAAATCA TGCCATCAGTGTCAAACCTG	0,48 µM	1	255 - 401	73
Pca9	AJ279811	VIC-ACCCACTGTCCAGAGCAGGG AGGACTGCAGCAGTTTGTGGG	0,3 µM	3	111 - 135	13
Phtr3 [1]	AM056070	NED-ATTTGCATCCAGTCTTCAGTAATT CTCAAAGAAGTGCATAGAGATTTCAT	1,4 µM	2 [1]	118 - 148 [1]	16 [1]
PK11	AF041465	PET-CTTTAAGAATTCAAATACAGAGTAGG GTTTTCTCCTTTCTACACTGAGG	0,54 µM	4	63 - 97	14
PK12	AF041466	VIC-CCTCCTGCAGTTGCCTCCCG CGTGGCCATGTTTATAGCCTGGCACTAAGAAC	1,14 µM	4	168 - 226	27
PmaTAGAn71 [1]	AY260537	NED-TCAGCCTCCAAGGAAAACAG GCATAAGCAACACCATGCAG	0,3 µM	2 [1]	190 - 310 [1]	29 [1]
POCC1	U59113	6FAM- TTCTGTGCTGCAATCACACA GCTTCCAGCACCACTTCAAT	0,8 µM	3	219 - 255	25
POCC6	U59117	VIC-TCACCCTCAAAAACACACACA ACTTCTCTCTGAAAAGGGGAGC	0,25 µM	1	195 - 253	28
P2/P8	AF006659-62	6FAM-CTCCCAAGGA TGAGRAAYTG TCTGCATCGC TAAATCCTTT	0,3 µM	2	319, 383	2

[1] Phtr3 was replaced by PmaTAGAn71 from 2018 onwards.

Table S2. Results of generalized linear mixed-effect models (GLMM) and linear mixed-effect models (LMM) examining the effect of the presence of extra-pair young in a brood and the proportion of nests in the direct neighbourhood (1st order) containing extra-pair young on aspects of reproductive success.

Dependent variable	**Explanatory variable**	**Estimate ± SE**	**z**	***P***	***P adj.***
Brood failure (GLMM)	Intercept	- 1.69 ± 0.32	- 5.24	<0.001	
	Proportion of nests with EPY	- 0.71 ± 0.37	- 1.90	0.06	0.11
	EPY in focal nest (yes)	- 0.06 ± 0.17	- 0.33	0.75	0.94
Fledging success (GLMM)	Intercept	3.01 ± 0.27	11.34	<0.001	
	Proportion of nests with EPY	- 0.28 ± 0.23	- 1.20	0.23	0.41
	EPY in focal nest (yes)	0.02 ± 0.11	0.15	0.88	0.99
Mean weight (LMM)	Intercept	12.00 ± 0.20	59.19	<0.001	
	Proportion of nests with EPY	- 0.03 ± 0.12	- 0.27	0.79	0.99
	EPY in focal nest (yes)	- 0.06 ± 0.05	- 1.13	0.26	0.59
	Number of hatchlings	**- 0.18 ± 0.01**	**- 14.10**	**<0.001**	**<0.001**

Table S3. Results of the model examining the effect of the occurrence of extra-pair young in a brood and the proportion of neighbouring nests (in the 1st order neighbourhood) containing extra-pair young on the probability of survival of either fledglings or adults. Each model controls for other variables known to affect survival.

Dependent variable	**Explanatory variable**	**Estimate ± SE**	**z**	***P***	***P adj.***
Local recruitment*	Intercept	- 6.01 ± 1.32	- 4.55	<0.001	
	Proportion of nests with EPY	0.64 ± 0.33	1.96	0.051	0.22
	EPY in focal nest (yes)	-0.03 ± 0.16	- 0.20	0.63	0.99
	Number of fledglings	**0.21 ± 0.04**	**5.44**	**<0.001**	**<0.001**
	Mean nestling body mass	**0.34 ± 0.09**	**3.81**	**<0.001**	**<0.001**
	Brood sex ratio	- 0.02 ± 0.41	- 0.04	0.97	1.00
Adult survival (females)	Intercept	- 0.39 ± 0.19	-2.01	0.05	
	Proportion of nests with EPY	0.33 ± 0.32	1.03	0.30	0.77
	EPY in focal nest (yes)	0.12 ± 0.14	0.82	0.41	0.88
	Age	0.18 ± 2.14	0.09	0.93	0.99
	Age^2	**-5.11 ± 2.13**	**-2.41**	**0.02**	**0.06**
Adult survival (males)	Intercept	0.18 ± 0.23	0.77	0.77	
	Proportion of nests with EPY	0.04 ± 0.32	0.12	0.91	0.99
	EPY in focal nest (yes)	-0.13 ± 0.14	-0.92	0.36	0.74
	Age	-0.11 ± 0.08	-1.45	0.15	0.38

* At least one fledging surviving until the next breeding season

Results when only considering data of nests with completely genotyped clutches

Table S4. Results of the models examining the effect of extra-pair young and the proportion of nests with extra-pair young (once for the extended neighbourhood: 1st and 2nd order, and once for the direct neighbourhood: 1st order only) on complete brood failure containing only data of completely genotyped clutches (N=564 of which in 92 cases complete failure occurred). Shown are the estimates ± the standard errors, the z and *P* values.

	Estimate ± SE	**z**	***P***	***P adj.***
Intercept	- 1.44 ± 0.41	- 2.24	0.03	
Proportion of nests with EPY in the extended neighbourhood	- 2.11 ± 1.23	- 1.71	0.09	0.17
EPY in focal nest? (yes)	0.08 ± 0.30	0.26	0.80	0.96
Intercept	- 1.94 ± 0.51	- 3.82	<0.001	
Proportion of nests with EPY in the direct neighbourhood	- 0.88 ± 0.66	- 1.33	0.19	0.34
EPY in focal nest? (yes)	0.07 ± 0.30	0.22	0.83	0.97

Table S5. Results of the model examining the effect of EPY and the proportion of nests with EPY (once for the extended neighbourhood: 1st and 2nd order, and once for the direct neighbourhood: 1st order only) on the proportion of nestlings that fledged containing data of only completely genotyped clutches (N=477 of which in 73 partial brood failure occurred). Shown are the estimates ± the standard errors, the z and *P* values.

