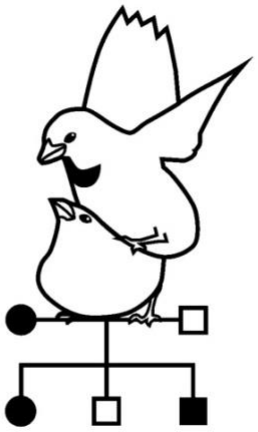
Animal Social Networks and Female Extra-pair Paternity



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Dedicated to my parents,
and to William Field, with whom I missed discussing the details.

“Social behaviour involves so many things happening at the same time, that it is impossible to see everything…
Only by watching, writing down, drawing, realizing how much you are not certain about, watching again, and thus completing your description step by step, can you attain a reasonable accuracy and completeness.”

- Niko Tinbergen
  Social Behaviour in Animals (1953)

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i. General Abstract

How animals choose to organise themselves socially has consequences for their subsequent survival and reproductive output, shaping evolutionary processes. However, the mechanisms by which such organisation influences their life history are complex and remain poorly understood; for example, the behaviour of reproductive partners, fine-scale social connections within non-reproductive groups, the broader social environment, and the physical environment all play a role in shaping the expression of social behaviours at the individual scale. In this thesis, which is separated into two parts, we consider the influence of social behaviour on reproductive choices. In the first part, we explore how researchers define a social association between individuals and then test the relationship between individual social behaviour and fitness at the annual and lifetime scales. In the second part, we apply concepts from animal social research to the question of female extra-pair paternity, which has long puzzled evolutionary ecologists. We conducted our research using a long-term study on wild house sparrows *Passer domesticus*, breeding on Lundy Island, and using a twenty-year genetic pedigree. We also used data from three other systems to compare the influence of association definition on social network structure. Our results suggest that individual sociality shapes reproductive choice in the short term, where the number of opposite-sex associates is correlated with reproductive success, but that social traits are likely to be subject to stabilising selection over a lifetime. Likewise, the inclusion of the social environment and social partner's behavioural preference as an indirect genetic effect on female behaviour increased variance in quantitative genetics models for female extra-pair paternity, suggesting a role for social behaviour. Finally, we found a correlation between the female divorce rate (or propensity to switch social mates) and the solicitation of extra-pair males. Together, our results suggest that the social preference of individual animals, when appropriately defined, is a powerful force in the mediation of behavioural traits and subsequent fitness.

ii. Acknowledgments

First, I would like to thank Dr Julia Schroeder for her patient supervision and constant shaping of exciting ideas, many of which I have benefitted from and are included throughout this thesis, as well as Dr Tim Evans and Prof Terry Burke for their guidance and supervision. I also thank HY Janet Chik, HH Alex Chan, Sarah Dobson, Živa Alif, Liam Paulson, and Daniel Dunlevy for their advice, support and good company in the lab and field. I would like to thank my progress panel, Dr James Rosindell and Dr Lauren Cator, for their valuable comments (and reassurance in the face of an unplanned pandemic) on early ideas for this thesis.

Well before my PhD, Dr Steve Christmas pointed me down the academic road I have followed since. Steve, Dr Tom Finch, Mick Pearson, Prof Lukas Jenni, and Prof John Endler, (as well as those listed above) have helped to keep that journey exciting and interesting, collaborating on various satellite and side-projects.

A PhD thesis is an enormous undertaking, not just for the candidate but, I now see, also for those around us. I would like to thank my wife, Matilda, who supported my decision to uproot our life, and who has always supported my interests and research, even and especially when our circumstances were difficult. I also thank my parents, Caroline and Mike, Ian and Amanda. I appreciate the opportunities that have enabled me to build a happy life around watching birds, but that is in no small part down to their love, support, and perseverance.

Lastly, I spent three summer field seasons on Lundy Island as part of this project, and I feel lucky to have been welcomed into that eclectic family - Dean and Zoe, Ash, Kobe and Meaghan, Pete and Erin, Rosie, Helen, the Tims (Jones and Davis), Matt and Sam, Tom, Alice, Rob and Sue, and Rob and David (and their long willow warbler days at Brambles Villa), and later, Stu and Megan and Luke.

Jade Fitton included a beautiful account of life on Lundy during the Covid-19 lockdown of 2021 – my second field season – and I recommend her book, *Hermit*, to anybody interested in adding colour to people and place at that time.

Chapter 2 – I would like to thank the various teams associated with the four systems that contributed data to this chapter (see the section below for funding associated with the Lundy system). The sociable weaver research was supported by funding from the FitzPatrick Institute of African Ornithology (DST-NRF Centre of Excellence) at the University of Cape Town (South Africa), the European Research Council (project 866489 'cooperative partner' to Rita Covas), FCT-Fundação para a Ciência e a Tecnologia (Portugal; project PTDC/BIA-EVF/5249/2014 to Rita Covas and project SFRH/BD/122106/2016 to ACF), ANR (France; project ANR- 15-CE32-0012-02 to Claire Doutrelant). The Broken Hill House Sparrow project is funded by an Australian Research Council Discovery Project grant (DP200100832) to SCG. The research in Wytham Woods was funded by a grant from the ERC (AdG 250164) awarded to Ben C. Sheldon.

Chapters 3 – 5 – As well as my co-authors, I would like to thank the Lundy Landmark Trust and Lundy Bird Observatory for their ongoing support of our fieldwork. All the research presented in these chapters was supported by the Quantitative Methods in Ecology and Evolution (QMEE) CDT funded by NERC NE/P012345/1 (JD), a fellowship from the Volkswagen Foundation (JS), a grant from the German Research Foundation: Deutsche Forschungsgemeinschaft (JS), CIG PCIG12-GA-2012-333096 from the European Research Council (JS), and NERC grant NE/J024597/1 (TB). Dr Isabel Winney and Dr Jarrod Hadfield made useful comments on aspects of the research in Chapter 4, and HH Alex Chan in Chapter 5. I would also like to thank the Imperial College Research Computing Service (DOI: 10.14469/hpc/2232). Finally, I want to thank the various editors and anonymous reviewers who commented on either submitted or published versions of these chapters and greatly improved the research methods and presentation therein.

iii. Author Declaration

Unless otherwise stated, the research presented in this thesis is entirely my own work. However, all chapters have been compiled with the supervision and co-authorship of my main supervisor, Dr Julia Schroeder, as well as Dr Tim Evans and Prof Terry Burke (see author contributions, and thus, the use of ‘we’, rather than ‘I’ throughout the research chapters). The work presented in Chapters 3, 4 and 5 has been published in Behavioural Ecology, Evolution and the Journal of Avian Biology respectively (see Associated Papers), and so my co-authors on those papers also serve as co-authors for the associated thesis chapters. Chapter 2 has been submitted for publication and is subject to peer review at the time of writing (December 2023). All fieldwork was carried out with explicit permission from the landowner and under the licence of the British Trust for Ornithology (BTO) S/6308 (JD) and Home Office Project Licence PPL 7009092 (JS).

iv. Associated Publications

1) Živa Alif, Jamie Dunning, Heung Ying Janet Chik, Terry Burke, and Julia Schroeder. 2022. What is the best fitness measure in wild populations? A case study on the power of short-term fitness proxies to predict reproductive value. *PLoS ONE.* 17(4): e0260905. DOI:10.1371/journal.pone.0260905

2) Jamie Dunning, Terry Burke, Alex Hoi Hang Chan, Heung Ying Janet Chik, Tim Evans, and Julia Schroeder. 2023. Opposite-sex associations are linked with annual fitness, but sociality is stable over a lifetime. *Behavioral Ecology.* 34(3):315-324. Doi:10.1093/beheco/arac124

3) Sarah Dobson, Jamie Dunning, Terry Burke, Heung Ying Janet Chik, and Julia Schroeder. 2023. Indirect genetic effects increase heritability estimates for male and female extra-pair reproduction. *Evolution.* Doi:10.1093/evolut/qpad100 (Joint first authorship)

4) Alex Hoi Hang Chan, Jamie Dunning, Kristina B. Beck, Terry Burke, Heung Ying Janet Chik, Daniel Dunleavy, Tim Evans, André Ferreira, Babette Fourie, Simon C. Griffith, Friederike Hillemann, and Julia Schroeder. 2023. Comparing animal social network structures using different definitions of association. **[Submitted]**. (Joint first authorship)

5) Jamie Dunning, Terry Burke and Julia Schroeder. 2023. Divorce is linked with extra-pair paternity in a monogamous passerine. Journal of Avian Biology. Doi:10.1111/jav.03171

v. Thesis Author Contributions

Jamie Dunning

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JD contributed to all aspects of research in this thesis, including experimental design, analytical techniques, and manuscript/chapter preparation and led three breeding seasons and four non-breeding field trips to Lundy Island. JD conceived and prepared all chapters presented in this thesis, with additional support, detailed below.

Dr Julia Schroder (main supervisor)

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JS provided intellectual input on all aspects of this thesis as the main supervisor and principal investigator of the Lundy Sparrow project. Also, JS co-authored all thesis chapters (and subsequent published papers) and offered guidance on analytical methods and scientific writing.

Dr Tim Evans (co-supervisor)

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TE provided intellectual input, provided guidance on analytical methods, and co-authored Chapters 2 and 3 related to network analysis.

Professor Terry Burke (Advisor)

Ecology and Evolution, Sheffield University

TB provided intellectual input to all aspects of the research in this thesis, including commenting on chapters/manuscripts and experimental design, and co-authored all chapters of this thesis. TB's lab at Sheffield carried out the genetic works included in this thesis.

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SD ran GLMM models used in Chapter 4 and intellectually contributed to the direction and preparation of that research, including a manuscript submitted for publication based.

Heung Ying Janet Chik (co-author of Chapters 2, 3, and 4)

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HYJC contributed to fieldwork and offered guidance on the analytical methods used throughout this thesis.

vi. Figures, Insets and Tables

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Chapter 1

An Introduction to Concepts in Animal Social Research

Publication Statement: This chapter has not been submitted for publication at the time of writing (December 2023).

General introduction

Social behaviour is an essential aspect of life on Earth and plays a critical role in processes determining the survival and reproductive success of individual animals (Smith and Maynard-Smith 1978; Krause and Ruxton 2002; Kotrschal, Scheiber, and Hirschenhauser 2010), and has consequences for the conservation of social species (Snijders et al. 2017; Overveld et al. 2020; Brakes et al. 2021; Greggor and Goldenberg 2023).

The study of these processes was made possible by first defining the ways in which individual animals can be socially linked, in other words, the various patterns of association and interaction between wild animals (Tinbergen 1953; Hinde 1976) and later by the application of social network theory to animal social research (Scott 2011; Wey et al. 2008; Krause, Lusseau, and James 2009). However, the evolutionary context of social behaviour remains challenging for behavioural ecologists. For example, we do not yet fully understand how social behaviours are maintained between individuals or within populations, their influence on life history (Wey et al. 2008; Maldonado-Chaparro et al. 2018), and how social behaviours are selected, and variation maintained (Silk 2007; Silk et al. 2009). Likewise, social behaviours and how they are measured are often poorly defined (Krause and Ruxton 2002; Krause, Lusseau, and James 2009).

In this thesis, we first address how a social association may be defined in a gregarious system of passerine birds (Chapter 2) before applying that definition to test how social associations are linked with fitness in the short and long term (Chapter 3). We then use these principles to test the long-standing question of female promiscuity in the context of the social environment (following Maldonado-Chaparro et al. 2018). First, by testing the influence of fine-scale social links, the influence of the social father's behaviour on female propensity to extra-pair behaviour (Chapter 4), and then by testing the hypothesis that female fecundity is linked to the solicitation of extra-pair partners (Chapter 5).

Defining Animal Social Behaviour

The language used to describe animal social behaviours has developed over time (Silk 2002), and as such, is often poorly unified across systems. Throughout this thesis, we use associate/association conventionally, to describe an overlap in space and time between two or more individuals (Croft, James, and Krause 2008; Wey et al. 2008; Krause, Lusseau, and James 2009). The term 'social' can be applied in different ways and to a broad spectrum of animal behaviours; for example, 'social' is commonly used to describe one extreme on the spectrum describing an individual's propensity to group with others. A flock of birds, comprised of multiple cooperating individuals, is considered social, whereas a hunting raptor is considered solitary, avoiding the company of others (Tinbergen 1953). However, in that context, when the raptor interacts with her partner or offspring, she too may be considered social. Individual social behaviour is therefore defined by context, where the benefits of being part of a group outweigh the costs (Krause and Ruxton 2002).

More often though, and throughout this thesis, 'social' describes a repeatable association (or bond) between two individuals (Krause, Lusseau, and James 2009)—akin to human friendship (Silk 2002; Massen, Sterck, and Vos 2010; Brent et al. 2014). Likewise, 'sociality' describes an individual's propensity to social association. Although linked, separating social behaviours from grouping or aggregation is important—an individual's

propensity to form groups, herds, or flocks (Krause and Ruxton 2002). For example, moths gathering around a lamp on a warm summer evening are not necessarily socializing; they are attracted to the light and linked only through coincidence (Tinbergen 1953; Webber et al. 2022). Similarly, a large flock of Eurasian starlings *Sturnus vulgaris* is unlikely to be socializing with every other individual within the flock, but they are all cooperating, and possibly, socially interacting with their immediate neighbours (Ballerini et al. 2008; King and Sumpter 2012; Ling et al. 2019).

Unlike the previous example, the group of starlings represents the intention of the group's members, who choose to interact. An interaction is a discrete and often directed behaviour between associates, such as when individuals overlap in space and time, and choose to direct some behaviour towards another (Hinde 1976; Krause, Lusseau, and James 2009), for example, a primate grooming a neighbour (Brent et al. 2014; Siracusa et al. 2023) or poking another in the eye (Perry, 2011). In some cases, non-physical behaviours used to signal some intention or maintain coordination may also constitute interactions (Bradbury, Vehrencamp, et al. 1998), for example, a starling maintaining proximity with another during flight (Bradbury, Vehrencamp, et al. 1998; Ballerini et al. 2008), or jackdaws *Corvus monedula* calling to coordinate leaving a communal roost site (Dibnah et al. 2022).

In mammalian systems, where the concept of animal social networks was first developed (Hinde 1952), social relationships (Hinde 1952; but also see Ostner and Schülke 2014; Brent et al. 2014) are commonly defined by the quality and frequency of non-aggressive (and often, non-sexual; Brent et al. 2014) interactions between pairs of individuals (Hinde 1976). However, in non-mammalian systems (including many avian systems, the focus of this thesis), such interactions are difficult to observe (Krause, Lusseau, and James 2009). Therefore, researchers must make assumptions based on time spent in physical proximity. Throughout this thesis, we define a social association as two individuals consistently sharing the same space at the same time, and from which we assume intention (see Chapter 1; Whitehead and Dufault 1999; Franks, Ruxton, and James 2010). Where they are essential to the content of the research in Chapters 2 and 3, we refer to

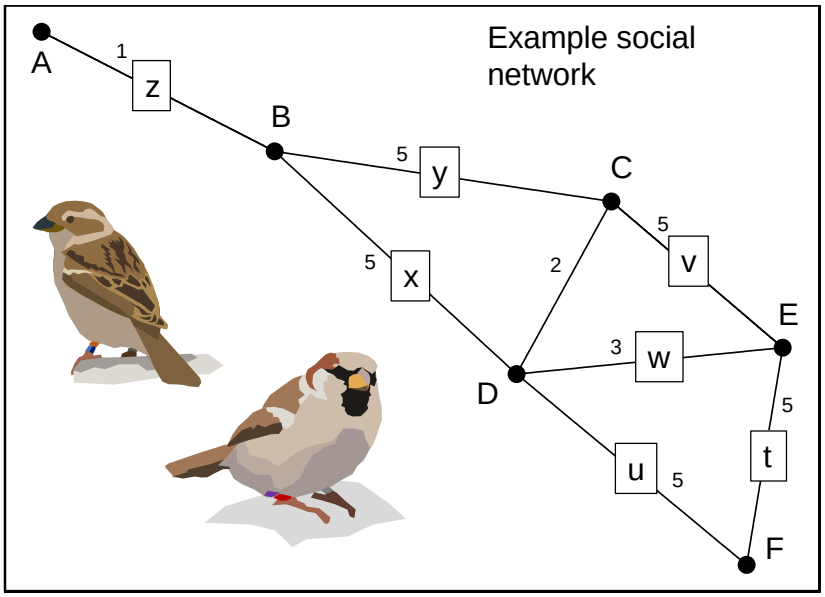
social associations as ‘associations’ for brevity. Note that the precise method of identifying associations, individuals overlapping in time and space, varies and is the subject of the first chapter of this thesis.

Early studies into the consequences of animal social behaviour used coarse, indirect measures of social complexity, for example, group size (Hinde 1976; Côté and Poulinb 1995; Brown and Brown 1996; see also Wey et al. 2008), but as a consequence assumed homogeneity of social preference. However, we now understand that social behaviour is one aspect of an individual’s personality—a repeatable behavioural trait that varies between but is consistent within individuals, and across contexts (Krause, James, and Croft 2010; Aplin et al. 2013, 2014; Aplin, Firth, et al. 2015). An individual’s social behaviour may be further mediated by their physical (Voelkl, Firth, and Sheldon 2016; Firth et al. 2017) or social environment (Ward and Webster 2016; Culina, Hinde, and Sheldon 2015; Culina, Firth, and Hinde 2020). Thus, to understand the evolution of social behaviour, we must first measure social preference at the individual scale.

Measuring Social Behaviour—Social Networks

Animal social network analysis (often, SNA) is the application of mathematical graph theory (see Wey et al. 2008; Silk 2023) to social systems and allows researchers to measure individual sociality directly by quantifying associations or interactions between a focal individual and their immediate (and more distant) neighbours (Wey et al. 2008; Farine and Whitehead 2015). Thus, a social network is a graph, defined by a set of nodes and edges in which the nodes represent individuals, and the interconnecting edges between the nodes, either associations or interactions (see Box 1). For example, individual A interacts with B, and is represented in the social network as two nodes, one to represent each individual, and an interconnecting edge, representing the interaction between them. Two nodes connected by an edge are represented as a single dyad. In this case, an interaction may be represented with a directional edge, indicating an agonist

and an antagonist (Wey et al. 2008; Silk 2023). Throughout this thesis, edges represent passive association (defined above) and are therefore non-directional.