	Estimate ± SE	**z**	***P***	***P adj.***
Intercept	7.48 ± 0.88	8.47	<0.001	
Proportion of nests with EPY in the extended neighbourhood	- 2.86 ± 1.48	- 1.93	0.054	0.11
EPY in focal nest? (yes)	- 0.32 ± 0.41	- 0.78	0.43	0.68
Intercept	6.70 ± 0.74	9.07	<0.001	
Proportion of nests with EPY in the direct neighbourhood	- 0.53 ± 0.86	- 0.61	0.54	0.79
EPY in focal nest? (yes)	- 0.30 ± 0.42	- 0.72	0.47	0.72

Table S6. Results of the model examining the effect of the occurrence of extra-pair young in a brood, the proportion of neighbouring nests containing extra-pair young (once for the extended neighbourhood: 1st and 2nd order, and once for the direct neighbourhood: 1st order only), the number of young that fledged and the average body mass (at day 14) on the likelihood of a nest to produce at least one local recruit, containing data of only completely genotyped clutches (N=499 nests of which 207 produced at least one local recruit). Shown are the estimates ± the standard errors, the z and *P* values.

	Estimate ± SE	**z**	***P***	***P adj.***
Intercept	- 6.19 ± 2.11	- 3.07	0.002	
Proportion of nests with EPY in the extended neighbourhood	- 0.01 ± 0.81	- 0.01	0.99	1.00
EPY in focal nest? (yes)	0.12 ± 0.21	0.57	0.57	0.99
Number of fledglings	**0.15 ± 0.06**	**2.43**	**0.02**	**0.07**
Mean nestling body mass	**0.33 ± 0.14**	**2.38**	**0.02**	**0.08**
Sex ratio	0.88 ± 0.59	1.50	0.13	0.50
Intercept	- 6.60 ± 2.08	- 3.17	0.002	
Proportion of nests with EPY in the direct neighbourhood	0.22 ± 0.45	0.50	0.62	0.99
EPY in focal nest? (yes)	0.12 ± 0.21	0.59	0.56	0.98
Number of fledglings	**0.14 ± 0.06**	**2.43**	**0.02**	**0.07**
Mean nestling body mass	**0.33 ± 0.14**	**2.40**	**0.02**	**0.08**
Sex ratio	0.87 ± 0.59	1.49	0.14	0.52

Table S7. Results of the model examining the effect of the occurrence of extra-pair young in a brood and the proportion of neighbouring nests containing extra-pair young (once for the extended neighbourhood: 1st and 2nd order, and once for the direct neighbourhood: 1st order only) on mean nestling body mass, only containing data of completely genotyped clutches (N=499 nests). Shown are the estimates ± the standard errors, the t and *P* values.

	Estimate ± SE	**t**	***P***	***P adj.***
Intercept	12.33 ± 0.24	50.83	<0.001	
Proportion of nests with EPY in the extended neighbourhood	- 0.31 ± 0.26	- 1.19	0.23	0.55
EPY in focal nest? (yes)	- 0.10 ± 0.07	- 1.47	0.14	0.37
Number of hatchlings	**- 0.19 ± 0.02**	**- 10.25**	**<0.001**	**<0.001**
Intercept	12.26 ± 0.23	54.26	<0.001	
Proportion of nests with EPY in the direct neighbourhood	- 0.15 ± 0.14	- 1.02	0.31	0.67
EPY in focal nest? (yes)	- 0.10 ± 0.07	- 1.48	0.14	0.36
Number of hatchlings	**- 0.19 ± 0.02**	**- 10.27**	**<0.001**	**<0.001**

Table S8. Results of the model examining the effect of the occurrence of extra-pair young in a brood and the proportion of neighbouring nests containing extra-pair young (once for the extended neighbourhood: 1st and 2nd order, and once for the direct neighbourhood: 1st order only) on the probability of adult survival, containing only data of completely genotyped clutches. Shown are the estimates ± the standard errors, z and *P* values. $N_{FEMALES}$=406, N_{MALES}=379).

	FEMALES				**MALES**			
	Estimate ± SE	**z**	***P***	***P adj***	**Estimate ± SE**	**z**	***P***	***P adj***
Intercept	-1.05 ± 0.39	-2.69	0.007		0.50 ± 0.43	1.17	0.24	
Proportion of nests with EPY in the extended neighbourhood	**2.07 ± 0.82**	**2.53**	**0.01**	**0.045**	-0.55 ± 0.80	-0.69	0.49	0.87
EPY in focal nest (yes)	-0.08 ± 0.21	-0.39	0.70	0.99	-0.22 ± 0.21	-1.07	0.29	0.63
Age	1.11 ± 2.15	0.52	0.61	0.98	-0.12 ± 0.13	-0.89	0.37	0.75
Age^2	-3.29 ± 2.15	-1.53	0.13	0.42				
Intercept	-0.52 ± 0.29	-1.80	0.07		0.03 ± 0.28	0.09	0.93	
Proportion of nests with EPY in the direct neighbourhood	0.77 ± 0.47	1.64	0.10	0.34	0.28 ± 0.45	0.62	0.54	0.90
EPY in focal nest (yes)	-0.06 ± 0.21	-0.27	0.79	1.00	-0.21 ± 0.18	-1.16	0.25	0.57
Age	1.03 ± 2.48	0.41	0.68	0.99	-0.07 ± 0.10	-0.72	0.47	0.85
Age^2	-3.05 ± 2.15	-1.42	0.16	0.49				

Results when removing edge territories. Note that we here only examined the direct neighbourhood.

Table S9. Results of generalized linear mixed-effect models (GLMM) and linear mixed-effect models (LMM) examining the effect of the presence of extra-pair young in a brood and the proportion of nests containing extra-pair young in the direct neighbourhood (1st order) on aspects of reproductive success.

Dependent variable	**Explanatory variable**	**Estimate ± SE**	**z**	***P***	***P adj.***
Brood failure (GLMM)	Intercept	- 1.56 ± 0.36	- 4.32	<0.001	
	Proportion of nests with EPY	- 0.91 ± 0.53	- 1.73	0.08	0.16
	EPY in focal nest (yes)	- 0.05 ± 0.21	- 0.26	0.80	0.96
Fledging success (GLMM)	Intercept	3.08 ± 0.29	10.77	<0.001	
	Proportion of nests with EPY	- 0.34 ± 0.33	- 1.03	0.30	0.51
	EPY in focal nest (yes)	- 0.08 ± 0.14	- 0.58	0.56	0.81
Mean weight (LMM)	Intercept	12.13 ± 0.23	52.78	<0.001	
	Proportion of nests with EPY	- 0.02 ± 0.16	- 0.12	0.90	1.00
	EPY in focal nest (yes)	- 0.08 ± 0.07	- 1.22	0.22	0.53
	Number of hatchlings	**- 0.20 ± 0.02**	**- 12.37**	**<0.001**	**<0.001**

Table S10. Results of the model examining the effect of the occurrence of extra-pair young in a brood and the proportion of neighbouring nests (in the 1st order neighbourhood) containing extra-pair young on the probability of survival of either fledglings or adults. Each model controls for other variables known to affect survival.