Box 1. Social network structure and social centrality. A social network (or graph) is defined by a set of *Nodes* (N: A-F, here representing individual house sparrows *Passer domesticus*) and a series of interconnecting *Edges* (E: t-z, here representing social associations, from shared membership of foraging groups). Edges may be *weighted* and/or *directed***.** Edge *weight* denotes in this case, the number of occasions upon which two sparrows were members of the same feeding group (and given here along each edge – e.g., individuals N[D] and N[E] were associated on three occasions, denoted by E[w]). *Directed edges* (not shown here) denote the direction of interaction from a sender to a receiver. Individual measures of sociality are calculated between a focal individual and their neighbours – measures of *Network centrality*. Although definitions vary between studies, we follow those described by Wey et al (2008) for use in animal social networks, commonly:

- **Node *Degree* –** the number of direct edges defined between a focal individual and all others. For example, N[A] had a degree of 1, and N[D] has a degree of 4. In this case, degree represents the number of unique individuals a sparrow has shared a feeding group with.
- **Edge weight (Strength)** - the number of groups shared by a pair of individuals. The sum of weights represents the total number of feeding groups that a focal individual took part in, for example, N[D] took part in 15 feeding events. Measures of strength may also be corrected against the density of a social network using Simple Ratio Indices (SRI, for more information see Farine 2013).

Other measures of network centrality measure individual importance in the context of a wider social group, including indirect (non-neighbour) associations, commonly: *Betweenness* centrality measures network influence and is defined by the number of shortest paths (*geodesics*) between all network dyads that must travel through the focal individual. For example, N[A] has a betweenness centrality of 0 because it does not sit on the path between any other potential dyad, whereas N[B] has a high betweenness of 9, because for all other individuals to be connected to N[A] they must pass N[B]. An alternative method is *Eigenvector centrality*, which also accounts for the influence of neighbouring individuals (for more details see McDoanld 2007; Wey et al. 2008).

Additionally, depending on how nodes and edges are defined, graph centrality measures can be extracted from a social network and used to describe aspects of an individual's social behaviour. In this thesis, we are interested in the influence of social behaviours on reproductive traits. Specifically, the number and strength of association may influence reproductive outcomes and, thus, drive selection (Ryder et al. 2009; Oh and Badyaev 2010; McDonald et al. 2013; Beck, Farine, and Kempenaers 2020, 2021). For example, Oh and Badyaev (2010) used a 'betweenness' centrality measure to measure the social lability (propensity to move, in this case between social groups) of house finches *Carpodacus Mexicanus*. Betweenness centrality measures the influence on the transfer of information through a social network, defined by the shortest paths between any two nodes (individuals) in the network that travel through a focal individual (Box 1). House finches are a classic study system for sexual selection, with variations in male plumage ornamentation selected by the female as a measure of individual quality (Hill and Hill 2002; Hill 1991). Oh and Badyaev (2010) suggested that house finches with higher-quality ornamentation benefitted from low social lability. For lesser quality but socially labile males, social information could be used to select groups within which they would be competitive during the pre-breeding period.

Similarly, Beck, Farine, and Kempenaers (2021) also used two alternative measures of social centrality—degree and strength during the non-breeding period—to measure the likelihood of individual blue tits *Cyanistes caeruleus* finding a reproductive partner during the following breeding season. Degree is defined by the number of unique nodes connected by an interconnecting edge (Box 1), in this case denoting individual blue tits that were members of the same foraging flock (Psorakis et al. 2012, 2015), and strength represented the extent to which two individuals were associated during the non-breeding period. Similarly, this study also found that male social lability was correlated with breeding success. However, adult males associated with a greater number of females had more extra-pair offspring than those with more male associates. Such studies highlight the role that sociality plays in shaping the evolutionary trajectory of a population,

but how social behaviours are maintained is complex and should be considered in the context of the costs and benefits they provide to the individual.

Measuring Consequences – Fitness

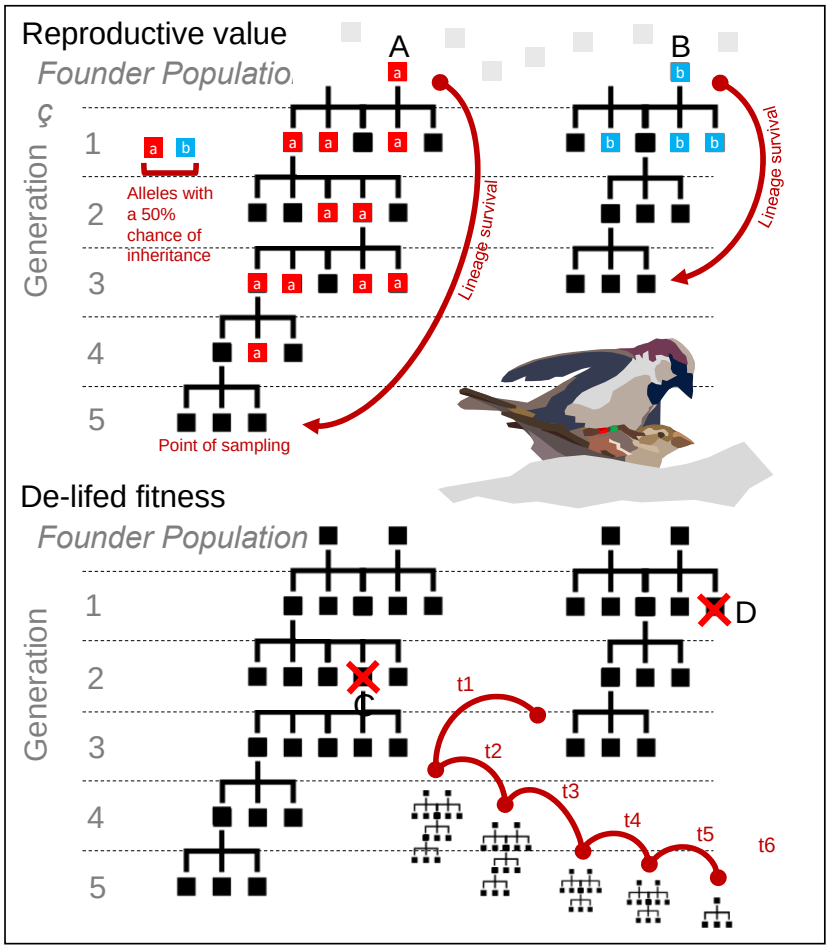
The ability to precisely define fitness is central to evolutionary theory, allowing researchers to measure the consequences of trait expression. In evolutionary ecology, consequences are defined explicitly by the costs and benefits to an individual's ability to pass genetic information on to subsequent generations.

Although there is no unified definition of fitness, it is difficult to measure accurately, and so is often instead defined by its components (Reid et al. 2019; Alif et al. 2022). For example, to pass genes on to subsequent generations, an individual must first survive from hatching to the age of the first reproduction. Likewise, that individual must compete with others and successfully attract a reproductive partner, and finally, that reproductive pair must produce viable offspring and raise them to the point of recruitment into the population. Thus, although realised fitness can be quantified retrospectively using a genetic pedigree (see Chapter 3 of this thesis; Coulson et al. 2006), these components such as an individual's ability to survive, are often used as fitness proxies, see for example, Schroeder et al. (2011); Schroeder et al. (2012); Stanton and Mann (2012); or raise and recruit offspring (lifetime reproductive success; Alif et al. 2022), see for example, Schmoll et al. (2003); Gerlach et al. (2012); Schroeder et al. (2012); Schroeder et al. (2015). Alternatively, some studies have also used other fitness measures for specific applications, such as individual growth rate (McGraw and Caswell 1996) and de-lifed fitness (Coulson et al. 2006). The individual growth rate was developed for young and expanding populations and works similarly to lifetime reproductive success but adds weight to offspring produced at younger ages (McGraw and Caswell 1996). De-lifed fitness (Coulson et al. 2006) is a retrospective measure of realised fitness and

encompasses both survival and reproductive success for each individual, in the context of the broader population, see Box 2; Coulson et al. (2006); Alif et al. (2022).

However, fitness proxies are not necessarily correlated with each other (see Box 2; Reid et al., 2019; Alif et al., 2022), and so a definition of fitness must be selected in the context of and appropriate to the study system. Alif et al. (2022) compared how lifetime fitness proxies, measured at different life stages, predicted the expected number of allele copies an individual passed on to future generations and overall lineage survival (Box 2). The study found that only annual recruits measured over a lifetime, and in the first year of life, and de-lifed fitness correlated with reproductive value. Thus, in Chapter 1 of this thesis, where we describe how selection pressure may act upon social traits, we used recruits and de-lifed fitness at the lifetime and annual scales.

Box 2. Fitness proxies and reproductive value. Fitness describes an individual's ability to survive and produce viable offspring, which in turn carry their genes on into future generations – the persistence of an individual's genes. The ability to precisely measure fitness is central to understanding trait evolution, yet without complete genetic information, and continuous monitoring of all births and deaths within a population, fitness is difficult to quantify. To compensate, many studies use some measure of fecundity as a proxy for fitness – for example, eggs laid, or chicks recruited.



Alif et al (2022) compared fitness proxies with realised reproductive value, measured as expected individual allele copies in future generations from surviving lineages (see Barton and Etheridge 2011; Alif et al 2022; red[a]-blue[b] opposite) and founder lineage survival at the point of sampling (opposite generation 5).
The study found that in the Lundy sparrow system only Lifetime reproductive success and individual growth rate (measured during the first year of life) at the recruitment stage, but not eggs, hatchlings or fledglings, and de-lifed fitness (for a detailed description see Coulson et al. 2006) were significantly correlated with reproductive value.

In the example given above, the allele (a) from A is passed down multiple generations with a 50% chance of inheritance (representing the contributions of genes from only one of the parents), whereas allele b cannot be passed down this lineage because it was not inherited by the recruited individual in generation 1. Lineage survival is a binary trait where a founding lineage either survives to a point of sampling (1, as A), or not (0, as B). De-lifed fitness estimates the influence of an individual on population growth at the annual scale but can also be summed to an accumulative lifetime metric. It is calculated by removing (de-lifing) individuals at each time step (t1-6), as well as any of the offspring, and re-calculating population growth without their influence. This approach takes the realized, retrospective population growth over time and quantifies the contribution of each individual to the population structure (Coulson et al 2005). For example (simplified above) removing individual C would also remove three subsequent generations of sparrows from the pedigree, whereas the removal of D would have no consequence for the structure of the population over time. Should D recruit offspring in future (at t2-6), their de-lifed fitness may increase.

The Evolution of Social Behaviour

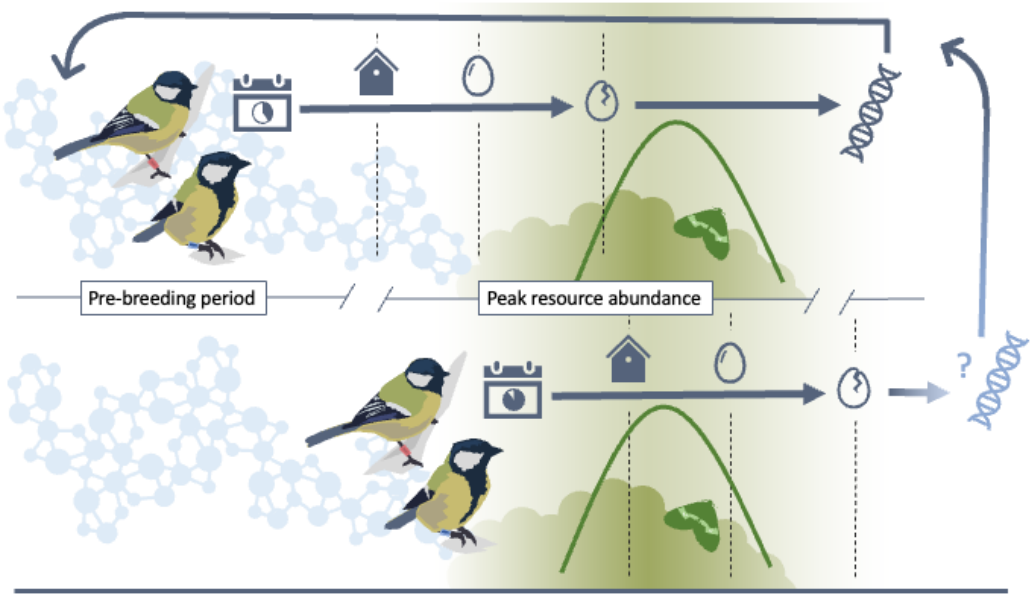
Understanding the consequences of a behaviour and the costs and benefits experienced by an individual due to its expression is critical to understanding its evolution. That is, where there is a benefit to an individual's survival or reproductive success, that individual will likely pass on genes to the next generation, driving selection. Likewise, costs to survival or reproductive success prevent genes from being passed on, suppressing behavioural expression. Although linked, the consequences of aggregation differ from those of social association, so separating the two is essential for research into the evolution of animal social behaviour (Webber et al. 2022). For example, in many gregarious animals, the dilution of predation risk is an important driver of group behaviour (Krause and Ruxton 2002). The *many-eyes* (Pulliam 1973; Roberts 1996) and *selfish herd* (Hamilton 1971; Vine 1971) hypotheses suggest that predation risk is diluted by increasing group size, through reduced odds of predation and coordinated vigilance (Hamilton 1971; Foster and Treherne 1981). These principles are demonstrated across the animal kingdom, including in flocking birds (Cresswell 1993, 1994; McBlain, Jones, and Shannon 2020). In these cases, the social association between aggregated individuals is likely inconsequential, where the derived benefit is a function of group size, and not the identity of its membership (but predator–prey interactions may also influence the structure of social networks (Voelkl, Firth, and Sheldon 2016), whereas, where the identity of a group's members is known, aggregation provides a mechanism for information transfer and the emergence of novel behaviour (Krause and Ruxton 2002 ; Dall et al. 2005; Aplin et al. 2012; Aplin, Farine, et al. 2015; Ling et al. 2019; Hillemann et al. 2020; Beck, Sheldon, and Firth 2023), and, importantly, facilitates the formation of social and reproductive bonds (Oh and Badyaev 2010; Beck, Farine, and Kempenaers 2020; Chapter 3). In these cases, groups (or subgroups of a larger group) may represent socially tolerant and socially associated individuals (Whitehead and Dufault 1999; Franks, Ruxton, and James 2010; Psorakis et al. 2015).

Unlike aggregation, the consequences of social association are likely to be influenced by the identity of others in the broader social environment, for example, where an individual's

behaviour is influenced by a social association with another (Firth and Sheldon 2016; Bebbington et al. 2017; Culina, Firth, and Hinde 2020, Box 3), or where group behaviours converge to exploit some environmental benefit (Milligan 2015; Culina, Firth, and Hinde 2020). Where social behaviour influences the spatial structure of a breeding population (Firth and Sheldon 2016; Bebbington et al. 2017), neighbours may reduce aggressive interactions towards those with whom they are affiliated, improving reproductive fitness (Bebbington et al. 2017); or, where individuals who form social bonds in the early pre-breeding period begin their breeding cycle earlier (Firth and Sheldon 2016; Culina, Firth, and Hinde 2020), and may be better placed to exploit variable resources that otherwise constrain reproductive fitness (McCleery et al. 2004; Chik et al. 2022, illustrated in Box 3). In both circumstances, benefits are only experienced when behaviours are plastic to the sociality of others, shaping reproductive decision making (Aplin et al. 2014, 2015; Firth et al. 2018).

Social network theory is widespread in behavioural ecology and has been applied broadly, for example, on the maintenance of group structures (Oh and Badyaev 2010; Albery et al. 2022), the transfer of information and the formation of culture in animal systems (Aplin et al. 2013; Aplin, Firth, et al. 2015; Farine et al. 2015; Firth, Sheldon, and Farine 2016; Dibnah et al. 2022; Beck, Sheldon, and Firth 2023), and the transmission of disease (Poiani and Wilks 2000; Hamede et al. 2009; Albery et al. 2021). However, more recently, network approaches increasingly seek to encompass the dynamism inherent to social behaviour, although the techniques used to measure the dynamic nature of social networks are in their infancy (Farine 2018; Silk 2023), the realization that social networks are dynamic—the result of a more complex interplay between life history and the environment—emphasizes the role of social factors in the evolution of animal behaviour. Furthermore, the application of social research to long-standing questions in ecology and evolution may provide new perspectives (Maldonado-Chaparro et al. 2018).

Box 3. Social association as a mechanism of selection.



The mechanisms by which an individual's social connections drive selection are complex and often linked with the wider social environment via indirect genetic effects. Indirect genetic effects relate to the expression of a phenotype in one individual, in response to the expression of a gene in another. For example, adapting behaviour in response to a reproductive partner - aligning social behaviour following a pair-bond (depicted above; Culina, Firth and Hinde, 2020), increasing mate-guarding or reducing parental care in response to extra-pair behaviour (Schroeder et al. 2016).

Culina, Firth and Hinde (2020) suggested that great tits *Parus major* that mediate their social preference within pairs, form pair bonds and initiate their breeding cycle earlier, than less socially labile individuals. This early breeding phenology may better align hatch dates with peak prey abundance (green curved line, depicting the distribution of winter moths over time, and breeding events, nest building, egg laying and egg hatch dates) giving socially labile individuals a reproductive advantage and driving selection on a social trait.

The influence of the social partner (or others in the wider social environment) is likely an overlooked mediator in behavioural expression. In this thesis, we similarly considered the influence of the social partner by including indirect genetic effects in quantitative models for female extra-pair behaviour (Chapter 4 – Indirect genetic effects improve female extra-pair heritability estimates).

Sociality and female extra-pair paternity

One such question is that of female extra-pair paternity (for a detailed review, see Maldonado-Chaparro et al. 2018). Extra-pair paternity was first demonstrated using DNA fingerprinting while assigning genetic parentage to a house sparrow *Passer domesticus* chick (Burke and Bruford 1987; also see Wetton and Parkin 1991), where the genetic father (or sire) was found to be different from the social father providing parental care. In the decades since, we now understand that extra-pair behaviours are common across birds (Petrie and Kempenaers 1998; Griffith, Owens, and Thuman 2002; Brouwer and Griffith 2019), and the evolutionary context of extra-pair behaviours continues to attract research attention (Kempenaers and Schlicht 2010).

Extra-pair behaviours are often described from either the male or female perspective because the evolutionary consequences are dependent on the sex of the individual. For example, evolutionary theory predicts that for males, who can sire many extra-pair offspring without investing in costly parental care, extra-pair paternity is beneficial (Trivers 1972; Lebigre, Arcese, and Reid 2013; Raj Pant et al. 2022); whereas, for females, whose reproductive output is limited by the number of eggs they can produce (Arnqvist and Kirkpatrick 2005; Forstmeier et al. 2014), extra-pair males must offer some additional benefit, either directly to the female or indirectly (to the survival of her offspring). However, empirical studies consistently fail to detect the benefits to extra-pair offspring required to support the indirect benefits (or, good genes) hypothesis, and instead often report costs to females who engage in extra-pair behaviour (Akçay and Roughgarden 2007; Schmoll et al. 2009; Sardell et al. 2012; Hsu et al. 2014, 2015; Arct, Drobniak, and Cichoń 2015; Grinkov et al. 2022). Despite this, and contrary to evolutionary theory, females actively solicit extra-pair copulations (Smith 1988; Lifjeld and Robertson 1992; Sheldon 1994; Forstmeier 2007; Girndt 2018).