Dependent variable	Explanatory variable	Estimate ± SE	z	*P*	*P adj.*
Local recruitment*	Intercept	- 8.42 ± 1.81	- 4.65	<0.001	
	Proportion of nests with EPY	0.83 ± 0.48	1.73	0.08	0.35
	EPY in focal nest (yes)	0.15 ± 0.19	0.78	0.44	0.94
	Number of fledglings	**0.26 ± 0.05**	**4.88**	**<0.001**	**<0.001**
	Mean nestling body mass	**0.46 ± 0.12**	**3.84**	**<0.001**	**<0.001**
	Brood sex ratio	0.36 ± 0.53	0.68	0.49	0.97
Adult survival (females)	Intercept	- 0.65 ± 0.28	-2.29	0.02	
	Proportion of nests with EPY	0.80 ± 0.48	1.66	0.10	0.34
	EPY in focal nest (yes)	0.06 ± 0.19	0.32	0.75	1.00
	Age	-0.91 ± 2.98	-0.31	0.76	1.00
	Age^2	-2.30 ± 2.20	-1.05	0.30	0.75
Adult survival (males)	Intercept	0.03 ± 0.28	0.09	0.93	
	Proportion of nests with EPY	0.33 ± 0.46	0.62	0.54	0.90
	EPY in focal nest (yes)	-0.21 ± 0.18	-1.16	0.25	0.57
	Age	-0.07 ± 0.10	-0.72	0.47	0.85

* At least one fledging surviving until the next breeding season

General discussion

Social structure and extra-pair paternity

In 2018, Maldonado-Chaparro and colleagues highlighted in their review how linking the fine-scale social environment to mating decisions can create interesting new insights for the study of extra-pair paternity. Their work provided an excellent base for this PhD thesis in which we explored the link between social environment and extra-pair paternity. We investigated 1) whether the relationship strength between females and males prior to breeding predicts their likelihood to become extra-pair partners, 2) whether the prior direct and indirect social environment of individuals influence future pairing success, 3) whether changes in the individual-specific social breeding environment explain within-individual changes in extra-pair paternity, and lastly 4) whether extra-pair paternity increases the fitness of whole nests.

Main findings

In this work, we studied patterns of extra-pair paternity in a model species, the blue tit. We explored the unique social environment that each individual experiences across two different contexts (prior and during breeding) from three different social perspectives, i.e. the dyadic relationship (**Chapter 1**), the direct social environment (**Chapter 2, 3, 4**) and the indirect social environment (**Chapter 2**).

During the winter 2017/18, we examined the fine-scale social environment of blue tits by quantifying their foraging associations at bird feeders. In **Chapter 1**, we show that females and males with stronger social relationships (i.e. that foraged more often together) were more likely to become i) social partners, ii) close breeding neighbours and iii) extra-pair partners in the subsequent breeding season (Figure 1, 2; Table 1). Furthermore, we examined temporal aspects of the associations of social and extra-pair partners and show that their relationship strengths increased towards the breeding season (Figure S3).

Using the same dataset on the foraging associations in winter, we quantified the direct and indirect social environment of each individual (**Chapter 2**) and show that males that moved more often between different social groups were more likely to breed in the subsequent breeding season (Figure 1, Table 1). Further, among those individuals that managed to breed, adult males connected to more females in winter had a higher proportion of familiar females in their breeding neighbourhood (Table S4) and were more likely to sire extra-pair young (Figure 1, 3; Table 2).

In **Chapter 3**, we investigated the within-individual variation of extra-pair paternity in females and males using eleven years of paternity data. We show that extra-pair paternity is to some extent a repeatable trait in females and males (Table 2). Within-individual changes in the direct social breeding environment (quantified based on the spatial proximity of birds) did not explain changes in extra-pair paternity in females (Figure 2; Table 5). In adult males, however, a decrease in the average body size of male neighbours was linked to an increased extra-pair siring success (Figure 1; Table 4).

Finally, in **Chapter 4** we tested predictions of a framework proposed by Eliassen and Jørgensen in 2014. Analysing twelve years of data from more than 1100 breeding attempts, we found no evidence that nests containing extra-pair young or nests simply located in breeding neighbourhoods with a higher prevalence of extra-pair paternity do have higher breeding success and increased male survival (Figure 1, 2; Table 1, 2). However, females breeding in a neighbourhood with more extra-pair paternity seemed to be more likely to survive (Table 2).

Implications

The pre-breeding social environment and extra-pair paternity

Most studies on extra-pair paternity investigated aspects of the current breeding environment (Dunn et al. 1994; Komdeur 2001; Thusius et al. 2001; Schlicht et al. 2015a), neglecting that individuals often interact long before the actual reproduction. Using social network analysis, we demonstrate that different levels of the pre-breeding social environment (i.e. dyadic relationships, the direct and indirect social environment) can impact (extra-pair) mating outcomes of blue tits in the subsequent breeding season (**Chapter 1, 2**).

When and how different relationship types get established are long standing questions in behavioural ecology. More and more research shows that social pair bonds form long before the actual reproductive event and that the prior social relationships between females and males can predict future social partners (Rodway 2007; Psorakis et al. 2012; Teitelbaum et al. 2017), the breeding spatial structure (Firth and Sheldon 2016) and potentially divorce (Culina et al. 2015; Gilsenan et al. 2017). Our work corroborates these findings and extends it with new knowledge on the formation of extra-pair partners (**Chapter 1**). Furthermore, we show that not only the relationship strength to potential mates but an individual’s overal social position prior to breeding can influence its future mating success (**Chapter 2**).

Our findings raise the question how social aspects during winter translate into the observed mating patterns. We speculate that familiarity between close breeding neighbours may be the mechanism driving the results on extra-pair paternity in **Chapter 1** and **2**. For instance, familiar individuals may visit each other’s territories more often during the breeding season which can increase opportunities for extra-pair copulations. However, it remains to be tested whether the observed patterns in **Chapter 1** and **2** emerge from an active extra-pair mate choice (i.e. preferences for familiar individuals) or whether extra-pair copulations are indirectly facilitated due to decreased aggression between neighbours. Data on the fine-scale associations after breeding settlement and particularly during the fertile period of the female (Schlicht et al. 2015b) could shed light on whether familiarity from the winter drives for instance extra-territorial visits.