Such misalignment between empirical research and theory has resulted in a return to non-adaptive hypotheses to explain why females engage in extra-pair behaviour (Halliday and Arnold 1987; Forstmeier et al. 2014). This non-adaptive hypothesis posits that

variation in female extra-pair behaviours is maintained through pleiotropic effects acting on two sets of linked genes. For example, female extra-pair behaviours may be genetically linked to another trait under positive selection, where the benefits of one behaviour outweigh the cost of the other. The expression of female extra-pair behaviours may then be the derived from behaviours beneficial to either male extra-pair behaviour (intersexual pleiotropy) (Halliday and Arnold 1987; Reid and Wolak 2018; Forstmeier et al. 2014), or female fecundity (intrasexual pleiotropy) (Wang et al. 2020). Although male extra-pair paternity is clearly beneficial (Albrecht et al. 2009; Webster et al. 2007; Raj Pant et al. 2022), any empirical test of intersexual pleiotropy must also demonstrate that extra-pair behaviour is heritable and positively genetically correlated between sexes (Reid et al. 2011). As a result, empirical examples of intersexual pleiotropic effects are scarce (Zietsch et al. 2015; Wang et al. 2020; Reid and Wolak 2018). However, few studies have included variables for male social behaviour or the broader social environment (see Chapter 4), which has been demonstrated to improve heritable variations in parental care behaviour (Schroeder et al. 2013).

Until recently, the social environment has scarcely been considered in the question of female extra-pair behaviour (Maldonado-Chaparro et al. 2018). However, early hypotheses assumed that social behaviour should serve a function. For example, where breeding is synchronized, males must engage in mate guarding, reducing the opportunity for extra-pair copulation (Stutchbury and Morton 1995), or where breeding density is high and extra-pair copulations increase as a function of proximity (Westneat and Sherman 1997). Contemporary works have also explored extra-pair behaviour as opportunistic (Fossøy, Johnsen, and Lifjeld 2006; Brommer et al. 2007, 2010), but much like the breeding synchrony and density hypotheses that explain the influence of the encounter rate between potential extra-pair partners, they do not suggest an evolutionary mechanism. Early applications of social network theory to the question of female extra-pair paternity (following Maldonado-Chaparro et al. 2018) have provided insights, mostly related to bond strength and reproductive behaviours (Beck, Farine, and Kempenaers 2020; Beck, Valcu, and Kempenaers 2020; Wang et al. 2020), but the field of study is still in its infancy.

The Lundy Sparrow System

Throughout the research chapters (Chapters 2 – 5) of this thesis, we used a closed study system of house sparrow that live and breed on Lundy Island (51.11N, 4.40W), with no movement on or off the island beyond exceptionally rare vagrancy. This population has been intensely studied using colour rings to track individual life histories since 1991 when the first 80 nest boxes were erected. The first genetic assignment of parentage and the first genetic proof of extra-pair paternity in a bird was a house sparrow chick (Burke and Bruford 1987; also see Wetton and Parkin 1991) and this method has become central to the Lundy study. Following a crash in the native population in 1996-1997, 49 sparrows were released onto Lundy (from Sheffield, UK) in 2001 and we have maintained a complete genetic pedigree of all sparrows breeding on Lundy since, making this system well-suited to studies in behavioural genetics (Davis and Jones 2007; Schroeder et al. 2015, 2016). Lundy has no native predators of house sparrow, beyond migrant sparrowhawk *Accipiter nisus,* none of which remain to breed on the island. There is however likely some inter-specific competition with starling for 'wild' (non-nest box) nest cavities, but almost all sparrows on Lundy use nest boxes that are inaccessible to starling.

Nest boxes on Lundy are arranged into loose neighbourhoods broadly associated with farm or village infrastructure. We checked boxes every three days during the core breeding period (April – July). Once we located an active nest, we confirmed the colour rings of both social parents. On day two and seven all chicks in the nest are blood sampled to assign genetic parentage (and later inclusion in the genetic pedigree; Dawson et al. 2012). We metal-ringed and colour-marked chicks by day twelve, before which they are identified by clipped toenails.

The ecology of house sparrows also make them a useful study system for behavioural ecologists (Andersson 2006). House sparrows are locally territorial of nest sites but breed in lose, non-cooperative colonies. On Lundy, house sparrows have 2 to 3 broods (mean 2.3 as of 2022) of 4 or 5 eggs each per breeding season (Westneat et al. 2014). Between

2001 - 2022, the mean hatchlings per female was 7.4, the mean genetic (non-extra pair) fledglings is 3.1 and each female recruited a mean of 1 offspring into the breeding population per year. Although they are socially monogamous, almost 25% of nests contain extra-pair offspring (Schroeder et al. 2016; Box 4). The sex ratio is broadly stable, and the mean lifespan of recruits is three years (Alif et al. 2022).

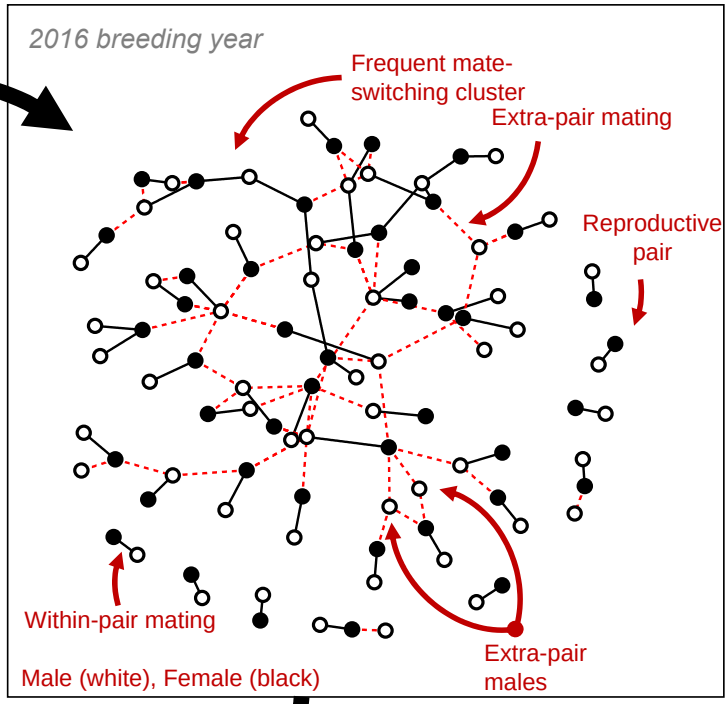
Outside of the breeding period they are gregarious and form large flocks in search of food and communal roost sites (Summer-Smith 1954; 1963). We also caught fully grown sparrows at roosts over winter to colour mark and sample the minority of birds which were not monitored in nest boxes during the breeding period.

Box 4. The Lundy sparrow system

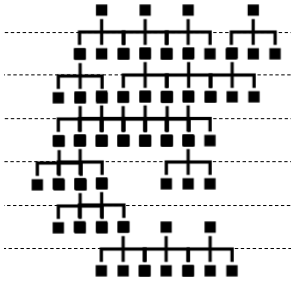
Fieldwork

House sparrows have been intensively studied on Lundy Island since 2000. The sparrows breed in nest boxes that are checked every other day during the breeding period. Most birds are ringed at the nest box, or using mist nets. Once captured each sparrow is fitted with a unique sequence of coloured leg rings to enable identification in the field. Then, tissue samples are taken at chick days 2 and 7 and when recaptured as adults. These samples are used to allocate offspring paternity, using ~23 microsatellite loci. Sparrows on Lundy have a mean 7.4 hatchings over 2.3 broods per year, and 0.2 are sired by a male outside of the established pair bond.

These annual data are then used to construct a genetic pedigree encompassing the entire sedentary population since 2000.



Genetic pedigree



The combination of the closed population (lack of immigration/emigration), intensive year-on-year monitoring, and the long-running genetic pedigree mean that the Lundy system is well-placed for longitudinal studies on the evolution of behaviour and empirical demonstrations of theoretical hypotheses.

Thesis outline and aims.

The broad theme of this thesis is the influence of social behaviour on life history, including female extra-pair behaviour, and the research chapters were designed to address specific questions associated with this theme. We used the long-running study of house sparrows on Lundy Island and a 20-year genetic pedigree to test hypotheses from the arguments presented above (Box 4).

Each of the four research chapters is presented as an independent study designed to address a set of research objects outlined below (also see Box 5). Aims 1 and 2 relate to social networks and the fitness consequences of individual sociality, whereas Aims 3 and 4 relate to how social behaviour can be applied to female extra-pair behaviour.

Aim 1: Test the suitability of existing definitions for social associations between animals and their influence on the structure of a social network (Chapter 2).

- Objective 1: Review how social associations are defined between animals (specifically birds).
- Objective 2: Introduce arrival networks to define social associations in gregarious systems.
- Objective 3: Define how the definition of association influences the structure of social networks across social study systems.

Aim 2: Test the link between social traits and fitness at the annual and lifetime scales (Chapter 3)

- Objective 1: Build non-breeding social networks using an appropriate definition of association.
- Objective 2: Define and extract meaningful measures of fitness (Box 2) for sparrows involved in social networks.
- Objective 3: Test the link between social traits, each representing a different aspect of social behaviour, with fitness over the short- and long-term.

Aim 3: Apply concepts from Chapters 2 and 3 to test whether the inclusion of the social environment in quantitative behaviour models improves heritability for female extra-pair behaviour (Chapter 4)

- Objective 1: Introduce the problem of female extra-pair paternity, and some of the hypotheses suggested to explain the behaviour in birds.
- Objective 2: Use quantitative genetic models to demonstrate how the social environment and partners' social preferences (lumped together as indirect genetic effects) improve heritable variance for the trait.

Aim 4: Building on Aim 3, identify empirical evidence for a pleiotropic driver of female extra-pair behaviour (traits beneficial to female fecundity, linked to extra-pair solicitation, Chapter 5)

- Objective 1: Describe the prevalence of extra-pair behaviour within the Lundy sparrow system.
- Objective 2: Define a trait as representative of female fecundity (social mate-switching – divorce).
- Objective 3: Test for a correlation between social mate switching and extra-pair partners and offspring.

Box 5. Thesis structure with key findings from research chapters.

Animal social networks and female extra-pair paternity.

How do we define social associations in aggregations of gregarious foraging birds?

Chapter 2 – Comparing animal social network structures using different definitions of association.

Finding – Social network structure is broadly robust to changing the definition of a social association. However small differences are explained by inappropriate definitions in the context of system biology.

What is driving variation in individual social preference – what are the consequences for individual fitness?

Chapter 3 – Opposite-sex associations are linked with annual fitness, but sociality is stable over lifetime

Finding – Selection on individual sociality is stable over a lifetime, but the number of opposite-sex associates is correlated with annual fitness benefits.

Can the inclusion of the social environment (an indirect genetic effect on individual behaviour) explain the long-standing question of female extra-pair paternity?

Chapter 4 – Indirect genetic effects improve female extra-pair heritability estimates

Finding – The inclusion of indirect genetic effects (that encompasses the social environment and partners' social preferences) improved heritable variation in extra-pair paternity models.

Is there empirical support for intersexual pleiotropy as a driver of female extra-pair paternity – is EPP linked to female fecundity?

Chapter 5 – Divorce is linked with extra-pair behaviour in a monogamous passerine

Finding – Females who switched social partners often (a trait beneficial to female fecundity) also engaged more extra-pair partners but did not have a greater proportion of EPP than monogamous females.

Chapter 2

Comparing Animal Social Network Structures Using Different Definitions of Association

Publication statement: A version of this chapter has been submitted for publication at the time of writing (December 2023):
Alex Hoi Hang Chan, Jamie Dunning, Kristina B. Beck, Terry Burke, Heung Ying Janet Chik, Daniel Dunleavy, Tim Evans, André Ferreira, Babette Fourie, Simon C. Griffith, Friederike Hillemann, and Julia Schroeder. 2023. Comparing animal social network structures using different definitions of association. **[Submitted]**.
(Joint first authorship)

Author contributions: JD conceived and prepared this chapter and the associated submitted publication and contributed to all aspects. AHHC prepared the code to build arrival networks and intellectually contributed to the direction and preparation of this research, including the manuscript submitted for publication; KB, HYJC, DD, AF, BF SCG, FH contributed data from other RFID systems, technical input on analyses and contributed a draft manuscript; TB, TE and JS provided supervision and commented on a draft manuscript.

Abstract: The interconnecting links (edges) between individuals (nodes) of an animal's social network are often defined by discrete, directed behaviours (interactions). However, where interactions are difficult to observe, a network edge is often defined instead as individuals sharing space or overlapping in time (an association). The precise definition of an association depends on the ecology of the study system, design, and research question. Yet, despite an increasingly accessible toolkit to assemble and analyse animal social networks, defining associations remains a challenge in behavioural ecology. Here, we apply three methods of defining social associations, by 1) time window, 2) co-occurrence in a group, and 3) arrival time, to four avian systems. We describe how each method alters the structure of the resulting social network. First, we test the ability of each method to detect individually repeatable social traits, then we describe the structure of each network using Jaccard similarity and Mantel tests, and finally, we test the sensitivity of the network structure to changing parameters within the three definitions. Network structure was robust to changing how associations were defined but did result in subtle differences. We suggest that these differences are the result of an inappropriate definition of association in the context of experimental design and system ecology.

Background

Individual sociality—one's propensity to socialise with others—has important consequences for animal life history and evolutionary processes (Wey et al. 2008; Maldonado-Chaparro et al. 2018). For example, more sociable individuals may have increased survival or reproductive success (Silk et al. 2009; Oh and Badyaev 2010; Stanton and Mann 2012; Maldonado-Chaparro et al. 2018; Chapter 3) or better access to resources (Aplin et al. 2012) than less sociable individuals. These links have now been demonstrated across several natural systems (e.g., in birds: Covas et al. 2006; McDonald 2007; Oh and Badyaev 2010; Firth, Sheldon, and Farine 2016, and mammals: reviewed in Silk 2007), commonly using social network analysis to capture the social connections between animals (Croft, James, and Krause 2008; Way et al. 2008). Likewise, social network structure also has implications for other biological processes (Kurvers et al. 2014), e.g. disease transmission (Keeling and Eames 2005; Albery et al. 2020; Albery et al. 2021) or selection (McDonald et al. 2013; Kurvers et al. 2014).

Despite wide research interest, the terminology used to describe animal social behaviour varies between studies. Throughout this manuscript, we will use *association* to refer to any link or connection between animals inferred from an overlap of two individuals in space and time (Croft, James and Krause 2008; Wey et al. 2008). The properties of an association may vary (e.g., in their intentionality, intensity, and duration), and associations may be the outcome of similar spatial preference or coincidence (social or non-social; Webber et al. 2022). For example, moths gathering around a lamp on a summer evening are likely not intending to socialize (Tinbergen 1952). Likewise, mixed-species groups aggregating around some resource (e.g., waterhole) are not socializing between species, but exploiting the same resource at the same time (Hinde 1952; Morse 1970, but also see Goodale, Beauchamp, and Ruxton 2017, for further discussion). We refer to these non-social associations as *aggregations* throughout the manuscript (Krause and Ruxton 2002). Researchers of animal behaviour and related fields often refer to social associations (defined above) as *relationships*, where individuals repeatedly associate,

maintaining some form of social bond (Croft, James, and Krause 2008; Franks, Ruxton, and James 2010; Ostner and Schülke 2014; Gomes et al. 2021). Socially related individuals are identified through their interactions with one another, and so relationships can be inferred by recording relevant behaviours. Subsequent networks are built by linking interacting, and therefore related, individuals. However, where interactions are difficult to observe (for example, in passerine birds; Iserbyt et al. 2018), associations—an overlap in time and space—are used as a proxy for relationships otherwise based on observed behaviours. Thus, throughout this manuscript, we use association in its social context, distinct from aggregation. However, separating association from aggregation in this context remains a challenge.

The importance of separating association from aggregation is dependent on the research question; for example, in some cases, group sizes are more important than the strength and identity of the associations, as in the case of diluting predation risk (e.g. Cresswell 1994; Krause and Ruxton 2002; Sorato et al. 2012; Voelkl, Firth, and Sheldon 2016), whereas for other questions, e.g., mate choice, fitness consequences are dependent on the identity of associating individuals (Oh and Badyaev 2010; Beck, Farine, and Kempenaers 2021; Chapter 3). Similarly, the identity of associates may be important for understanding the path of information transmission through a network (Krause and Ruxton 2002; Wascher et al. 2015).

Several methods have been used to define associations between individual animals without directly observed interactions, e.g., using a static antenna or WiFi networks to detect animals equipped with GPS tags or proximity loggers (Ripperger et al. 2020; Ripperger and Carter 2021; He et al. 2022; Wild et al. 2023). However, in small birds (Aplin et al. 2012; Sánchez-Tójar et al. 2017) and mammals (Godsall, Coulson, and Malo 2014; Evans, Lindholm, and König 2021; Raulo et al. 2021) that feed and shelter communally, networks are commonly constructed by recording the identity of Passive Integrated Transponder (PIT)-tagged animals visiting a static Radio Frequency Identification (RFID) antenna at a feeder or shelter (Ringsby et al. 2009; Mariette et al. 2011; Farine 2017A; Sánchez-Tójar et al. 2017; Bandivadekar et al. 2018; Firth et al.

2018; Broughton, Maziarz, and Hinsley 2019; Hillemann et al. 2020). This approach does not measure interactions explicitly but instead a data stream of temporal individual presence/absence at one location, from which associations can be inferred. In some cases, additional information can also be inferred from the strategic placement of the antenna; for example, at a breeding site, associated individuals likely have the intention to associate with each other in a reproductive or family context (Sánchez-Tójar et al. 2017; Firth et al. 2018; Iserbyt et al. 2018).

Recent methodological advances include published algorithms, guidelines, and software to quantify social associations from such temporal data streams (Farine 2017A; Iserbyt et al. 2018; Bridge et al. 2019; Youngblood 2019; Hart et al. 2021; Hart, Franks, and Brent 2022). Most of these advances commonly seek to define social associations among small mammals or passerine birds through membership of discrete social groups, known as the gambit of the group method (Whitehead and Dufault 1999; Franks, Ruxton, and James 2010). This assumes that individuals who overlap in space and time interact with one another and are thus assumed to be socially associated. Most definitions of an association follow this in principle, but the method by which group membership, and therefore the associations, are defined, varies. For example, associations have been defined between PIT-tagged house sparrows *Passer domesticus* foraging at the same RFID feeder within three seconds of each other (Plaza et al. 2019), sociable weavers *Philetairus socius* feeding together at a communal bird feeder (Ferreira et al. 2020), and flamingos *Phoenicopterus sp.* standing within one neck length of each other at the same time (McCully and Rose 2023). Thus, the definition of a social association varies depending on the definition of a meaningful spatiotemporal overlap. This poses a methodological challenge to behavioural ecologists interested in measuring animal social behaviour (Carter, Lee, and Marshall 2015), because different definitions for association have the potential to alter the structure of social networks (for discussion, see Castles et al. 2014; Farine 2015; Farine and Whitehead 2015). Some studies have used randomizations (Farine 2014, 2017) or observations to validate association definitions (Farine 2014; Boogert, Farine, and Spencer 2014), for example, when demography or

familial ties inform social structures (Haddadi et al. 2011; Davis, Crofoot, and Farine et al. 2018; Ferreira et al. 2020; Gomes et al. 2021). However, where this is not possible, an association must be defined, considering the context of the study species and the observed behaviour, and distinguishing intentional association from aggregation presents a specific challenge (Croft et al. 2008; 2011; Gomes et al. 2021).