Social networks often represent a static snapshot of the social life of animals. However, the social environment is highly dynamic changing over time (Farine 2018). Here, we created social networks separately for each month and then examined potential temporal differences in the effect of winter associations on future mating patterns (**Chapter 1**). We show that the association patterns of future social and extra-pair partners increased towards the breeding season (**Chapter 1**, Figure S3, S4). For extra-pair partners, the effect of the social associations was strongest shortly before breeding, whereas the effect on social pairs was clear throughout the winter (**Chapter 1**, Figure S3, S4). Further, in males the social factors that predicted success in acquiring a breeding partner and extra-pair partner(s) differed (**Chapter 2,** Figure 1, Table 1, 2). These findings provide new insights into the dynamics of pair formation and suggest that social pairs may get established earlier than extra-pair partners (**Chapter 1**) and that the formation of the two different relationship types may follow different mechanisms (**Chapter 2**).

The social structure during winter and its effect on extra-pair paternity may simply emerge from the preceding breeding social structure. However, we show that patterns of extra-pair paternity were not solely influenced by the previous breeding social structure (**Chapter 1**) and by between-year changes in the local, social breeding environment (**Chapter 3**) but also by the winter social structure itself (**Chapter 1, 2**). This makes sense for short lived species such as the blue tit as they may only reproduce once in their life and populations experience high turnover rates from one breeding season to the next. Thus, only few individuals will experience multiple breeding seasons whereas every individual necessarily experiences a non-breeding season. Taken together, our work highlights the importance of the pre-breeding social environment in predicting future mating patterns and the need for further research to assess the generality of our results.

Extra-pair paternity: individual-specific or environment-dependent trait?

Variation in extra-pair paternity was often linked to individual phenotypic traits (Sundberg and Dixon 1996; Yezerinac and Weatherhead 1997; Cleasby and Nakagawa 2012; Knief et al. 2017) or aspects of the (social) breeding environment such as the breeding synchrony and density (Dunn et al. 1994; Westneat and Sherman 1997; Thusius et al. 2001; Schlicht et al. 2015a). Teasing apart the contribution of intrinsic, individual-specific traits from environmental conditions is important for our understanding of the variation in extra-pair paternity and consequently the potential for sexual selection to act on phenotypes. Here, we found low, but significant repeatability of extra-pair paternity patterns in female and male blue tits (**Chapter 3,** Table 2). This suggests that extra-pair paternity is to some extent an individual-specific trait (**Chapter 3**). This can be the case if there is individual differences in the tendency to engage in extra-pair copulations (Forstmeier 2007), individual differences in the frequency of within-pair copulations, or if specific individual characteristics increase the probability to successfully gain extra-pair paternity (Yezerinac and Weatherhead 1997; Schlicht et al. 2015a; **Chapter 2**) or to successfully defend paternity. However, as the observed repeatabilities were low, extra-pair paternity may not cause strong sexual selection (Schlicht and Kempenaers 2013; **Chapter 3**).

Between-year changes in the local breeding environment did explain little of the within-individual changes in extra-pair paternity (**Chapter 3**). Extra-pair paternity inherently involves multiple individuals and likely depends on a whole array of behavioural events and physiological processes. Thus, extra-pair paternity may depend more strongly on recent interactions between individuals (see **Chapter 1**) and/or opportunities to copulate without disturbance rather than on events from the previous breeding season or individual traits. Furthermore, the exact timing of within- and extra-pair copulations in relation to the fertile period of the female and the amount of sperm transferred (Girndt et al. 2019) potentially play an important role in predicting patterns of extra-pair paternity. Thus, we speculate that extra-pair paternity may be in general a less predictable trait that depends, at least to some extent, on “chance events”.

One limitation of our studies is that we only investigated the occurrence of extra-pair paternity and not extra-pair behaviour or copulations itself. Individual extra-pair behaviour may be a highly repeatable and heritable trait whereas the occurrence of extra-pair paternity depends on several incidents in between, such as opportunities to copulate without disturbance and post-copulatory mechanisms. Also aspects of the social environment likely influence the expression of extra-pair behaviour and/or extra-pair copulations, whereas patterns of extra-pair paternity will also depend on post-copulatory processes. Thus, more research on the expression of extra-pair behaviour and/or copulations rather than the resulting extra-pair paternity could provide important new insights.

Fitness benefits through extra-pair paternity?

In some bird species, extra-pair males were reported to provide direct benefits to the extra-pair female(s) they copulated with. For instance, males may provide additional parental care (Kempenaers 1993; Townsend et al. 2010), help with predator mobbing (Kempenaers 1993), or become more tolerant towards the extra-pair female(s) (Gray 1997b). Consequently, extra-pair copulations may lead to fitness benefits (Gray 1997a), which is suggested to be one of the reasons why females actively engage in extra-pair copulations. Eliassen and Jørgensen (2014) proposed that extra-pair copulations, and the emerging paternity uncertainty among males, incentivizes males to cooperate towards public goods, resulting in "nicer" breeding environments. In our study, we did not measure cooperative behaviour directly but tested one of their key predictions, namely that extra-pair copulations should lead to increased fitness of whole nests (**Chapter 4**). Females breeding in neighbourhoods with a higher prevalence of extra-pair paternity had a somewhat increased survival (**Chapter 4**). However, breeding success and male survival were not related to either the presence of extra-pair young in the brood or to the proportion of nests with extra-pair young within the neighbourhood (**Chapter 4**). Thus, our findings provide little evidence for the "cooperative neighbourhood hypothesis" and the occurrence of direct benefits. In blue tits, extra-pair copulations may rather provide indirect, genetic benefits (Foerster et al. 2003; but see Charmantier et al. 2004) or insurance against male infertility (Santema et al. 2020). However, extra-pair copulations may lead to fitness benefits of whole nests in other species. Data on the social interactions between extra-pair partners after the copulation (such as during the provisioning phase of the young) would be a valuable addition to explore this topic in more detail.

Outlook

Research exploring the link between the fine-scale social environment and extra-pair mating decisions is still in its infancy, awaiting further exploration. There are several interesting aspects and hypotheses that remain to be explored and our work provides an ideal base for future studies. We highlight three potential future directions below.

Experimental manipulation of the social environment

The presented links between the social environment and extra-pair paternity in blue tits are solely correlational. In order to create ultimate links, experimental manipulations are needed. While some studies experimentally explored effects on social structure by removing or adding individuals (Croft et al. 2008; Jacoby et al. 2010), manipulating social relationships between individuals is a major challenge, particularly in the wild. However, new technologies such as selective bird feeders constitute promising tools (Firth et al. 2015; Firth et al. 2016). Here, only specific individuals are granted access (i.e. can forage together at the same location) which allows to create differences in the composition of the local social environment (e.g. varying population size, stability or phenotypic composition) and even allows to split specific relationship types such as breeding pairs. Such experimental approaches could provide exciting new insights into the link between social features and the expression of mating patterns.