When using the gambit of the group method, group membership and thus social associations between individuals also depend on the method by which groups are defined. A common approach is to define a *time window* (**Δ**t; Figure 2.1Aa) within which all individuals co-occurring at the same location within a given period (e.g. consecutive detections at a bird feeder) are defined as socially associating (hereafter association defined by time window). If the time window is too short, individuals that are socially associated may not be detected as belonging to the same group, yet, if the time window is too long, there is a risk of generating false associations between aggregating individuals (Croft, James, and Krause 2008; Psorakis et al. 2015). To solve this problem, an alternative approach was developed. Here, discrete grouping events are identified, typically using a Gaussian mixture model (GMM; Psorakis et al. 2012, 2015, hereafter, association defined by GMM; Figure 2.1Ab). This GMM approach considers dynamically changing time windows determined based on periods of increased activity in the presence/absence temporal data stream (Psorakis et al. 2012) in an automatic manner. This approach to identifying group membership was developed for the blue tit *Cyanistes caeruleus* and great tit *Parus major* study systems in Wytham Woods, Oxford, UK. The publication of the associated R package “asnipe” (Farine 2013; Farine 2017A; R Core Team 2023) led to its use across many avian systems (for examples, see Madsen, Vander Meiden and Shizuka 2021; Moyers et al. 2018; Broughton, Maziarz, and Hinsley 2019; Evans and Morand-Ferron 2019; Whiteside et al. 2019; Taff, Zimmer and Vitousek 2019; Brandl et al. 2021; Beltrão, Gomes and Cardoso 2022), and non-avian systems (Findlay et al. 2016; Poirier and Festa-Bianchet 2018; Zeus, Reusch and Kerth 2018; Skinner and Miller 2020).

However, the biological validity of the associations extracted using the GMM approach heavily depends on the biology and experimental design of the species and study system. For example, great tits form small fission–fusion flocks of loose social groups over the non-breeding season. In contrast, house sparrows form very large nomadic, gregarious flocks over the non-breeding period with loose group-level social preferences (Tóth et al. 2009; Havlíček, Riegert, and Fuchs 2022; Chapter 3). In gregarious systems like sparrows, the power of the commonly used GMM approach, or the fixed time windows, may not be appropriate because groups of foraging flocks cannot be easily identified (Chapter 3). Likewise, Ferreita et al. (2020) found that physical proximity based on the proportion of time two individuals spend on the same feeder best identified groups in gregarious flocks of sociable weavers, compared to the GMM approach. An alternative definition based on the differences in individual arrival time to a feeder (hereafter Arrival time; Chapter 3; Chan and Dunning 2023; Figure 2.1Ac) may be more appropriate to define associations in highly gregarious species, especially where a limited number of locations are available for observation (e.g., only one RFID feeder). A definition for associations based on arrival time assumes that individuals who are strongly associated are more likely to arrive together at a resource than those who are not because it is likely that they also associate with each other at locations where they cannot be observed (Atton et al. 2012; Hilleman et al. 2020). This arrival time definition requires researchers to define arbitrary thresholds to filter out random aggregations.

Here, we describe how different definitions of associations affect the structure of social networks. We used four avian study systems (two house sparrow populations, one great tit population, and one sociable weaver population) that collect data via PIT tags and RFID reader antennas, each with different ecologies and experimental designs. We compare the robustness of global social networks and individual network metrics, using three association definitions (time window, GMM, and arrival time). First, we compared the repeatability of individual social network metrics between definitions. Individual social network metrics can be used as an aspect of an individual's animal personality (Bell, Hankison, and Laskowski 2009; Aplin et al. 2015; Hillemann et al. 2019; Tkaczynski et al.

2020; Proops et al. 2021) and are expected to be, to some extent, consistent within individuals over time. Next, we describe the similarities of the global social networks built using these three association definitions. Finally, we demonstrate the sensitivity of the parametrisation of the definitions of the network structure. Our results will assist behavioural ecologists in making methodological choices for animal social behavioural studies.

Materials and methods

Systems

We built social networks from RFID data, collected from wild birds at four study systems: two house sparrow populations, at Broken Hill, Australia, and Lundy Island, UK; one sociable weaver population at Benfontein Nature Reserve, South Africa; and a great tit population at Wytham Woods, UK. In each, we captured birds using mist nets, or at nest boxes, and fitted each bird with a PIT tag and an individually coded metal ring. In all four systems, RFID antennas were mounted at a bird feeder, but otherwise system ecology and experimental design varied:

1) House sparrows on Lundy Island, Devon, UK (51.11 N, 4.40 W): We collected RFID data between November 2015 and January 2016 from the long-term study of house sparrows on Lundy Island where they breed and winter around a small village on the island's southern end. House sparrows are socially monogamous and territorial during the breeding season, nesting in cavities and often in loose colonies. During the non-breeding period, house sparrows form gregarious flocks, and often aggregate around food sources (Havlíček, Riegert, and Fuchs 2022). On Lundy, we caught > 95% of the house sparrow population (Simons et al. 2015) and fitted subcutaneous PIT tags, which did not affect fitness (Schroeder et al. 2011). Individuals were recorded visiting a single, 7.8" x 7.8" RFID antenna (DorsetID, Netherlands) mounted below a large seed reservoir and positioned centrally in the study system (Figure 2.1Ba) within the home range of all sparrows in the population. Several sparrows can access the feeder at the same time. PIT tags were read approximately every 0.25 seconds. The RFID system was active when power was available between 6:00 and 00:35 daily (Schroeder et al. 2012).

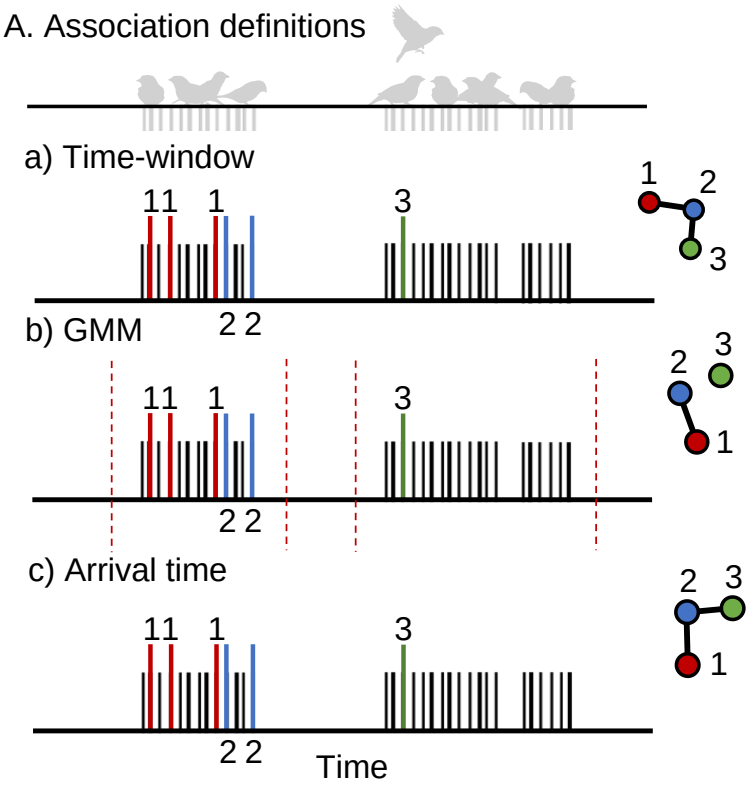
2) House sparrows at Broken Hill, New South Wales, Australia (31.57S, 141.27E): We used data from house sparrows visiting one RFID feeding station throughout the non-breeding period in July and August 2022 in Broken Hill, a town of around

1,900 hectares. The ecology of the house sparrows here is broadly like those on Lundy Island. A single feeding station had an RFID antenna fitted around an entrance hole (Priority 1 RFID, Melbourne, Australia) that led to a feeding chamber inside a metal net cage (Figure 2.1Bb). This feeder was in the home range of only a small proportion of the Broken Hill sparrow population of approximately 19,000 individuals, of which less than 2% were tagged. Sparrows were implanted with subcutaneous PIT tags (Micro Products Australia Mini Microchips, 1.4 × 8.5 mm, 0.52 g) and were recorded when they entered and exited the feeding chamber. PIT tags were read approximately every 0.5 seconds.

3) Great tits in Wytham Woods, Oxfordshire, UK (51.46 N, 01.20 W): We used data collected between December 2011 and February 2012 from eight feeders at the northern extent (the Great Woods) of Wytham Woods, a largely broadleaf deciduous woodland surrounded by open arable farmland. Pairs of great tits establish territories during the breeding season, but this territoriality breaks down during the autumn and winter when birds form loose fission–fusion flocks with unrelated individuals that forage together (Hinde 1952; Ekman 1989). The bird feeders had two access ports, both fitted with an RFID antenna (Dorset ID, Netherlands, Figure 2.1Bc). The feeders were operational every week, from pre-dawn Saturday morning until after dusk on Sunday evening, and PIT tags were read approximately every 0.25 seconds. A PIT tag enclosed in a plastic ring was fitted to 90% of breeding great tits (Aplin et al. 2013).

4) Sociable weavers in Benfontein Nature Reserve, Northern Cape, South Africa (28.51S, 2.46E): Sociable weavers are highly social, colonial nesting passerines endemic to southern Africa. They form large gregarious foraging flocks composed of colony members all year round (Ferreira et al. 2020). We collected social data at two feeder boxes placed next to each other on the ground (Figure 2.1Bd) between December 2017 and February 2018. Each feeder box had four perches, each with an attached RFID antenna (Priority 1 RFID, Melbourne, Australia) over

four feeding trays. Although this setup allowed only one bird to access a feeding tray at once, four birds could feed at adjacent perches at the same time. All captured weavers were fitted with a PIT tag mounted to a plastic leg ring. The PIT tags were read approximately every 0.5 seconds.


A. Association definitions
a) Time-window
11 1
3
2 2
1
2
3
b) GMM
11 1
3
2 2
2
3
1
c) Arrival time
11 1
3
2 2
2
3
1
Time

B. RFID systems
a
b
c
d

Figure 2.1A. Three association definitions applied to Radio Frequency Identification (RFID) data streams. Black lines denote individuals visiting a feeder where three are highlighted (1, 2, and 3), representing tagged individuals. The time window definition (Aa) is where individuals are considered associating when they overlap in space within (**Δ**t) of each other, illustrated with a transparent buffer zone. In this case, individuals 1 and 2 as well as 2 and 3 are associated. The GMM (Ab) definition identifies the start and the end of gathering events, denoted here with red dotted lines. In this instance, 1 and 2 are connected, whereas 3 is not connected to either. Arrival time (Ac) defines an association in which individuals overlap by **Δ**t of their arrival (first detection) at the RFID antenna. An individual can only be recorded as arriving again after a period of absence, defined by **Δ**i. In this case, the network would be identical to that of the time window, where 1 and 2 and 2 and 3 are connected.

Figure 2.1B. **Radio Frequency Identification (RFID) experimental setup in four wild systems**: a) Single, open RFID antenna mounted below a large feed reservoir on Lundy Island, Devon, UK; b) RFID antenna at the entrance to an open feeding chamber (the wire prevents access by larger species) at Broken Hill, New South Wales, Australia; c) Great reservoir tit *Parus major* interacting with one of two RFID antennas mounted in front of the access hole to a sunflower seed feeder at Wytham Woods, Oxfordshire, UK; d) Sociable weaver visiting four RFID antenna mounted over four separate seed reservoirs at Benfontein Nature Reserve, Northern Cape, South Africa.

Social network construction using different association definitions.

We built three networks for the four study systems, one for each association definition (Figure 2.1A), an association based on the time window definition (Figure 2.1Aa), the GMM definition (Psorakis et al. 2012, 2015; Farine 2017; Figure 1Ab), and the arrival time definition (Chapter 3; Figure 2.1Ac). Each network was weighted, where multiple associations between dyads were scaled using the simple ratio index (Farine and Whitehead, 2015) and undirected (associations did not represent directed interactions), using R (R Core Team 2023). We applied the following methods and general parameters between systems:

1) Time window (Figure 2.1Aa): We used R (R Core Team, 2023) to build time window networks. This approach has a single overlap parameter (**Δ**t), where any two individuals visiting a feeder within **Δ**t of each other are defined as associates. We defined **Δ**t as one second across all four systems, which captured absolute physical and temporal proximity at the feeder (see, e.g., McCully, and Rose 2023; Farine 2015).

2) GMM (Figure 2.1Ab): We used the asnipe R package (Farine 2013; Farine 2017 A) to detect associations using GMM. This package requires no set parameters—only information on the ID, time, and location of individual visits. The GMM function detects the start and end points of gathering events and links all individuals within each distinct event as associates (Psorakis et al. 2012; 2015). We used this function across all four systems but combined the date and location parameters within each system into a unique location parameter to reduce processing times and memory requirements (Farine 2017A).

3) Arrival time (Figure 2.1Ac): We built arrival networks using a series of custom functions, available on an online repository (Chan and Dunning 2023). We defined two parameters for the arrival time associations: 1) A time overlap to define two or more birds arriving and recorded at the RFID antenna for the first time (**Δ**t). 2) A

period of inactivity, after which a bird is considered to have left the feeder (**Δ**i). That is, only birds which are recorded for the first time within **Δ**t of each other are considered associates, regardless of how long they then spend at the feeder. Birds can only be first recorded again after a period of absence defined by **Δ**i. We defined these parameters for all four systems the same: **Δ**t as 150 seconds, which we considered was long enough to record the arrival time of a group of birds to each interact with the RFID antenna across systems. We defined **Δ**i as 300 seconds. Multiple feeders (in this case, only Benfontein and Wytham) were treated separately and then combined to calculate edge weights within the same algorithm.

We used the iGraph package in R (Csardi and Nepusz 2006; R Core Team 2023) to extract three node-based network measures from the three association datasets for each of the four systems: degree, the number of unique associates connected to a focal individual; strength, the total number of associations between a focal individual and all associates; and betweenness, the number of geodesics (shortest paths between any focal dyad of nodes within the network) that pass through a focal individual. We removed all individuals from networks who had a degree of 0 across the recording period – those that were not associated with any other individuals in the network. Consequently, the number of individual vertices in each did not represent the number of individual birds recorded.

Analysis

Within-system comparisons in the social network structure

We used three definitions to compare each association approach within the four study systems. First, we estimated the repeatability of social traits. Second, we examined how association definitions alter the structure of social networks within systems, using Jaccard similarity indices. Third, within the arrival definition, we explored how parameterisation affected the network structure. Therefore, we computed repeatability and similarity indices with varying **Δ**t.

a) Repeatability of social traits

We first constructed sub-graphs representing a whole week across each recording period for each of our four systems: 9 weeks at Broken Hill, Australia, 14 weeks on Lundy Island (see Chapter 3), 13 weeks at Benfontein Nature Reserve, South Africa, and 14 weeks at Wytham Woods (see Aplin et al. 2015). We extracted three network measures from each subgraph for each week and then z-transformed to normalise the measures due to differences in network structure across weeks. In all cases, we removed individuals with a degree of 0 (no associations) because they could not contribute to the network structure. We calculated repeatability using repeated measures among weeks for individual birds within each system and the association definition.

We ran repeatability models using the R package MCMCglmm (Hadfield 2010; R Core Team 2023), using package default model parameters and priors. We modelled each social trait as a response variable against the model intercept and with BirdID as a random effect. Repeatability was then defined as the variance explained by individual ID over the total variance (Nakagawa and Schielzeth 2010). We interpreted repeatability in the context of three levels, low (< 0.3), medium (< 0.5) and high (> 0.5; following Bell, Hankison, and Laskowski 2009; Winney et al. 2018); however, we also considered credible intervals for our interpretation.

b) Similarity in network structures

We first described the cardinality of each network for each association definition, that is, the number of individuals (Vertices; V), and the number of associations (Edges, E) detected by each system, as well as the network density (D). The density of a network is defined by the number of observed edges (in this case associations) over the maximum potential edges in each network (assuming every possible dyad represents an association). Then, we used four Jaccard similarity indices to compare global network structures between association definitions but within systems. We compared the three possible network pairs: GMM – time window; GMM – arrival time; and time window – arrival time. We used four comparisons to describe aspects of network structure, from the multinet R package (Magnani, Rossi, and Vega 2021), following Bródka et al. (2018); but also see Emmert-Streib, Dehmer, and Shi (2016): 1) We used Jaccard actors to compare the identity of individuals detected by association definitions, where 1 indicates that all of the individuals are identical between networks, and 0 indicates that neither shares an individual. 2) We used Jaccard edges to compare common edges where two individuals connected with each other in multiple networks. Here, 1 indicates that dyadic edge links are identical between networks, and 0 indicates that neither network shares a common edge. 3) We used Jaccard triangles as a measure of common clusters of individuals between networks. where 1 indicates that triads are identical between networks, and 0 where neither network shares a common triad of individuals. We describe Jaccard similarities using equivalent qualitative terms to repeatability analyses, namely, low similarity (< 0.3), medium (< 0.5) and high similarity (> 0.5) as arbitrary thresholds to aid interpretation. 4) We used Pearson's degree, a Pearson's correlation coefficient between the degree distribution of networks. Here, -1 indicates no correlation between the distribution of individual degrees between association definitions, and 1, indicating that networks are perfectly correlated.

Finally, we ran Mantel tests to account for edge weights (Mantel 1967; Croft, James, and Krause 2008) between networks within systems. Unlike Jaccard similarity measures, Mantel tests account for network edge weights by comparing the correlation of values

between two matrices. We extracted the weighted adjacency matrices for each network and computed the Mantel coefficient using the Pearson correlation method and 999 matrix permutations with the 'Vegan' R package (Dixon 2003). The results produce a correlation between network layers that varies between -1 and 1, with -1 and 1 representing matrices being negatively and positively correlated, respectively. The p-value and 95% confidence intervals were computed using the null distribution obtained by the permutations.

c) Sensitivity Analyses – Arrival time definition

Finally, we computed repeatability and network similarity measures again but varied the arrival **Δ**t parameter within each system for the arrival time definition. We maintained **Δ**i at 300 seconds, but varied **Δ**t**,** defining associations between birds arriving from within 1 second, to within 300 seconds of each other. For each **Δ**t interval (per second), we re-calculated the repeatability for three social traits, Jaccard similarities, and Mantel correlation coefficients. We compared these variable results with the GMM and time window networks. We did not do this for time window or GMM networks, since **Δ**t for time window networks were fixed at 1 second to replicate association by physical proximity, and associations defined by GMM automatically set parameters within the detection algorithm.