Advances in data collection

We quantified the social environment during winter based on foraging associations and the social environment during breeding based on the spatial proximity of breeding pairs. Both only represent a vague picture of the social environment that individuals experience. For instance, birds will also associate during other contexts than foraging that may even have a more predictive power of future mating patterns. In addition, social associations or the spatial proximity do not provide information on the social interactions between individuals (i.e. whether they are affiliative or agonistic). Future research using more fine-scale tracking (Alarcón-Nieto et al. 2018; Ripperger et al. 2020) during various contexts or continuously, and information on the value and direction of interactions, could provide better evidence for the link between social environment and variation in extra-pair paternity.

Interacting phenotypes and social selection

Extra-pair behaviour is a social trait that is always expressed in interaction with other individuals. Thus, the expression of extra-pair behaviour of a focal individual may not only be influenced by its own phenotype but by the phenotype(s) of its social associate(s) (i.e. "interacting phenotypes"; Moore et al. 1997; Wilson et al. 2011). For instance, a highly promiscuous male may influence the expressed extra-pair behaviour of his social female. This could be the case if increased extra-pair behaviour in the male coincides with less effort in mate-guarding or other pair-bond related behaviours that can lead to increased extra-pair behaviour in the female. In such a case, extra-pair behaviour could spread among individuals, potentially leading to changes in the overall expressed mating system. Research examining such links may provide exciting new insights into the causes of the variation in extra-pair paternity.

In species that exhibit social behaviour, selection can be mediated by the interaction between a focal individual's phenotype and the phenotypes of its associates, known as social selection (West-Eberhard 1979; Wolf et al. 1999; McGlothlin et al. 2010). In blue tits, several male attributes have been linked to extra-pair siring success (Delhey and Kempenaers 2006; Poesel et al. 2006; Schlicht et al. 2015a). For instance, larger males are more successful in siring extra-pair young (Kempenaers et al. 1997; Schlicht et al. 2015a). However, this success may depend on the average body size of male conspecifics the focal male interacts with or on the body size of the extra-pair female's social partner. Thus, the relative fit of individuals to their social environment may create variation in extra-pair siring success and alter selection pressure. Research on sexual selection and extra-pair paternity may benefit from taking into account the detailed social environment that individuals experience.

Conclusion

The presented thesis is of essential interest to behavioural ecologists working on mating behaviour and animal sociality. We present that the social environment that individuals experience prior to breeding is an important determinant of future (extra-pair) mating patterns. In addition, we reveal that measures of extra-pair paternity show low repeatability and that changes in the breeding environment explained only little of the changes in extra-pair paternity. As extra-pair paternity always involves multiple individuals and emerges from a whole series of behavioural and physiological events, we suggest that extra-pair paternity is a trait that remains difficult to predict. Lastly, we show that the prevalence of extra-pair paternity in breeding neighbourhoods is unlikely to affect the fitness of whole nests. Our research on extra-pair paternity in blue tits will hopefully encourage further research to improve our understanding of the link between the unique social environment and variation in (extra-pair) mating behaviour.

References

Alarcón-Nieto G, Graving JM, Klarevas-Irby JA, Maldonado-Chaparro AA, Mueller I, Farine DR. 2018. An automated barcode tracking system for behavioural studies in birds. Methods Ecol Evol. 9(6):1536–1547.

Cleasby IR, Nakagawa S. 2012. The influence of male age on within-pair and extra-pair paternity in passerines. Ibis. 154(2):318–324.

Croft DP, Morrell LJ, Davis A, Faria JJ, Dyer JRG, Piyapong C, Ramnarine I, Ruxton GD, Krause J. 2008. Does defection during predator inspection affect social structure in wild shoals of guppies? Anim Behav. 75(1):43–53.

Culina A, Hinde CA, Sheldon BC. 2015. Carry-over effects of the social environment on future divorce probability in a wild bird population. Proc R Soc B Biol Sci. 282(1817):20150920.

Delhey K, Kempenaers B. 2006. Age differences in blue tit Parus caeruleus plumage colour: within-individual changes or colour-biased survival? J Avian Biol. 37(4):339–348.

Dunn PO, Whittingham LA, Lifjeld JT, Robertson RJ, Boag PT. 1994. Effects of breeding density, synchrony, and experience on extrapair paternity in tree swallows. Behav Ecol. 5(2):123–129.

Eliassen S, Jørgensen C. 2014. Extra-pair mating and evolution of cooperative neighbourhoods. PLoS One. 9(7):e99878.

Farine DR. 2018. When to choose dynamic vs. static social network analysis. J Anim Ecol. 87(1):128–138.

Farine DR, Sheldon BC. 2015. Selection for territory acquisition is modulated by social network structure in a wild songbird. J Evol Biol. 28(3):547–556.

Firth JA, Sheldon BC. 2016. Social carry-over effects underpin trans-seasonally linked structure in a wild bird population. Ecol Lett. 19(11):1324–1332.

Firth JA, Sheldon BC, Farine DR. 2016. Pathways of information transmission among wild songbirds follow experimentally imposed changes in social foraging structure. Biol Lett. 12(6):20160144.

Firth JA, Voelkl B, Farine DR, Sheldon BC. 2015. Experimental evidence that social relationships determine individual foraging behavior. Curr Biol. 25(23):3138–3143.

Gilsenan C, Valcu M, Kempenaers B. 2017. Difference in arrival date at the breeding site between former pair members predicts divorce in blue tits. Anim Behav. 133:57–72.

Girndt A, Cockburn G, Sánchez-Tójar A, Hertel M, Burke T, Schroeder J. 2019. Male age and its association with reproductive traits in captive and wild house sparrows. J Evol Biol. 32(12):1432–1443.

Gray EM. 1997a. Do female red-winged blackbirds benefit genetically from seeking extra-pair copulations? Anim Behav. 53(3):605–623.

Gray EM. 1997b. Female red-winged blackbirds accrue material benefits from copulating with extra-pair males. Anim Behav. 53(3):625–639.

Hasselquist D, Bensch S, von Schantz T. 1996. Correlation between male song repertoire, extra-pair paternity and offspring survival in the great reed warbler. Nature. 381(6579):229.

Jacoby DMP, Busawon DS, Sims DW. 2010. Sex and social networking: the influence of male presence on social structure of female shark groups. Behav Ecol. 21(4):808–818.

Kempenaers B. 1993. A case of polyandry in the blue tit: female extra-pair behaviour results in extra male help. Ornis Scand. 24(3):246–249.

Knief U, Forstmeier W, Pei Y, Ihle M, Wang D, Martin K, Opatová P, Albrechtová J, Wittig M, Franke A. 2017. A sex-chromosome inversion causes strong overdominance for sperm traits that affect siring success. Nat Ecol Evol. 1(8):1177.