Network Permutations

To test whether our analyses could have yielded similar repeatability scores from randomised data, we also ran network permutations for each analysis (Farine 2017). We created 1,000 random networks for repeatability by shuffling individual IDs within each weekly subgraph, while maintaining network structure (Aplin et al., 2014; Farine 2017). We constructed a possible “null distribution” of repeatability scores from the randomised data, and calculated the proportion of randomised data that were more extreme than the observed estimate. The result is significant at p = 005 if fewer than 25% of the random values are greater than the observed value or if more than 97.5% of the random values are greater than the observed value.

For network comparisons, to randomise the link between social associates of birds in the population, we used an alternative permutation method by shuffling individual IDs in the edge list for each network 1,000 times with replacements, randomising the whole social network structure. For each network constructed by each approach for each study system, we computed the Jaccard comparison indices for each of the 1,000 random networks with the original network to obtain a distribution of comparisons with a random network.

Results

a) Repeatability of social traits

We found that three social traits, degree, strength, and betweenness, are repeatable in all four systems, with little variation between association definitions (Figure 2.2). All three definitions displayed low repeatability in the Lundy systems; low to moderate repeatability in the Wytham system; and high repeatability for degree and strength, but low to moderate repeatability for betweenness in the Broken Hill and Benfontein systems. We found significantly lower repeatability of degree and strength in the Wytham system when associations were defined by the time window definition (Figure 2.2C). The arrival time and GMM definitions were performed equally across systems (Figure 2.2). All repeatability measures were statistically significant, except for betweenness in the GMM and arrival definition in Benfontein (Table 2.1).

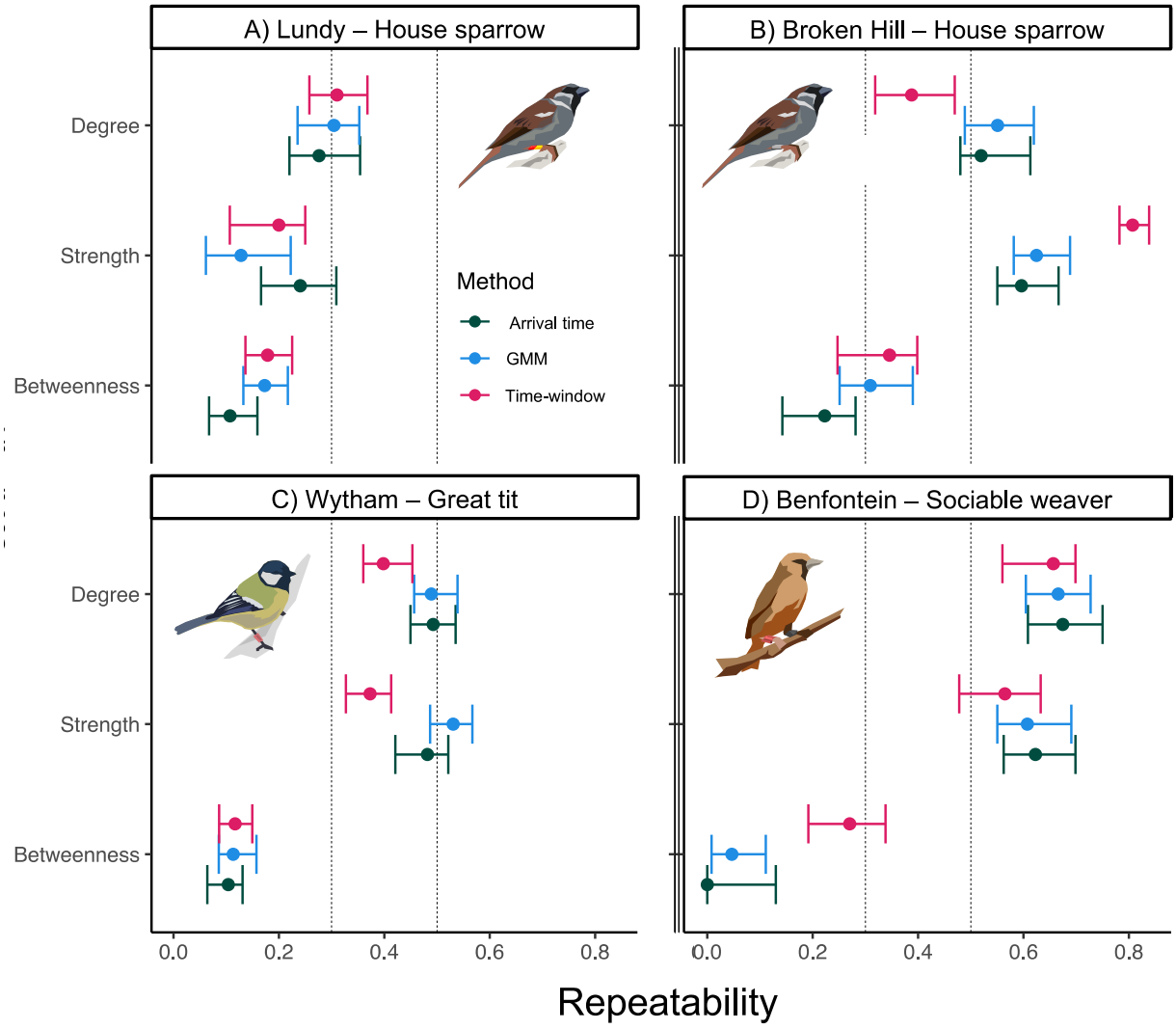


Figure 2.2. **Repeatability of social traits between association definitions**. Between-week repeatability for three individual social traits (Degree, Strength, and Betweenness centrality) across three association definitions (by colour) in four systems: A) 14 weeks of house sparrow data collected at Lundy Island, UK; B) 9 weeks of house sparrow data from Broken Hill, Australia; C) 14 weeks of great tits data from Wytham Woods, UK; and D) 13 weeks of sociable weaver data from Benfontein National Park, South Africa. Points denote the mean repeatability, and error bars denote the 95% credible intervals (CI). Dotted lines denote thresholds for low (< 0.3), medium (< 0.5) and high (> 0.5) repeatabilities (also see Table 2).

b) Similarity in network structures

We used two methods to compare network structures: Jaccard similarity indices and Mantel tests. We compared networks in three dyads: GMM/Time window; GMM/Arrival time; and Time window/Arrival time (Table 2). Our results suggest that network structures are robust to changing association definitions. However, where the number (vertices; cardinality V) and identity (Jaccard actors, range 0.86–1) of individuals detected are similar between network pairs, metrics to capture clustering (Jaccard triangles; 0.01–0.77), dyad identity (Edges, cardinality E), and associated edge weights (Mantel coefficient; 0.46–0.92) varied more. We found the highest similarity scores between the GMM and arrival time definitions (15 high/ 1 medium/ 0 low similarity scores), followed by GMM and time window definitions (11 high/ 2 medium/ 3 low similarity scores), then time window and arrival definitions (10 high/ 3 medium/ 3 low similarity scores). All definitions identified a similar number of individuals between networks within systems, but the number of edges differed. Specifically, networks based on time windows produced less dense networks, with fewer edges given the potential edge density. This was particularly true for Broken Hill, where house sparrows were only recorded individually entering and leaving a feeding chamber. Using the arrival time definition resulted in denser networks. All network comparisons were significantly different from comparisons with randomly generated networks (Table 2.2; Figure S2.1), suggesting that all comparison metrics were meaningful and did not arise due to random chance.

c) Sensitivity Analyses – Arrival Networks

Finally, we explored how altering the time parameter (**Δ**t) affected the network structure within the arrival time definition. Our results demonstrated that social traits have low repeatability with a low **Δ**t but with higher values, repeatability increased and then plateaued. The repeatability of betweenness was more sensitive to changes, especially in Broken Hill and Benfontein (Figure 2.3 – 2.4). We report a similar plateau in similarity between association methods, consistent across study systems. In general, the arrival definition produced networks more like the GMM definition, compared to the time window definition as the time parameter **Δ**t varied. Differences were consistent across study systems other than Broken Hill, where a low **Δ**t produced very similar networks to the time window definition.

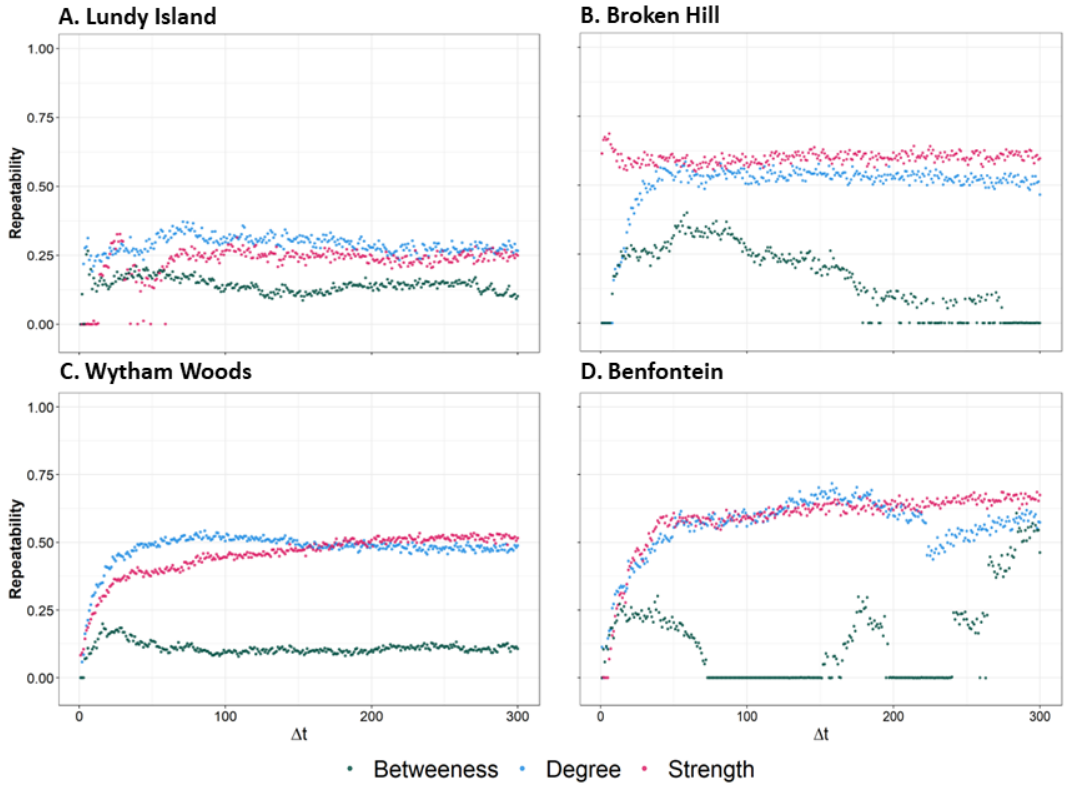


Figure 2.3. Sensitivity of association definitions. Sensitivity analysis of between-week repeatability of individual metrics for arrival networks with varying **Δ**t from 0 to 300 s, and fixed **Δ**I = 150 s, for four systems: A) House sparrow data in Lundy Island, UK; B) House sparrow data in Broken Hill, Australia; C) Great tits data in Wytham Woods, UK; D) Sociable weaver data in Benfontein Nature Reserve, South Africa. Arrival networks were built using RFID data across study systems, and repeatability was calculated for degree (number of edges per node; blue), strength (weighted degree; pink), and betweenness (number of shortest paths passing through a node; green).

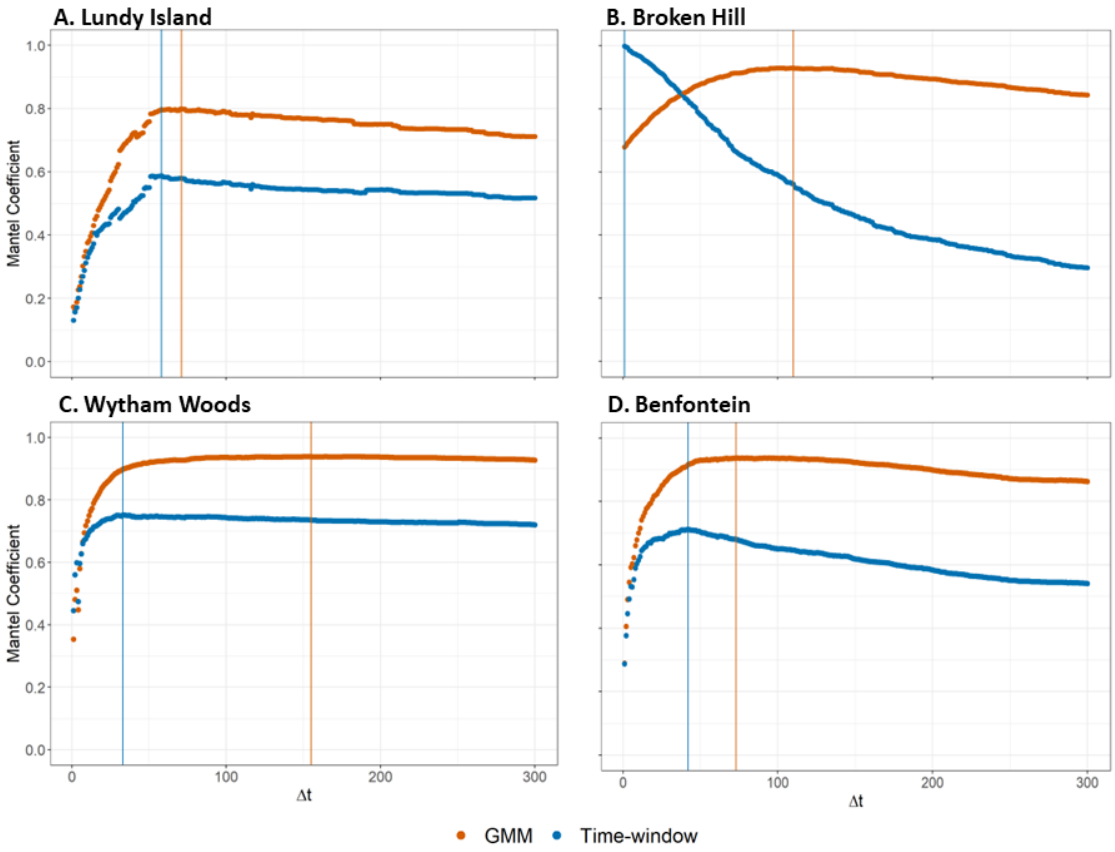


Figure 2.4. Sensitivity of arrival network parameters. Sensitivity analysis of the Mantel correlation coefficient of arrival networks with varying **Δ**t from 0 to 300 s, with fixed **Δ**I =150 s, for four systems. Mantel coefficients describe the similarity between two networks, taking edge weights into account. A) House sparrow data on Lundy Island, UK; B) House sparrow data in Broken Hill, Australia; C) Great tits data in Wytham Woods, UK; D) Sociable weaver data in Benfontein National Park, South Africa. Arrival networks were compared to GMM (orange line), and time window networks (time window, **Δ**t=1; blue line) built using RFID data across study systems. Vertical lines represent the point at which the networks are the most similar.

Table 2.1. Descriptive statistics of social traits between association definitions. Repeatability and mean measures for three social network traits (Degree, Strength, Betweenness) across weeks in four study systems (Lundy Island House Sparrows, Broken Hill House Sparrows, Wytham Woods great tits, and Benfontein Sociable Weavers) using three association definitions. We calculated each metric across all weeks within study systems, with the standard deviation provided in parentheses. P-values were obtained by running 1,000 random permutations and calculating repeatability in the same way, then calculating the proportion of data that was more extreme than the observed value.

System	Method	Trait	Mean (sd)	R	95% CI	p-value	System	Mean (sd)	R	95% CI	p-value
Lundy	Time-window	Degree	13.38 (16.08)	0.32	0.27-0.37	0	Broken Hill	3.41 (2.8)	0.4	0.32-0.47	0
		Strength	0.12 (0.12)	0.19	0.11-0.25	0.001		0.06 (0.13)	0.81	0.79-0.84	0
		Betweenness	44.25 (123.06)	0.28	0.23-0.36	0.001		25.22 (64.08)	0.34	0.25-0.4	0
	GMM	Degree	23.35 (24.17)	0.30	0.24-0.35	0.001		26.27 (13.83)	0.55	0.49-0.61	0
		Strength	1.7 (1.7)	0.13	0.06-0.22	0.005		1.67 (0.86)	0.62	0.58-0.69	0
		Betweenness	31.11 (86.7)	0.17	0.13-0.22	0.002		19.94 (31.1)	0.31	0.25-0.38	0.001
	Arrival	Degree	32.33 (31.93)	0.28	0.23-0.36	0.003		25.01 (13.93)	0.55	0.48-0.61	0
		Strength	0.27 (0.18)	0.26	0.17-0.31	0.004		0.37 (0.17)	0.6	0.56-0.67	0
		Betweenness	24.75 (72.21)	0.12	0.07-0.16	0.016		17.55 (22.83)	0.21	0.13-0.28	0
Wytham Woods	Time-window	Degree	12.84 (7.8)	0.41	0.36-0.45	0	Benfontein	18.36 (10.11)	0.62	0.56-0.7	0
		Strength	0.09 (0.05)	0.37	0.33-0.41	0		0.18 (0.1)	0.55	0.49-0.64	0
		Betweenness	135.59 (302.98)	0.11	0.09-0.15	0		26.8 (45.29)	0.28	0.2-0.34	0
	GMM	Degree	30.41 (14.51)	0.49	0.46-0.54	0		30.2 (11.28)	0.67	0.60-0.73	0
		Strength	4.15 (1.96)	0.53	0.49-0.56	0		2.13 (0.96)	0.60	0.55-0.69	0
		Betweenness	140.48 (385.07)	0.11	0.09-0.16	0		19.75 (28.49)	0 .05	0-0.11	0.019
	Arrival	Degree	29.26 (14.35)	0.5	0.45-0.54	0		34.74 (10.67)	0.7	0.62-0.75	0
		Strength	0.44 (0.13)	0.48	0.43-0.53	0		0.44 (0.14)	0.62	0.55-0.69	0
		Betweenness	133.69 (389.62)	0.1	0.07-0.13	0		14.7 (32.42)	0	0-0.13	0.136

Table 2.2. **Descriptive statistics of network structure between association definitions.** We compared three network structures, built using three association definitions (see methods for parameters), for four systems: A) House sparrow data on Lundy Island, UK. B) House sparrow data in Broken Hill, Australia; C) Great tits data in Wytham Woods, UK; D) Sociable weaver data in Benfontein National Park, South Africa. 1) First, we measured the cardinality of each network, given in the first row of each panel as n Vertices (V; individuals in each network), Edges (E; associations between individuals) and Network density (D; the number of edges over the total number of potential edges); 2) We described four Jaccard similarity measures (left matrix A–D): Actors (common vertices between network layers); Edges (common dyadic edges between network layers); Triangles (to a proxy for network clustering, common clusters of triangles between network layers); and Pearson's degree (a comparison of the degree correlation coefficient between network layers) – where 0 denotes a strong negative correlation and 1, a strong positive correlation; 3) Finally, we used Mantel correlations to compare network similarity accounting for edge weights (right matrix A–D), given as the correlation between two networks where -1 is a strong negative correlation and 1 is a strong positive correlation. P-values and 95% CI of the null distribution (given in parentheses) denote the extent to which comparisons differ from 999 random matrix permutations (where $p<0.05$ denotes a significant difference from random).