Komdeur J. 2001. Mate guarding in the Seychelles warbler is energetically costly and adjusted to paternity risk. Proc R Soc London B Biol Sci. 268(1481):2103–2111.

Maldonado-Chaparro AA, Montiglio P, Forstmeier W, Kempenaers B, Farine DR. 2018. Linking the fine-scale social environment to mating decisions: a future direction for the study of extra-pair paternity. Biol Rev. 93(3):1558–1577.

McGlothlin JW, Moore AJ, Wolf JB, Brodie III ED. 2010. Interacting phenotypes and the evolutionary process. III. Social evolution. Evolution. 64(9):2558–2574.

Moore AJ, Brodie III ED, Wolf JB. 1997. Interacting phenotypes and the evolutionary process: I. Direct and indirect genetic effects of social interactions. Evolution.:1352–1362.

Oh KP, Badyaev A V. 2010. Structure of social networks in a passerine bird: consequences for sexual selection and the evolution of mating strategies. Am Nat. 176(3):E80–E89.

Poesel A, Kunc HP, Foerster K, Johnsen A, Kempenaers B. 2006. Early birds are sexy: male age, dawn song and extrapair paternity in blue tits, Cyanistes (formerly Parus) caeruleus. Anim Behav. 72(3):531–538.

Psorakis I, Roberts SJ, Rezek I, Sheldon BC. 2012. Inferring social network structure in ecological systems from spatio-temporal data streams. J R Soc Interface. 9(76):3055–3066.

Ripperger SP, Carter GG, Page RA, Duda N, Koelpin A, Weigel R, Hartmann M, Nowak T, Thielecke J, Schadhauser M. 2020. Thinking small: Next-generation sensor networks close the size gap in vertebrate biologging. PLoS Biol. 18(4):e3000655.

Rodway MS. 2007. Timing of pairing in waterfowl I: Reviewing the data and extending the theory. Waterbirds. 30(4):488–505.

Santema P, Teltscher K, Kempenaers B. 2020. Extra-pair copulations can insure female blue tits against male infertility. J Avian Biol.

Schlicht E, Kempenaers B. 2013. Effects of social and extra-pair mating on sexual selection in blue tits (cyanistes caeruleus). Evolution. 67(5):1420–1434.

Schlicht L, Valcu M, Kempenaers B. 2015a. Spatial patterns of extra-pair paternity: beyond paternity gains and losses. J Anim Ecol. 84(2):518–531.

Schlicht L, Valcu M, Kempenaers B. 2015b. Male extraterritorial behavior predicts extrapair paternity pattern in blue tits, Cyanistes caeruleus. Behav Ecol. 26(5):1404–1413.

Sundberg J, Dixon A. 1996. Old, colourful male yellowhammers, Emberiza citrinella, benefit from extra-pair copulations. Anim Behav. 52(1):113–122.

Teitelbaum CS, Converse SJ, Mueller T. 2017. Birds choose long-term partners years before breeding. Anim Behav. 134:147–154.

Thusius KJ, Dunn PO, Peterson KA, Whittingham LA. 2001. Extrapair paternity is influenced by breeding synchrony and density in the common yellowthroat. Behav Ecol. 12(5):633–639.

Townsend AK, Clark AB, McGowan KJ. 2010. The direct benefits and genetic costs of extrapair paternity in the cooperatively breeding American crow. Am Nat. 175:E1–E9.

West-Eberhard MJ. 1979. Sexual selection, social competition, and evolution. Proc Am Philos Soc. 123(4):222–234.

Westneat DF, Sherman PW. 1997. Density and extra-pair fertilizations in birds: a comparative analysis. Behav Ecol Sociobiol. 41(4):205–215.

Wilson AJ, Morrissey MB, Adams MJ, Walling CA, Guinness FE, Pemberton JM, Clutten-Brock TH, Kruuk LEB. 2011. Indirect genetics effects and evolutionary constraint: an analysis of social dominance in red deer, Cervus elaphus. J Evol Biol. 24(4):772–783.

Wolf JB, Brodie III ED, Moore AJ. 1999. Interacting phenotypes and the evolutionary process. II. Selection resulting from social interactions. Am Nat. 153(3):254–266.

Yezerinac SM, Weatherhead PJ. 1997. Extra–pair mating, male plumage coloration and sexual selection in yellow warblers (Dendroica petechia). Proc R Soc London B Biol Sci. 264(1381):527–532.

Acknowledgments

First and foremost I would like to thank my supervisor Bart. I'm deeply grateful for all your scientific guidance, your patients, your critical mind and perfectionism that improved the scientific quality of this work immensely and that shaped me in becoming a better scientist. I'm thankful for all your support and motivating words, not only scientifically but also personally when I was feeling stressed. I also would like to thank you for giving me a lot of freedom during my PhD such as allowing me to help with shorebird fieldwork in Alaska or when applying for a Postdoc position (even if it was probably way too early). Finally, I would like to thank you for making some of the best pancakes I ever ate!

I also would like to thank my supervisor Mihai, for his theoretical and analytical insights, the maintenance of the database and scientific guidance. I'm very grateful for all your help with statistics and coding that you very, very patiently taught me.

Further, I would like to thank my external supervisor Damien. I'm very grateful for all your support, your help with social network analysis and coding, your creative and intellectual mind and your scientific guidance through all this time. During motivational crisis you always managed to bring me back on track. Whenever I visited you and your lab in Radolfzell, I felt highly welcomed and enjoyed the vibrant and lively scientific and non-scientific chats, lab dinners, happy hours and "distractions" by Gilli. Thank you for always believing in me as a scientist and especially for convincing me to apply for a Postdoc position that I thought I would never get.