Definition		**A.** Lundy			**B.** Broken Hill		
		GMM	Time-window	Arrival time	GMM	Time-window	Arrival time
	Cardinality (V/E/D)	118/2274/0.32	118/1619/0.23	118/3783/0.54	66/1862/0.73	57/290/0.18	66/1534/0.71
GMM	–	–	0.82 p = 0.001 (-0.04 – 0.04)	0.77 p = 0.001 (-0.06 – 0.06)	–	0.69 p = 0.001 (-0.02 – 0.04)	0.92 p = 0.001 (-0.09 – 0.1)
Time-window	Actors	1	–	0.54 p = 0.001 (-0.05 – 0.06)	0.86	–	0.46 p = 0.001 (-0.02 – 0.05)
	Edges	0.7			0.15		
	Triangles	0.5			0.01		
	P Degree	0.97			0.51		
Arrival time	Actors	1	1	–	1	0.86	–
	Edges	0.58	0.42		0.82	0.18	
	Triangles	0.32	0.16		0.67	0.02	
	P Degree	0.85	0.79		0.93	0.65	
System		**C.** Wytham			**D.** Benfontein		
	Cardinality (V/E/D)	219/6774/0.28	204/4115/0.29	214/6688/0.19	62/1433/0.75	62/978/0.51	62/1583/0.83
GMM	–	–	0.82 p = 0.001 (-0.02 – 0.02)	0.94 p = 0.001 (-0.02 – 0.02)	–	0.64 p = 0.001 (-0.02 – 0.02)	0.92 p = 0.001 (-0.02 – 0.02)
Time-window	Actors	0.93	–	0.74 p = 0.001 (-0.02 – 0.02)	1	–	0.47 p = 0.001 (-0.10 – 0.1)
	Edges	0.6			0.68		
	Triangles	0.37			0.49		
	P Degree	0.92			0.9		
Arrival time	Actors	0.97	0.95	–	1	1	–
	Edges	0.94	0.61		0.87	0.61	
	Triangles	0.91	0.38		0.77	0.4	
	P Degree	0.99	0.92		0.92	0.81	

Discussion

In this study, we compared three association definitions applied to avian social networks in four study systems. These were time window (Farine 2015), GMM (Psorakis et al. 2012, 2015), and an alternative approach using arrival time instead of group delineation (Chan and Dunning 2023; also see Chapter 3; Methods). Our results suggest that association definitions were robust to the noise of visitations when applied to individuals attending a resource.

We found statistically significant and similar levels of repeatability within systems, but differences between association definitions. Likewise, the structure of networks, measured using similarity indices and Mantel coefficient correlations, were also similar within systems but between association definitions. Where we identified small differences in network structure, we found that some association definitions resulted in more similar networks between systems with more similar ecologies, for example, the highly gregarious and open-access antenna systems at Lundy and Benfontein. Altering the arrival time overlap (**Δ**t) within arrival networks did also subtly influence the structure of the networks, but not significantly, and generally network structure was robust to the definition of **Δ**t. Our results suggest that before inferring meaning from animal social networks, it is important to consider which social association definition, or parameter, is of interest to the research question at hand (Croft, James, and Krause 2008; Farine and Whitehead 2015), as this can influence network structure (Castles et al. 2014). RFID systems, often used in conjunction with some attractive resource, are a common approach for measuring social behaviour in passerine birds, which often forage and shelter communally. However, tools available to infer social associations from such data have been developed for specific systems, or questions, and may not be generalisable across contexts.

No single association definition we used resulted in a significant change in network size, defined by associations rather than raw antenna detections, or structure in any system, except for the use of a time window to define associations between sparrows entering a feeding chamber at Broken Hill. The similarity was expected because each association

method is trying to capture meaningful social associations from the same temporal data stream, highlighting that all definitions result in similar networks. However, our results also show that methodological decisions can result in differences specific to systems and study species. These differences can be explained by a mismatch between an appropriate definition of an association in the context of the research question, system ecology, and experimental design. Alternatively, association definitions may capture subtly different behaviours, such as the propensity to aggregation or exploration of novel food patches.

Our results also suggest that the design and layout of RFID feeders can influence the obtained social networks using different association methods. When using the time window definition, we observed lower repeatability of individual social traits in Wytham Woods but increased repeatability in Broken Hill and Benfontein compared to the other methods. Since we used a strict threshold of 1 s to define the time window (which we used to represent a measure of absolute proximity), the method was likely not appropriate for the RFID feeders in Wytham Woods because birds can only visit feeders one or two birds at a time, in which case meaningful associations would have been lost. Similarly, the time window definition in Broken Hill also resulted in smaller network sizes, which we attributed to the design of the RFID system. Here, sparrows were only detected as they entered and left a feeding chamber, making detection of groups difficult. In the Broken Hill sparrows, a higher **Δ**t value (e.g., 5 to 10 s) might be more appropriate to capture physical and temporal proximity. On the other hand, shorter time windows can be more appropriate for open RFID systems like in Benfontein and Lundy Island (Figure 2.1), where multiple individuals can access food resources at one time. Overall, the arrival and GMM approaches captured repeatability across RFID designs, highlighting the strength of the gambit of the group approach to define social links between individuals. The similarity in the networks observed in our study may be attributed to the inherent noise of aggregation present in social data collected at a resource, but visitation rates of individuals are influenced by several factors beyond the necessity to socialise, such as dominance (Oh and Badyaev 2010; Evans, Jones, and Morand-Ferron 2018) and behavioural preference (Aplin et al. 2013, 2014, 2015; Culina, Firth, and Hinde 2020). We also consider that each association definition may capture subtly different behaviours or

can be influenced by individual preferences. For example, individuals attending a resource and linked using time window and GMM definitions, network edges (associations) may also capture a tolerance to forage with con-specifics but also a propensity to monopolise a resource.

Overall, GMM and arrival definitions captured more similar networks compared to the time window, probably because the latter captures physical and temporal proximity, while the two former are based on the gambit of the group approach. Surprisingly, the pattern was not observed for house sparrows on Lundy Island, where GMM and time window produced more similar networks. This may reflect the inability of the GMM approach to identify group structures in large flocks visiting the feeder. To further determine how the choice of parameters can influence the networks built using the arrival approach, we performed a sensitivity analysis by varying **Δ**t and comparing repeatability and network similarity metrics across the study systems. We show that the arrival approach is generally robust against changes in parameters, where the values increase and then plateau consistently across study systems. We also confirm that the choice of **Δ**t =150 used in the current study was appropriate and can be a reasonable threshold for future researchers wishing to apply the arrival approach.

A core limitation of our study, and indeed other studies that compare wild animal social networks, is the inability to know the true social associations between individuals, because sociality measures are only ever a sample of a wider, complex behaviour. We have addressed this in part by running permutations to compare to randomised networks for some analysis (Farine 2017), but these methods have their own shortcomings (see Farine and Carter 2022 and Hart et al. 2022 for more detailed discussions). Further, we have also used data from systems that have developed methods specific to the biology of the animals they study: The Wytham Woods project developed the asnipe R package and GMM to build networks based on the behaviour of great tits, but also their own feeder design (Farine 2017). Likewise, Benfontein were able to test their social networks based on familial ties (Ferreira et al. 2020), and the arrival network is based on watching birds arrive at feeders on Lundy Island (Chapter 3). Measuring social behaviour as birds attend to a resource may be a factor in defining social associations, which may be less obvious

as birds prioritise feeding. Recent studies have shown the potential of wireless biologging networks (WBNs) to track animal behaviour and social interactions (Ripperger et al. 2020; Ripperger and Carter 2021), thereby providing a more accurate representation of social networks in the wild.

We suggest that future studies should define associations based on the specific ecology of their study system and sampling methodology, and that studies should explicitly define associations in their methods. Key considerations are: 1) the gregariousness of the study system, or their propensity to aggregate (without social association; Krause and Ruxton 2002) at a resource. For example, where a social association is equivalent to group membership, the gambit of the group definition is appropriate (Farine 2017; Psorakis et al. 2012, 2015), whereas in highly gregarious systems, where social associations are masked by aggregation of individuals at a resource, time window or arrival time are likely to be more appropriate (Chapter 3); 2) the sampling methodology, for example, in open-access systems where multiple individuals can access an RFID antenna at one time, gambit of the group definitions may be less appropriate than in systems that limit access to the antenna. Likewise, the number of sampling events (i.e., multiple RFID antennas) will likely influence network density. Where the concepts of social association are unclear, it may be beneficial to apply multiple definitions and compare them before hypothesis testing. Furthermore, we encourage future research to report association definitions in published research, providing a biological justification on the choice of association definitions when conducting animal social network studies. These could be empirically tested against another socially relevant variable (e.g., family ties; Ferreira et al. 2020) or based on observation of the study species (e.g., watching sparrows arrive at a feeder on Lundy Island; Chapter 3). While we show here that differing association definitions are generally robust and produce broadly similar networks, decisions that researchers make would nevertheless result in different network structures and may influence research outcomes.

Chapter 3

Opposite-Sex Associations are Linked with Annual Fitness, but Sociality is Stable Over a Lifetime

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Abstract: Animal sociality, an individual's propensity to associate with others, has fitness consequences through mate choice, for example, directly by increasing the pool of prospective partners, and indirectly through increased survival, and individuals benefit from both. Annually, fitness consequences are realised through increased mating success and subsequent fecundity. However, it remains unknown whether these consequences translate to lifetime fitness. Here, we quantified social associations and their link to fitness annually and over a lifetime, using a multi-generational, genetic pedigree. We used social network analysis to calculate the variables representing different aspects of an individual's sociality. Sociality showed high within-individual repeatability. We found that birds with more opposite-sex associates had higher annual fitness than those with fewer associates, but this did not translate to lifetime fitness. Instead, for lifetime fitness, we found evidence for stabilizing selection on opposite-sex sociality, and sociality in general, suggesting that reported benefits are only short-lived in a wild population, and that selection favours an average sociality.

Background

Some individuals are consistently more sociable than others, demonstrated by within-individual repeatability of social traits across vertebrate groups (Aplin et al. 2015; Thys et al. 2017; Dimitriadou, Croft, and Darden 2019; Plaza et al. 2019; Beck, Valcu, and Kempenaers 2020; Proops et al. 2021; Strickland et al. 2021). This variation in individual sociality is positively linked with fitness in some taxa (Silk 2007; Silk et al. 2009) and is therefore expected to be subject to selection (Krause and Ruxton 2002). Fitness is a relative measure of an individual's genetic contribution to the population in the next generation, and thus can only be represented comprehensively and precisely by measures of traits spanning an organism's lifetime (Endler 1986; Reid et al. 2019; Moiron, Charmantier, and Bouwhuis 2022). A comprehensive definition of fitness is fundamental to understanding the evolutionary pressures that shape variation in sociality. In practice, however, many studies must rely on fitness correlates instead (e.g., number of broods, or survival, instead of genetic contribution). For example, in mammal societies, variations both in within- and between-sex affiliations (Archie et al. 2014) have been linked to lifetime fitness correlates, survival, and longevity (Cameron, Setsaas, and Linklater 2009; Silk, Alberts, and Altman 2003; Silk et al. 2010; Stanton and Mann 2012; but also see Thompson and Cords 2018). However, in birds, the subject of this study, the use of fitness correlates (eggs laid, chicks fledged, within-year survival, etc.) is frequent over more precise fitness measures (Moiron, Charmantier, and Bouwhuis 2022) that require intensive field work over a long period of time.

Although some benefits are linked with sociality during the breeding period, most of these tend to be short-term and contextual (Bebbington et al. 2017; Riehl and Strong 2018). Instead, benefits associated with reproduction are often linked with non-breeding sociality (Firth and Sheldon 2016; Kohn 2017; Maldonado-Chaparro et al. 2018; Beck, Farine, and Kempenaers 2020) when group cohesion is stronger (Silk et al. 2014; Kurvers 2020). Sociality may influence fitness in different ways, through benefits to reproductive success or increased survival, and so the mechanism of selection acting on social traits may also differ. For example, communal foraging between socially associated individuals during the non-breeding period facilitates resource information transfer (Aplin et al. 2012; Firth,

Sheldon, and Farine 2016; Hillemann et al. 2020) and reduces predation risk (Cresswell 1994; Cresswell and Quinn 2011; Sorato et al. 2012), increasing survival. However, these benefits may also incur costs associated with competition for resources and mate choice (Birkhead and Biggins 1987; Forstmeier et al. 2011; Mayer and Pasinelli 2013; Grant and Grant 2019; see also Lea et al. 2010). Sociality may also benefit individuals who hold more central social network positions or have access to opposite-sex associates through enhanced mate choice (McDonald 2007; Oh and Badyaev 2010; Firth et al. 2018; Beck, Farine, and Kempenaers 2021). Although the association between annual fitness correlates and non-breeding sociality has been well described, testing how selection acts on social traits requires lifetime fitness measures, and remains unresolved.

With the recent development of tools to construct and analyse social networks (Wey et al. 2008; Farine and Whitehead 2015) the study of sociality has become popular among behavioural ecologists. Yet, to describe the association between sociality and fitness, any potential study must first overcome two problems: (1) A social association must be clearly defined relative to the behaviour of the study system (Figure 3.1; Psorakis et al. 2012, 2015), and (2) To study the evolution of social behaviour, precise measures of individual fitness must be quantified to test for correlation with a social trait, selection. Although annual fitness correlates are widely used, lifetime fitness is more precise and without the stochasticity of annual measures (Dobson, Murie, and Viblanc 2020; Alif et al. 2022); thus, it can better describe selection pressure acting on a trait (Endler 1986; Reid et al. 2019). However, lifetime fitness requires wild animals to be monitored throughout their whole lives, and all breeding attempts, and the fates of their offspring, must be recorded to determine recruitment. All of these require a multi-generational genetic pedigree (Kruuk 2004; Korsten et al. 2013).

Our study system, an island population of house sparrows *Passer domesticus* (hereafter, sparrow/s) where we monitor all individuals from birth to death, without capture bias (Simons et al. 2015), overcomes both problems. (1) We have sociality data from birds that are electronically registered visiting a feeder. Social centrality measures are repeatable across different timescales and contexts in this and other populations (Plaza et al. 2019). (2) We have lifetime recruitment data available, from a multi-generational

genetic pedigree that, because our population is closed, meaning that there is no movement of sparrows to or from the island, and since our study covers all the sparrows on the island, we can compute precise annual and lifetime fitness estimates (Schroeder et al. 2015; Alif et al. 2022).

We tested predictions based on the arguments presented above to understand the potential for selection on sociality: (1) We confirmed that the social traits we measured were meaningful by testing for individual repeatability of sociality; (2) We tested the prediction that non-breeding sociality has fitness benefits, either driven by reproductive success through opposite-sex association or through increased survival through network centrality measures and is subject to selection.

Materials and Methods

Study system

We used data from the Lundy sparrow system, a long-term study based on the island of Lundy (51.11N, 4.40W), ≈19 km off North Devon, UK, in the Bristol Channel. The sparrows on Lundy breed in nest boxes, situated in groups around the only village on the island. The island is rodent-free; therefore, the sparrows have no predators apart from the occasional vagrant raptor. House sparrows are a model organism in behavioural ecology and evolution, and much is known about their biology, physiology, and life history (Andersson 2006; Sánchez-Tójar et al. 2018). House sparrows are socially monogamous, but 25% of broods show they can be genetically promiscuous (Schroeder et al. 2016). On Lundy, they have on average 2 to 3 broods of 4 or 5 eggs each per breeding season (Westneat et al. 2014). The sex ratio is stable, and the mean lifespan of recruits is three years (Alif et al. 2022). Although sparrows are territorial during the breeding season, during the non-breeding period, they form gregarious groups that forage communally for seed and at supplementary bird feeders (Summer-Smith 1954; 1963), both of which are available year-round on Lundy.

Most sparrows were first captured, and tissue was sampled in nest boxes at their natal site during the breeding season (April to August) or using mist nets during the post-fledging period (Schroeder et al. 2011; Girndt et al. 2019). Tissue samples were either blood or mouth swabs, stored in ethanol, and refrigerated at 3°C prior to analysis. We genotyped sparrow DNA at <22 microsatellite loci suitable for parentage assignment in sparrows (Dawson et al. 2012). Using the genetic data, we assembled a near-complete genetic pedigree (Schroeder et al. 2015, 2016), which spans 20 years, 2000–2019, and 8,379 individuals. We fitted all sparrows with a unique combination of a coded metal ring and three coloured leg rings. We also provided each sparrow with a subcutaneous Passive Identification Transponder (PIT tag; TROVANID100: 11.5 × 2.1 mm and 0.1 g) under the skin of the breast, which we have previously shown has no detrimental effect on subsequent fitness (for details, see Schroeder et al. 2011). These tagged individuals were then recorded when they visited a custom-made 19.8 cm x 19.8 cm Radio

Frequency Identification antenna (RFID; DorsetID) mounted on a seed reservoir (for photos see Sánchez-Tójar et al. 2017; Brandl et al. 2019), positioned centrally within our study site. The feeder was open access, and explicitly not limited to a single bird feeding at one time, as is the case with hanging bird feeders (Youngblood 2019; Beck, Farine, and Kempenaers 2020). Our feeder recorded visiting birds every day that the island generators were running (from 6 am to midnight, seven days a week).

Social centrality measures

To quantify the sociality of individual sparrows, we calculated measures of social centrality (hereafter centrality measures) using presence data from the RFID antenna, collected during the non-breeding periods, from November 2015 to January 2016 (15 weeks) and 2016/17 (13 weeks, hereafter referred to events). An association between birds observed from these data can reflect either individuals that choose to maintain some social cohesion, which we consider to be a non-random association, or individuals without pre-established social cohesion who coincide in time and space, which we consider random mixing. These data record the presence of birds without distinguishing between these two types of associations. Further, dyadic interactions can also be aggressive, and our data cannot exclude these cases. Although in sparrows, dominance hierarchies are typically linear, there is no evidence of a correlation with reproductive fitness (Sánchez-Tójar 2018).

The 'gambit of the group' is a common approach used to identify discrete groups among all associating individuals (Whitehead and Dufault 1999; Figure 3.1A). However, given the gregarious nature of sparrows and the high activity at our feeder, at which non-discrete groups of sparrows accumulated, the gambit of the group approach overestimated associations between individuals (Figure 3.1A; also see Ferreira et al. 2020). One solution to this would be to define a non-random association in which two individuals overlapped by a defined period ($\Delta\mathbf{t}$) at our bird feeder. However, in our system, again due to the near constant visitations, this resulted in linear network structures, such as linking the first bird to the second, then the second to the third, and so on (Figure 3.1B).

To account for the social behaviour of sparrows, we derived a method to infer non-random associations that assumed that non-random social associations are established before they attend the feeder (suggested by Summer-Smith 1954). We, therefore, defined an association as two individuals that arrived at feed within 150 s (Δt) of each other. Here, an arrival is defined as the (re)appearance of the individual at the feeder after being absent for a period of minimally >300 s (Δ_I). We defined that $\Delta t = 150$ s was sufficient to detect and link individuals who arrived together in a group (see Figure 3.1C), and the resulting data better sampled non-random associations between individuals in our system, from watching sparrows in the field and on pre-recorded footage, arriving at our feeder (Plaza et al., 2019).

From the resulting association matrices of the two events, 2015/16 and 2016/17, we built a series of weighted, nondirectional, social networks (hereafter, network/s), where the vertices represent individual sparrows and interconnecting edges their associations. First, we built individual networks for each of the 15 weeks in 2015/16, and 13 weeks in 2016/17, to estimate within-individual repeatability in centrality network metrics. This was to validate these centrality measures against the individual repeatability already demonstrated in this system using both RFID and video data (Plaza et al. 2019). We then built a network for each event to extract non-breeding sociality. Finally, we also built two bipartite networks from each event (sub-graphs), which only considered the association strength between opposite-sex individuals.

From the first non-breeding networks, we extracted three centrality measures representing different aspects of sociality for each individual using the 'iGraph' R package (Csardi and Nepusz 2006): We selected centrality measures to reflect aspects of an individual's social preference, following similar studies on sociality (McDonald 2007; Farine and Whitehead 2015; Beck, Farine, and Kempenaers 2021). Degree represents the number of associates and may impact fitness through enhanced mate choice, where individuals position themselves alongside others of lesser quality (Oh and Badyaev 2010;), or where same-sex associates benefit reproduction in cooperative breeding species (Bebbington et al. 2017; Riehl and Strong 2018). Strength represents the quality of these relationships and may influence the structure and behaviour of reproductive

communities (Firth and Sheldon 2016; Culina, Firth, and Hinde 2020). We calculated strength following Farine (2013), using the sum of dyadic simple ratio indices (the association probability between a dyad, from 0, never associated, to 1, always associated), which we transformed to give a measure of net association quality (Eq. 1, where S denotes strength, $d_{(i)}$ and sum $SRI_{(i)}$ the degree and SRI of a given individual, respectively, and N(V) = the number of vertices in a network).

$$(Eq.1) \quad S = d_{(i)} \frac{SRI_{(i)}}{N(V)}$$

We used eigenvector centrality (following McDonald 2007, hereafter centrality) to quantify the influence of an individual on all others within the network (Newman 2004; Oh and Badyaev 2010). Finally, we extracted opposite-sex degree from the two bipartite sub-graphs, the number of opposite-sex associations, which we used to represent an individual's pool of potential reproductive partners, as a fourth measure of sociality (following Beck, Farine and Kempenaers 2021). Given the high density of sparrows visiting the feeder, and the frequency at which those birds were detected, we did not threshold our networks (using only a sample of the birds attending an antenna, following Farine and Whitehead 2015) to maintain network structure, although only birds who arrived in a dyad (where degree > 0) were included in our networks.

Fitness measures

For each of the sparrows that survived to the following breeding period, we used the genetic pedigree to calculate two fitness measures, and for each of these, we calculated one annual measure, and one across the lifetime of the sparrow. Both fitness measures are based on the number of recruits, and we have shown that they correlate well with reproductive value, thus representing fitness in an evolutionarily meaningful way (Alif et al. 2022). We defined recruits as offspring that survived and produced genetic offspring themselves.

(1) *Recruits*. For the number of annual recruits, we summed individual recruits within the breeding year following the social events. We then again summed individual recruits across a lifetime, or up to 2020, as a measure of lifetime recruits. Note that the latter category only contained five sparrows that were still alive at the point of the census; as such, our recruitment data can be considered near complete. We excluded birds that did not survive to breed, and yearlings that had zero recruits.

(2) *De-lifed fitness*. As a second fitness measure, we used de-lifed fitness (p_{ti}; Eq. 2), which estimates an individual's genetic contribution to the population (Coulson et al. 2006). De-lifed fitness is a retrospective measure of realised fitness relative to the population each year, calculated by removing (de-lifing) an individual and its offspring from the pedigree and recalculating the resulting change in population growth.

$$(Eq.2) \quad p_{ti} = \frac{\xi_{t(i)} - w_{t(i)}}{N_t - 1}$$

Here, p_{ti} is the contribution of individual ($_i$) to population growth during a specific period *t.* Further, $\xi_{t(i)}$ is a measure of individual performance; here, the number of surviving offspring of individual we at the end of the breeding period *t*. We added a value of one if the individual we itself survived the next breeding period *t* + 1. The population size at time *t* is N_t at the beginning of each breeding cycle (here, April). To estimate the individual's contribution to population growth, we use w_t, which represents the population size ratio

at $t + 1$ to the population size at t. This de-lifed fitness p_{ti} is an annual value per individual, and we calculated it for all birds that produced at least one recruit. We then also summed p_{ti}, within individuals as a lifetime de-lifed fitness measure, p_i.

Individual repeatability in sociality

First, we validated our centrality measures by confirming that they were repeatable within individuals between weeks. We modelled degree, strength, centrality, and opposite-sex degree, respectively, as response variables each in four Gaussian linear mixed models against the intercept, and with bird identity modelled as a random effect to compensate for repeat identities between years. We then divided the variance explained by bird identity by the total phenotypic variance of the trait to quantify repeatability (see Nakagawa and Schielzeth 2010). We ran repeatability models using package MCMCglmm default parameters and priors, and the models converged robustly and reliably.

Selection on sociality – annual and lifetime fitness

We quantified the association between centrality measures and fitness. As all four centrality measures are inherently correlated, we modelled each separately to avoid collinearity (Webster, Schneider, and Vander Wal 2020). For each centrality measure, we ran two models, with annual recruits and annual de-lifed fitness as the response variables. In the models with annual numbers of recruits as a response, we assumed a Poisson error distribution with a log link function, and in the models explaining de-lifed fitness we assumed a Gaussian error distribution. We mean-centred all centrality measures within each year, eliminating between-year differences, and modelled them as fixed covariates. We also added each sociality variable as a quadratic effect to test for stabilizing or disruptive selection, where averages are favoured over the extremes (Wolf et al. 2007). Bird identity was modelled as a random effect on the intercept to account for pseudo-replication, and cohort to account for environmental stochasticity. We modelled fixed effects for sex (male, 1 or female, 0) and age (in calendar years) and age as a quadratic

effect to account for variation in fitness as explained by demography (Schroeder et al. 2012). We added sex as an interaction term with age to account for the extra-pair behaviour of older males (Girndt et al. 2018).

We modelled lifetime recruits and lifetime de-lifed fitness in the same way as the annual ones, but instead of age, we used lifespan, or maximum age in 2020. Because each bird was only represented once in this dataset, we only modelled the cohort as a random effect.

We used Bayesian Markov Monte Carlo simulations, using MCMCglmm (Hadfield 2010), to run all models. For all models, we used inverse Wishart priors for random effects, and ran each over 343,000 iterations, with a burn-in of 3,000, and a thinning interval of 200. We visually checked the posterior trace plots for all model outputs and ensured that autocorrelation was below 0.1 and effective sample sizes were between 1,000 and 2,000. The fixed effects were considered statistically significant when the 95% credible interval (CI) of its posterior distribution did not span zero.

Null models and dominance interactions

We ran a node-permutation null model by shuffling the identities of birds visiting the feeder between existing arrival times in our association matrices, thereby breaking any link between sociality and fitness, over 1,000 randomized permutations (following Farine, 2017). We used these randomized association matrices to construct 1,000 new networks and extracted the mode for our four centrality measures. We used these randomized centrality measures to rerun all fitness models. Finally, to exclude the possibility that dominance interacted with our observed centrality measures, we tested for correlations between the centrality measures and dominance from videos recorded during the same period of our social network events. We represented individual dominance by calculating ELO ratings based on antagonistic interactions at the bird feeder (for further details, see Sánchez-Tójar 2018). We did not include the randomised centrality measures from our null models in these correlations.

Results

The data consisted of 150 individual birds making 410,114 visits to the RFID feeder within our study period (mean = 2,734 visits per bird, SD = 8,116) across both events. Excluding birds that died prior to the start of our study or those that were ringed after, 160 tagged birds survived in our system in November 2015; an additional 90 birds were tagged prior to the 2017 breeding period, although not all survived to sampling. After constructing the arrival networks, we identified 3,783 associations between 118 PIT-tagged individuals during 2015/2016, and 874 associations between 69 individuals in 2016/2017. These networks contained 66.3% of 122 and 26.3% of 205 breeding birds in 2016 and 2017, respectively. Combined, we had 130 records for annual and lifetime fitness from 102 individuals, 33 of which were recorded in both years (for summary statistics, see Table 3.1). Degree and opposite-sex degree are closely correlated, implying that those with more opposite-sex associates also tend to have more associates of either sex (Table S3.1)

Individual repeatability in sociality

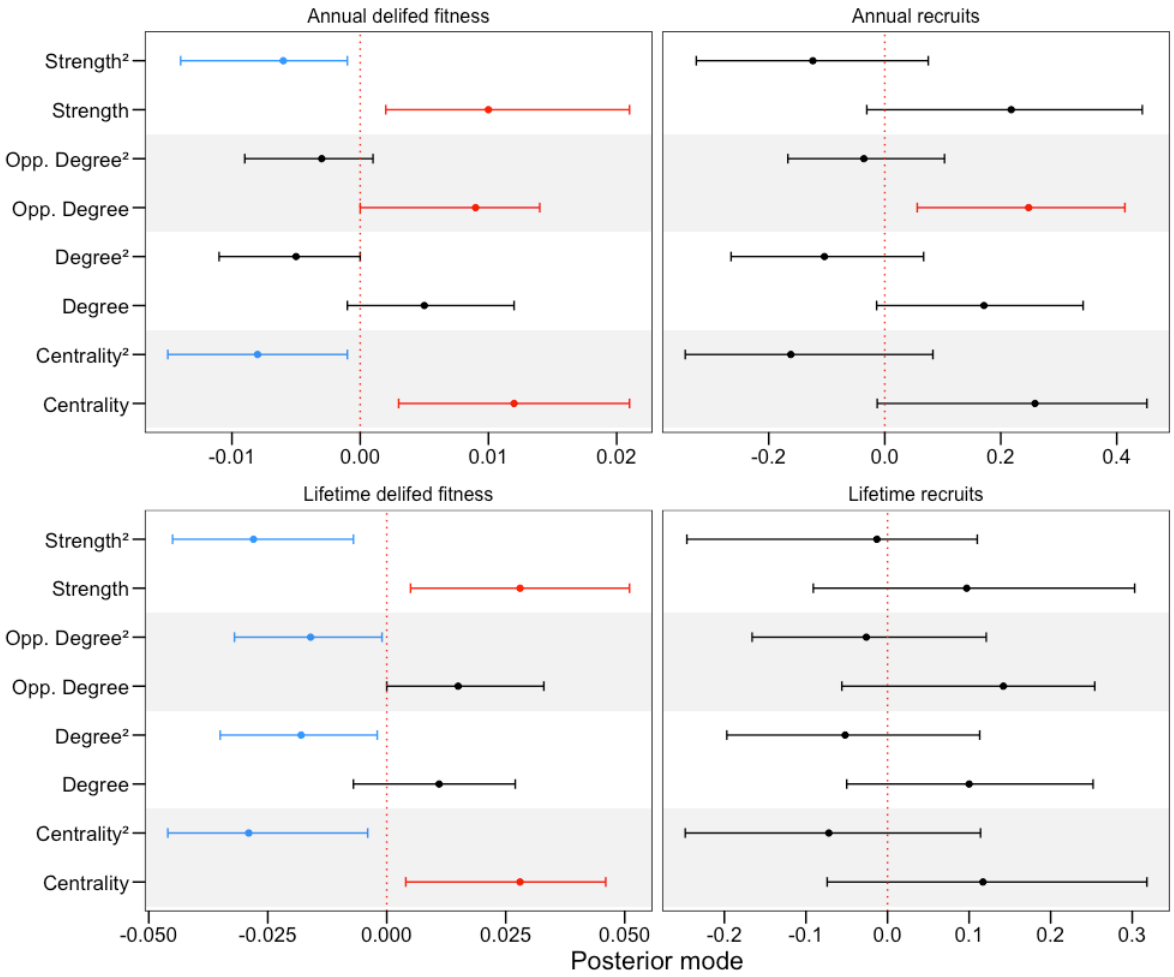
We confirmed individual repeatability by week in all four centrality measures between 15 weeks in 2015/16: Degree, R = 0.29 (0.15 – 0.39), Strength, R = 0.22 (0.10 – 0.32), Centrality, 015 (0.03 – 0.27) and Opposite-sex degree, 0.27 (0.13 – 0.4); and, 13 weeks in 2016/17: Degree, R = 0.29 (0.15 – 0.39), Strength, R = 0.22 (0.10 – 0.32), Centrality, 015 (0.03 – 0.27), and Opposite-sex degree, 0.27 (0.13 – 0.4) (Table 3.1).

Selection on sociality – annual and lifetime fitness

Opposite-sex degree had a statistically significant linear relationship with the number of annual recruits and annual de-lifed fitness. Strength and centrality had a negative quadratic association with annual delifed fitness (Figure 3.1; Table 3.2). Age and sex also predicted annual recruits, with younger individuals and females recruiting more offspring. Age also positively predicted annual de-lifed fitness (Table 3.2).

None of our centrality measures statistically significantly predicted lifetime recruitment (Figure 3.1; Table 3.3); however, all four had a statistically significant negative quadratic relationship with lifetime de-lifed fitness (Figure 3.1).

Figure 3.1. **Comparison of social variables** (also see Table S3.2 for non-social variables)**.** observed fitness as response variables against social measures from 8 linear mixed models, at two scales, from the Lundy Island house sparrows: Explanatory variables for Annual de-lifed fitness and Lifetime de-lifed fitness where ^{2} denotes a quadratic function and their 95% credible intervals. Credible intervals are given as solid bars for each explanatory variable, where a solid point denotes the posterior mode. Black bars denote no effect on the response variable; red denotes a positive and blue, a negative, relationship with the response. In adjacent panels, quadratic functions of each response variable are presented in A and B (on the Y axis: A Centrality, Degree, Opp. Degree, Strength, and B Centrality, Degree, Opp. Degree, Strength)



Null models and dominance interactions

We found no link between fitness and sociality, nor any evidence of selection from our null models (Figure S3.1). Likewise, dominance was not strongly correlated with any centrality measure, implying that our method of assigning associations based on arrival time, rather than shared space at a bird feeder, is unlikely to be influenced by dominance (Table 3.1).

Table 3.1. **Summary statistics for recruitment and centrality measures for individual house sparrows on Lundy Island during two non-breeding events** (November–January 2015/2016 and 2016/2017). Each measure is given as mean, standard deviation, and sample size, and includes repeatability (R) and 95% CI for centrality measures.

Summary Statistics of Recruitment					
Fitness		2015/16		2016/17	
Variable	Scale	Mean, SD (n = 118)		Mean, SD (n = 69)	
Recruits	Annual	2.65, 1.98		0.78, 1.07	
	Lifetime	5.34, 3.76		4.15, 3.86	
Summary statistics and repeatability of centrality measures					
Centrality measure		Mean, SD	R, 95CI	Mean, SD	R, 95CI
Degree		64.11, 32.03	0.29, 0.15–0.39	25.33, 17.37	0.35, 0.16–0.49
Strength		0.06, 0.05	0.22, 0.10–0.32	0.09, 0.13	0.33, 0.16–0.48
Centrality		0.35, 0.30	0.15, 0.03–0.27	0.25, 0.31	0.23, 0.10–0.36
Opposite-sex degree		32.00, 15.86	0.27, 0.13–0.4	12.18, 9.19	0.45, 0.24–0.61

Table 3.2. Annual recruitment model outputs. Annual recruitment model outputs from GLMMs for each of our four centrality measures (Degree, Strength, Centrality, and Opposite-sex degree), derived from 410,114 visits to an RFID baited feeder by 150 individuals. Centrality measure of house sparrows on Lundy Island, modelled against annual recruits. We inferred significance where the 95% CI did not span zero, positive effects on the response variable are highlighted in red, and negative in blue.