My time in Seewiesen and Radolfzell wouldn't have been the same without all the wonderful people that I met during this journey. I'm very grateful for all the colleagues at the Max Planck Institute for Ornithology and the Max Planck Institute for Animal Behavior, particularly members of Bart's and Damien's lab. Further, I would like to thank the International Max Planck Research School for Organismal Biology, particularly Mäggi Hieber, for providing scientific education, and financial and logistic support. I would also like to thank Ben Hatchwell, my PAC member, for providing scientific guidance at the beginning of my PhD and for showing me his fantastic work on long-tailed tits in Sheffield. I'm immensely grateful for the blue tit field team and I would like to especially thank Agnes and Andrea for all their support and guidance. Further, I would like to thank all the field assistants that helped me with data collection during many cold winter days: Carles, Friedi, Cecile, Giulia, Alice and Fenja. I also would like to thank P3, Lotte, Emmi, Carol, Sylvia, Alex, Kim, Melanie, Christine, Jakob, Carmen and Esteban for many wonderful days in the field and (scientific) chats. I'm also

grateful to Peter Loës and Peter Skripsky who took care of the maintenance of all the nest boxes and bird feeders, and Klaus Pichler and Felix Hartl for building the bird feeders. I'm grateful for all my colleagues with whom I did not only share the same working environment but many enjoyable moments to refuel my energy. Here, I would like to especially thank Hannes, Mäggi, P3, Carol, Peter Skripsky, Kim, Yifan, Eunbi, Luisana, Elena, Daiping and Luke for BBQs, beers, crafting evenings, movie nights, coffee breaks and hikes. In this spirit, I also would like to thank the Maisinger Seehof and the Georg Ludwig for many wonderful nights in the Biergarten with good food and many, many beers. Last but not least, I'm especially thankful for my office mate Hannes. I really enjoyed all our chats, working together in the field in Alaska and, at a later stage, "distractions" by Nuna!

I'm truly grateful for my parents who always supported me and my passion for nature throughout my whole life. As they do not speak English: Liebe Mama, lieber Papa, ich bin euch wahnsinnig dankbar für all eure Unterstützung! Obwohl ihr wahrscheinlich vieles von dem was ich in meiner Arbeit mache nicht versteht, habt ihr mich doch stets in allem was ich tue unterstüzt! Solche Eltern kann man sich nur wünschen und ich bin unendlich dankbar euch zu haben.

Last, I would like to thank my partner Matthias for all his unconditional support, his help through all my ups and downs, the endless scientific discussions, help with statistics and help to compete my good old imposter syndrome. You have been incredibly patient during these four years and I'm deeply grateful to have found such a wonderful partner who shares my passion for nature.

Kristina Beck
Juli 2020

Author contributions

Chapter 1: All authors conceived the idea and designed the study; B.K. conducted the paternity analyses; K.B. and D.F. analysed the data with input from B.K.; all authors wrote the manuscript.

Chapter 2: All authors conceived the idea and designed the study. B.K. conducted the paternity analyses; K.B. analyzed the data with input from D.F. and B.K.; all authors wrote the manuscript.

Chapter 3: B.K. and M.V. conceived the idea and designed the study; B.K. conducted the paternity analyses; K.B. and M.V. analysed the data with input from B.K.; K.B. and B.K. wrote the manuscript, with input from M.V.

Chapter 4: All authors conceived the idea and designed the study. B.K. conducted the paternity analyses; K.B. analyzed the data with input from B.K., P.S. and L.S. K.B. and B.K. wrote the paper with input from L.S. and P.S.

....

Bart Kempenaers, Doktorvater

Kristina Beck, Doktorand

Curriculum vitae

Kristina Beck
Max Planck Institute for Ornithology
Eberhard-Gwinner-Straße, 82319 Seewiesen

CURRENT POSITION AND ACADEMIC EDUCATION

September 2016 – present	**PhD student** at the Max Planck Institute for Ornithology within the International Max Planck Research School for Organismal Biology (IMPRS), Seewiesen, Germany
October 2014 – July 2016	**MSc** - University of Vienna, Austria, program: Behavioural, neuro- and cognitive biology
October 2010 – August 2014	**BSc** - Ludwig-Maximilian University, Munich, Germany, program: Biology

RESEARCH EXPERIENCE

September 2016 – present	**PhD thesis** in Germany. Dissertation project: Influence of the social environment on the mating system of blue tits (Supervisors: Prof. Bart Kempenaers, Dr. Mihai Valcu and Dr. Damien Farine)
February 2016	**Field assistant** in French Guiana. Project: Induced tadpole transport in a poison frog. (Supervisors: Dr. Andrius Pašukonis, Dr. Max Ringler, Dr. Eva Ringler)
February – March 2015	**Master thesis** in French Guiana. Project: Tadpole transport trajectories of the neotropical frog, *Allobates femoralis*. (Supervisors: Prof. Walter Hödl, Dr. Andrius Pašukonis, Dr. Max Ringler)
August – September 2014	**Research internship** at the Konrad Lorenz Research Station, Austria and the Max Planck Institute for Ornithology in Seewiesen, Germany. Project: Local and stimulus enhancement in juvenile ravens. (Supervisor: Prof. Thomas Bugnyar)
January – April 2014	**Bachelor thesis** at the Ara Project in Costa Rica**.** Project: Social interactions of juvenile scarlet macaws before and after a release. (Supervisor: Prof. Niels Dingemanse)
April – August, November –	**Research internship** at the Konrad Lorenz Research Station, Austria. Project: Effects of site fidelity on food caching behaviour of common

December 2013	ravens. (Supervisors: Dr. Matthias Loretto, Prof. Thomas Bugnyar)
August 2012	**Research internship** at the Department of Behavioural Ecology in Munich. Project: Distribution of the ant *Formica fuscocinerea* in urban playgrounds (Supervisor: Prof. Volker Witte)

PARTICIPATION IN WORKSHOPS

October 2019/ February 2020	Advanced scientific writing (IMPRS Workshop by Dr. Wolfgang Goymann, Dr. Robert Kraus, Dr. Kamran Safi, Dr. Dina Dechmann)
April 2017	Introduction to scientific writing (IMPRS Workshop by Dr. Brian Cusack)
January 2017	Social network analysis (IMPRS Workshop by Dr. Damien Farine)
November 2016	Introduction into R (IMPRS Workshop by Dr. Kamran Safi)
September 2015	Introduction into R; How to analyse an animal’s home range (Graduate Meeting “Studying Animal Behaviour in the Field” in Austria 2015)
April 2015	Animal social networks in behavioural research (University of Neuchâtel)
October 2014	Bio-logging – new ways of animal tracking (Max Planck Institute for Ornithology, Radolfzell)

TEACHING EXPERIENCE

Nov.2017 – Apr.2018 Nov.2018 – Apr.2019	**Instructor**: Handling and processing of blue tits. Max Planck Institute for Ornithology, Seewiesen
July 2015	**Instructor**: Workshop at the Children’s University Almtal and Ennstal, Austria: “Science for children.”
August 2014, 2015	**Instructor**: Seminar at the Children’s University Steyr, Austria: “Smart, black birds. How can you investigate the behaviour of Corvids?”
April-August 2012	**Teaching Assistant**: Practical course on animal biodiversity. Ludwig-Maximilian University, Munich, Germany
October - December 2011	**Teaching Assistant**: Practical course on zoology. Ludwig-Maximilian University, Munich, Germany

CO-ORGANIZED SCIENTIFIC EVENTS

January 2017	Student Conference and Workshop on “Social network analysis”, Radolfzell, Germany

PUBLICATIONS

PUBLICATIONS (PEER REVIEWED)

Beck KB, Valcu M, Kempenaers B. 2020. Analysis of within-individual variation in extra-pair paternity in blue tits (*Cyanistes caeruleus*) shows low repeatability and little effect of changes in neighbourhood. Accepted for publication in *Behavioral Ecology*, DOI:araa069.

Beck KB*, Loretto M-C*, Bugnyar T. 2020. Effects of site fidelity, group size and age on food caching behaviour of common ravens. *Animal Behaviour*, 164, 51-64.
https://doi.org/10.1016/j.anbehav.2020.03.015
*** shared first authors**

Beck KB, Farine DR, Kempenaers B. 2020. Winter associations predict social and extra-pair mating patterns in a wild songbird. *Proceedings of the Royal Society B*, *287*(1921), 20192606.
https://doi.org/10.1098/rspb.2019.2606

Beck KB, Loretto M-C, Ringler M, Hödl W, Pašukonis A. 2017. Relying on known or exploring for new? Movement patterns and reproductive resource use in a tadpole-transporting frog. *PeerJ* 5:e3745.
https://doi.org/10.7717/peerj.3745

Pašukonis A*****, **Beck KB***, Fischer MT, Weinlein S, Stückler S, Ringler E. 2017. Induced parental care in a poison frog: a tadpole cross-fostering experiment. *Journal of Experimental Biology*, 220(21), 3949-3954. http://jeb.biologists.org/content/220/21/3949
*** shared first authors**

Ringler E, **Beck KB**, Weinlein S, Huber L, Ringler M. 2017. Adopt, ignore, or kill? Male poison frogs adjust parental decisions according to their territorial status. *Scientific Reports*, 7, 43544.
http://doi.org/10.1038/srep43544

PUBLICATIONS SUBMITTED/IN PREPARATION

Santema P, Schlicht L, **Beck KB**, BC Sheldon, Kempenaers B (currently in revision for Animal Behaviour): Why do nestling birds fledge early in the day.

Cantor M, Maldonado-Chaparro AA, **Beck KB**, Carter GG, He P, Hillemann F, Klarevas-Irby JA, Lang SDJ, Ogino M, Papageorgiou D, Prox L, Farine DR (currently in revision for Journal of Animal Ecology): Animal social networks: revealing the causes and implications of social structure in ecology and evolution.

Beck KB, Farine DR, Kempenaers B (in preparation): Social network position predicts male mating success in a small passerine.

Beck KB, Santema P, Schlicht L, Kempenaers B (in preparation): Cooperative neighbourhood benefits are not a major driver of extra-pair paternity in blue tits.

POPULAR SCIENCE ARTICLES

Beck KB. 2014. Wanna be my friend? Papageienzeit (17): 32-41.

Beck KB, Frigerio D, Loretto M-C. 2016: Der Kolkrabe – Schwarzfedriges Genie oder doch nur ein Unglücksbote? Von Irrtümern und Mythen bis hin zur Forschung von Groß und Klein. ÖkoL (38): 3-11.

PEER REVIEW ACTIVITIES

Animal Behaviour, Biology Letters, Journal of Ornithology, Zoological Letters, Scientific Reports

CONFERENCE CONTRIBUTIONS

Beck KB, Valcu M, Kempenaers B. 2019: Within-individual variation in extra-pair paternity in blue tits. ASAB summer meeting, Konstanz, Germany, talk.

Beck KB, Farine D, Valcu M, Kempenaers B. 2017: Influence of the social environment on extra-pair paternity in blue tits. 11th Göttinger Freilandtage, Göttingen, Germany, poster.

Loretto M-C, **Beck KB**, Schuster R, Bugnyar T. 2017: From large scale movements to local food caches - the spatial behaviour of non-breeding ravens. 6th International Bio-logging Symposium, Konstanz, Germany, poster.

Loretto M-C, **Beck KB**, Schuster R, Bugnyar T. 2017: Variation in space use of non-breeding ravens: From large scale movements to local food caches. 35th International Ethological Conference, Estoril, Portugal, poster.

Beck KB, Ringler E, Fischer MT, Weinlein S, Hödl W, Pašukonis A. 2016: Tadpole cross-fostering induces complex parental and spatial behaviour in poison frogs. 8th ECBB, Vienna, Austria, poster **(*best poster award*)**.

Beck KB, Loretto M-C, Ringler M, Hödl W, Pašukonis A. 2016: Movement patterns and spatial orientation in tadpole transporting frogs. 8th ECBB, Vienna, Austria, poster.

Beck KB, Loretto M-C, Hödl W, Pašukonis A. 2015: Tadpole transport trajectories in the neotropical frog, *Allobates femoralis*. Graduate Meeting “Studying Animal Behaviour in the Field” in Grünau, Austria, talk.

Beck KB, Pašukonis A, Hödl W. 2015: Räumliche Orientierung von Pfeilgiftfröschen – Kaulquappentransport von *Allobates femoralis*. 39. Internationales Symposion Mensch-Tier-Umwelt, Vienna, Austria, talk.

GRANTS

Erasmus Internship Scholarship (1550 €)

Research Grant of the Ethological Society for master thesis (500 €)

Short-term grant abroad (KWA) (1400 €)

Research scholarship for master thesis (University of Vienna) (1000 €)

MEMBERSHIPS

Ethological Society

The Association for the Study of Animal Behaviour (ASAB)

LBV – Landesbund für Vogelschutz

International Bio-logging Society

PUBLIC RELATIONS AND MEDIA COVERAGE

Selected media responses on the published work on poison frogs where I was involved in:

https://www.nytimes.com/2017/10/24/science/tadpole-poison-frogs.html

https://derstandard.at/2000063406883/Wiener-Forscher-verpassten-Pfeilgiftfroeschen-Unterhosen-mit-Sendern

https://www.sciencedaily.com/releases/2017/09/170920104345.htm

Statutory declaration and statement

Eidesstattliche Erklärung

Ich versichere hiermit an Eides statt, dass die vorgelegte Dissertation von mir selbständig und ohne unerlaubte Hilfe angefertigt worden ist.

München, den 28.07.2020 ....

Kristina Beck

Erklärung

Hiermit erkläre ich, dass die Dissertation nicht ganz oder in wesentlichen Teilen einer anderen Prüfungskommission vorgelegt worden ist. Des Weiteren erkläre ich, dass ich mich nicht anderweitig einer Doktorprüfung ohne Erfolg unterzogen habe oder ohne Erfolg versucht habe, eine Dissertation einzureichen oder mich einer Doktorprüfung zu unterziehen.

München, den 28.07.2020 ....

Kristina Beck