Annual recruits	Posterior mode 95% Credible Intervals			
Variable	Degree	Strength	Centrality	Opposite-sex degree
Fixed terms				
(Intercept)	3.49 1.46—6.11	3.69 1.58—6.46	4.19 1.60—6.31	3.78 1.58—6.50
Centrality measure	0.17 -0.01—0.34	0.22 -0.03—0.44	0.26 -0.01—0.45	0.25 0.05—0.41
Centrality measure^2	-0.1 -0.26—0.06	-0.12 -0.32—0.07	-0.16 -0.34—0.08	-0.04 -0.16—0.10
Sex (male)	-0.67 -1.41—0.05	-0.7 -1.46— -0	-0.74 -1.48— -0	-0.57 -1.47—0
Age	-1.14 -2.03— -0.30	-1.15 -2.04— -0.28	-1.27 -1.99— -0.26	-1.07 -2.00— -0.26
Age^2	0.05 -0.07—0.17	0.04 -0.08—0.17	0.06 -0.08—0.16	0.03 -0.07—0.17
Age*Sex (male)	0.21 -0.01—0.48	0.22 -0.02—0.46	0.28 -0.02—0.49	0.21 0—0.49
Random terms				
*Bird ID	0 0—0.13	0 0—0.12	0 0—0.12	0 0—0.13
*Cohort	1.88 0.25—15.69	1.5 0.19—15.57	2.09 0—15.89	2.29 0.11—16.90
Residuals	0 0—0.27	0 0—0.28	0 0—0.29	0 0—0.24

Table 3.3. Lifetime recruitment model outputs. Lifetime recruitment model outputs from GLMMs for each of our four centrality measures (Degree, Strength, Centrality, and Opposite-sex degree), derived from 410,114 visits to an RFID baited feeder by 150 individuals. Centrality measure of house sparrows on Lundy Island, modelled against lifetime recruits. We inferred significance where the 95% CI does not span zero, positive effects on the response variable are highlighted in red, and negative in blue. († Age in lifetime models denotes either lifespan, or age in 2020, whichever is greatest)

Lifetime recruits	Posterior mode, 95% credible intervals (lower – upper)			
Variable	Degree	Strength	Centrality	Opposite-sex degree
Fixed term				
(Intercept)	0.85 0—1.93	0.85 0.02—1.95	0.99 -0.06—1.87	0.8 -0.03—1.83
Centrality measure	0.1 -0—0.25	0.1 -0.09—0.3	0.12 -0.07—0.31	0.14 -0.05—0.25
Centrality measure^2	-0.05 -0.19—0.11	-0.01 -0.24—0.11	-0.07 -0.24—0.11	-0.03 -0.16—0.12
Sex (male)	0.33 -0.35—0.99	0.28 -0.36—0.91	0.28 -0.33—0.98	0.48 -0.24—1.03
†Age	0.1 0—0.23	0.11 0—0.24	0.09 0.01—0.25	0.12 0—0.24
†Age*Sex (male)	-0.06 -0.20—0.07	-0.07 -0.19—0.07	-0.07 -0.2—0.06	-0.06 -0.21—0.04
Random effects				
*Cohort	NA 0.07—2.78	0.47 0.07—2.76	0.45 0.06—3	0.39 0.10—2.77
Residuals	NA 0—0.27	0.12 0.01—0.29	0.11 0.02—0.28	0.14 0—0.26

Discussion

We found evidence for annual fitness benefits of sociality, where individuals with more opposite-sex associates had higher fitness in the breeding period than those with fewer, but this did not translate to lifetime fitness. For lifetime fitness, we found evidence for stabilising selection on sociality, including opposite-sex degree, suggesting that such benefits are only short-lived, or contextual, in a wild population.

We constructed our networks by linking dyads of birds that arrived together at a bird feeder, but ignored the time that they spent there, to eliminate most random associations. Other studies have adopted similar approaches in high-density and open-feeder systems, or have considered the same implicit problems (Gomes, Boogert, and Cardoso, 2021). Ferreira et al. (2020), for example, identified flocks arriving but then defined associations by spatial proximity at a series of feeder boxes. Further research could optimize our approach for other systems, either by refining the time after which an individual is determined to have left the feeder ($\triangle_i$), or similarly, the time it takes for all members of a group to interact with the feeder upon arrival ($\triangle t$). Further work may also consider defining associations only where a dyad visits together more often than would be expected by chance, but doing so must also consider some method of retaining peripheral associations. Although RFID systems sample sociality well at a feeder, we cannot be sure that sociality traits are maintained in other contexts. Future researchers might consider tracking social behaviour across time and space (for example, see Ripperger and Carter 2021).

Where previous studies on wild birds have suggested links between aspects of sociality and annual reproductive success (for examples, see Firth and Sheldon 2016; Kohn 2017; Beck, Farine, and Kempenaers 2020), we were also able to use lifetime measures, which better reflect the genetic contribution of the individual to population growth, and thus, fitness. This also allowed us to describe how selection acts upon sociality across the population. We found that sociality had little influence on fitness at the annual scale, apart from opposite-sex association, which was linked to increased recruitment and de-lifed fitness. Our study corroborates that annual fitness benefits described elsewhere,

particularly regarding mate choice (Oh and Badyaev 2010; Beck, Farine, and Kempenaers 2021; Beck, Farine, and Kempenaers 2020), directly translate into increased annual fitness. At the lifetime scale, our study also provides some insight into the evolution of social behaviours, which we found to be maintained at the population average through stabilizing selection. Ours is, therefore, to the best of our knowledge, the first study to link sociality with lifetime fitness benefits in a wild bird (but see Formica et al. 2021; Philson and Blumstein 2023). Our results may also suggest a mechanism for the selection of sociality through enhanced mate choice, but the impact on survival was difficult to determine in this study. Sociality is predicted to increase survival through reduced predation risk or information transfer (Sorato et al. 2012; Hillemann et al. 2020), but we found no evidence to suggest that either was selected for, through higher centrality, in our analyses.

Stabilizing selection in this case may be driven by factors such as high mate fidelity or changing sociality with age (Oh and Badyaev 2010; Albery et al. 2022), removing the need to constantly maintain opposite-sex associations over a lifetime while maintaining individual fitness. However, these opposite-sex associations may also be beneficial in an extra-pair context from the male perspective (Beck, Farine, and Kempenaers 2020) and require further research.

Our centrality measures were associated with lifetime but not with annual de-lifed fitness, and only opposite-sex degree was associated with recruitment at the annual scale. We found no relationship between social centrality and dominance in our study using arrival time to define sociality, but aggressive interactions were probably also reduced over the non-breeding period (Summer-Smith 1954; 1964). None of our centrality metrics was linked with recruitment at the lifetime scales. Overall, de-lifed fitness better represents fitness, as it is a relative measure of the contribution to population growth (Alif et al. 2022). The number of recruits, while intuitively appealing, is not relative, and in good years, more birds may have a higher number of recruits, while in poor years, having one recruit may be an achievement. As such, this measure is not always comparable between years and may explain our results. Further, recruitment is also dependent on parental effects and relationships within the breeding season, which were not quantified here, although they

have been suggested elsewhere (Bebbington et al. 2017; Riehl and Strong 2018), whereas de-lifed fitness also captures long-term survival. We found that older males recruited more offspring, likely by virtue of older males siring more extra-pair offspring (Girndt et al. 2018). Likewise, younger birds had lower annual de-lifed fitness, because younger birds had not recruited any offspring in previous years that would contribute to their current de-lifed fitness.

In conclusion, we suggest a link between opposite-sex association and reproductive success on the annual scale, suggesting a mechanism for selection to shape social behaviour. At the lifetime scale, we suggest that selection on sociality is stable, suggesting greater fitness for those at the population mean in a wild population of passerine birds.

Chapter 4

Indirect Genetic Effects Increase Heritability Estimates for Male and Female Extra-Pair Reproduction

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Abstract: The question of why females engage in extra-pair behaviours is long-standing in evolutionary biology. One suggestion is that these behaviours are maintained through pleiotropic effects on male extra-pair behaviours (genes controlling extra-pair reproduction are shared between sexes, but only beneficial to one sex, in this case, males). However, extra-pair reproduction must be heritable and positively genetically correlated between sexes for this to evolve. Previous studies have suggested low heritability, with no evidence for between-sex genetic correlations in extra-pair reproduction. However, these have not considered indirect genetic effects (derived from the behaviour of others, IGEs) from the social partner or the influence of the social partner's genotype on the phenotype of an individual, despite the potential of IGEs to uncover hidden heritable variation. Using data from a closed house sparrow population with a genetic pedigree spanning two decades, we tested the influence of social partner IGEs on heritable variation and genetic correlation estimates of extra-pair reproduction. We found that the inclusion of IGEs resulted in larger heritable genetic variance for both male and female extra-pair heritability. While IGEs did not change between-sex genetic correlations, we found that they reduced uncertainty in those estimates. Future studies should consider the effect of IGEs on the mechanisms of sex-specific extra-pair reproduction.

Background

The question of why females engage in extra-pair behaviours has long puzzled evolutionary biologists (Griffith, Owens, and Thuman 2002; Brouwer and Griffith 2019). Extra-pair behaviours (hereafter extra-pair reproduction) occur outside of an established social pair bond, from copulation to realised paternity of extra-pair offspring, and are common in socially monogamous passerine birds (Griffith, Owens, and Thuman 2002; Cockburn 2006). Extra-pair reproduction between species has been linked to phylogenetic variation (Brouwer and Griffith 2019), suggesting a genetic basis for the trait, but the mechanism of selection is unclear and may vary between sexes. The benefit of engaging in extra-pair behaviour for the male is siring more offspring without investing in costly parental care (Trivers 1972; Lebigre, Arcese, and Reid 2013; Raj Pant et al. 2022), but this is not the case for females, who can only replace within-pair offspring with extra-pair offspring, and risk associated costs (Trivers 1972; Dixon et al. 1994; Valera, Hoi, and Krištín 2003; Poiani and Wilks 2000; Matysioková and Remeš 2013; Schroeder et al. 2016; Albery et al. 2021). Yet, females actively seek extra-pair copulation (Lifjeld and Robertson 1992; Forstmeier 2007; Girndt et al. 2018).

Adaptive hypotheses explain female participation in extra-pair behaviours with indirect benefits, such as genetic fitness benefits to her offspring. However, evidence for the indirect benefits hypothesis is sparse (Arct, Drobniak, and Cichoń 2015). In fact, empirical studies either fail to identify indirect benefits, or suggest costs to extra-pair offspring (Akçay and Roughgarden 2007; Schmoll et al. 2009; Sardell et al. 2012; Hsu et al. 2014; Hsu et al. 2015; Grinkov et al. 2022) and to promiscuous females (Forstmeier 2007; Matysioková and Remeš 2013; Schroeder et al. 2016). An alternative, non-adaptive hypothesis posits that variation in female extra-pair behaviours is maintained instead through intersexual pleiotropy (Halliday and Arnold 1987; Forstmeier et al. 2014). Intersexual pleiotropy may drive female extra-pair behaviour, where the trait is genetically linked to another trait under positive selection in males, for instance, male extra-pair reproduction (Halliday and Arnold 1987; Reid and Wolak 2018). However, empirically testing the intersexual pleiotropy hypothesis is challenging because any study must demonstrate that male extra-pair reproduction is beneficial, that extra-pair reproduction is

heritable, and that it is positively genetically correlated between sexes (Reid et al. 2011a; Forstmeier et al. 2014).

Multiple studies have found support for the idea that male extra-pair behaviours contribute to male lifetime reproductive success, including research by Albrecht et al. (2009), Webster et al. (2007), Lebigre, Arcese, and Reid (2013), Baldassarre and Webster (2013), Losdat, Arcese, and Reid (2015), and Raj Pant et al. (2022). However, heritability estimates for these behaviours are often low or without robust estimation (Reid et al. 2011a, 2011b, Reid and Wolak 2018; Grinkov et al. 2020). Additionally, so far, empirical studies have not found conclusive evidence for a between-sex correlation in extra-pair behaviour in either captive (Wang et al. 2020) or wild populations (Zietsch et al. 2015; Reid and Wolak 2018). However, these studies did not consider indirect genetic effects (IGEs). IGEs refer to the variance explained by shared genetic variance of interacting conspecifics (Maldonado-Chaparro et al. 2018; see Table 1). If present, IGEs can strongly mediate trait expression and therefore have the potential to reveal "hidden" heritable variation (Wolf et al. 1998; Bijma 2010). For example, female extra-pair reproduction may be influenced by genetic variation that determines the mate-guarding behaviour of her social partner, which in turn limits her access to extra-pair males (Maldonado-Chaparro et al. 2018).

Despite the potential of IGEs to contribute to heritable genetic variance, most quantitative genetic estimates for extra-pair behaviours only consider direct genetic effects (Table 1). Yet, extra-pair behaviour is inherently social and relies on the interplay of up to four individuals – the focal individual, the social partner, and the extra-pair partners of both the focal individual and social partner. Thus, not including IGEs may underestimate the total genetic variance in traits (Kruuk and Wilson, 2018; Schroeder et al., 2019). Moreover, IGEs can facilitate evolution in the presence of positive genetic covariance between the focal individual and their partner, even when heritability is low (Bijma 2010; Bailey, Marie-Orleach, and Moore 2018; Schroeder et al. 2019).

Here, we tested for social partner IGEs and between-sex genetic correlation of extra-pair reproduction using a closed and intensively monitored wild island passerine population, with a genetic pedigree spanning two decades.

Table 4.1. Quantitative genetic terms used in this study, their definitions and key references.

Term	Definition	Key references
Additive genetic variance (V_A)	The component of phenotypic variance in a trait, among individuals in a population, attributed to the additive effects of inherited alleles.	Falconer and McKay (1996); Charmantier, Garant and Kruuk (2014)
Direct genetic effects (DGE)	The effect of an individual's own genes on their own trait expression. For example, the black badge of the male house sparrow is the result of his own genes, with no outside influence.	Wolf et al., (1998); Bijma (2011)
Indirect genetic effects (IGE)	The effect of individual/s genes on the expression of another individual's trait. For example, male mate-guarding behaviour, a direct genetic effect of his own genotype, prevents a female from copulation with another male, an expression of her own phenotype. The male's genotype directly affects the expression of the female's phenotype.	Wolf et al., (1998); Bijma (2011)
Genetic correlations (r_g)	The magnitude and direction to which the expression of two traits are influenced by the same set of genes, ranging from (-1, genetic variation fully influences both traits in opposite directions) to (1, both traits are fully influenced in the same direction).	Charmantier, Garat and Kruuk (2014)
Pleiotropic effects	Pleiotropy describes a single gene, or set of genes, that influence multiple unrelated traits, where r_g describes the magnitude and direction of correlation, and pleiotropy	Halliday and Arnold (1987)

	describes a mechanism underlying the correlation between traits.	
Heritability (h^2)	The proportion of phenotypic variance in a trait that is due to additive genetic variance from additive direct genetic effects only, ranging from (0, direct additive genetic variance accounts for no phenotypic variation in a trait) to (1, direct additive genetic variance fully determines phenotypic variation in a trait).	Wilson et al. (2010); Charmantier, Garat and Kruuk (2014); Schroeder et al., (2019)
Total heritable variation (t^2)	The proportion of phenotypic variance in a trait that is due to genetic variation from direct and indirect genetic effects, and their covariance.	Bijma (2011); Schroeder et al., (2019)
Individual permanent environment (PE)	Environmental effects on an individual's phenotype that are constant across (or common to) repeated measures on that individual. For example, sparrows with nests in noisy environments provisioned offspring less often than those in quieter breeding locations.	Kruuk and Hadfield (2007); Charmantier, Garat and Kruuk (2014)
Social permanent environment (SE)	Environmental effects (see above; PE) on an individual's phenotype that are constant across (or common to) repeated measures on a conspecific (in this case the social partner). For example, how much parental care a social partner provides to a brood may change the amount of parental care provided by the focal individual.	Maldonado-Chaparro et al. (2018)

Methods

Study system

We have monitored the sedentary and closed population of house sparrow *Passer domesticus* (hereafter sparrow/s) breeding on Lundy Island in the Bristol Channel, UK (51°10'N, 4°40'W) systematically since 2000 (see Ockendon, Griffith, and Burke 2009; Schroeder et al. 2012; Chapter 3). All sparrows are marked with a unique sequence of three coloured leg rings and a BTO metal ring to allow identification of social parents at nesting boxes (for details, see Nakagawa et al. 2007). Annually, nearly all present sparrows are identified by observation and capture without bias (Simons et al. 2015). We collected DNA samples from nestlings at the natal site and from recaptured adults and used 22 microsatellite loci to allocate paternity (Dawson et al. 2012). Female house sparrows are socially monogamous but genetically promiscuous (Schroeder et al. 2016), and, on Lundy, our sparrows instigate a mean of 2.3 (sd 1.04) broods and lay a mean of 9.1 (sd 4.9) eggs annually (Westneat et al. 2014). Previous studies have described extra-pair behaviour but found no evidence for adaptive benefits to females of extra-pair behaviour in this system (Ockendon, Griffith, and Burke 2009; Hsu et al. 2014, 2015, Schroeder et al. 2016). Changing social partners is common, with 47% of individuals having more than one social partner across their lifetime (Schroeder et al. 2016).

We used these data to construct a genetic pedigree (Schroeder et al. 2015) spanning 20 years from 2000–2019 and comprised of 8151 individuals. We identified extra-pair offspring where the genetic sire differed from the social partner in the pedigree. We defined an extra-pair reproduction event differently from the perspective of each social partner: a male extra-pair reproduction event was measured by the count of extra-pair offspring he sired in other nests while he maintained his own social brood elsewhere. We did this by defining the start and end date of each social brood and checking the paternity of offspring against the list of present males. For females, the number of extra-pair offspring she can raise is limited by her egg production. Thus, we measured a female extra-pair reproduction event as a binary trait (extra-pair offspring present in brood, 1, or absent, 0). We considered all eggs in her nest to be her own, as our pedigree shows no nest parasitism (egg-dumping) as a strategy in our house sparrow system.

To avoid pseudo-replication and to measure male and female extra-pair reproduction using different scales in our models, we considered the perspectives of both social parents separately in our models. Because each individual may be involved in several broods over the course of their lifetime, the number of extra-pair samples exceeds the total number of unique individuals and initiated broods. Thus, each social brood was measured twice, once from the social female's perspective and once, separately from the social male's perspective.

Heritability and IGE models

We estimated within-sex heritability and between-sex genetic correlations of extra-pair reproduction using animal models. Animal models use a genetic pedigree within a mixed-effect model to differentiate between environmental and genetic influences on a phenotypic trait (Wilson et al. 2010). We ran a series of animal models using MCMCglmm (Hadfield 2010) in R, v3.6.3 (R Core Team et al. 2023).

We used a series of univariate and bivariate models with different random effects to determine whether social partner IGEs detected genetic variance within-sex extra-pair reproduction. We then used the same approach to test for genetic correlations between male and female extra-pair behaviour (see Tables 4.3 and 4.4 for model specifications). To improve confidence in our models, we repeated each using multiple sets of priors, which confirmed the results qualitatively (Table S4.1). We modelled male extra-pair reproduction as a Poisson trait and female extra-pair reproduction as a threshold trait (i.e., presence, 1, or absence, 0, of extra-pair offspring within a brood). To reflect the increased likelihood of older males siring extra-pair offspring, we included age as a fixed effect across all models (Girndt et al., 2018). We did not include fine-scale environmental or social effects, which can potentially bias heritability estimates in closed systems (Germain et al. 2016; Grinkov et al. 2022).

In models measuring heritability, we included the focal individuals' identities twice as random effects. The first random effect was used to estimate the effect of the individual permanent environment, and the second one was linked to a pedigree-based inverse relatedness matrix to estimate DGE (Table 4.3, Models 1.1 + 1.2). This separates

environmental and genetic causes of variance in extra-pair reproduction (Kruuk and Hadfield, 2007). In models measuring total heritable variation, considering both DGE and IGE, we also included the identity of the social partner twice: first to estimate the social partner's permanent environment and then, to generate a pedigree-based relatedness matrix linked to the partner, to estimate the IGE. In univariate models, we also modelled covariation between DGEs and IGEs, but we could not do this in bivariate models due to MCMCglmm package constraints (Table 4.4). We constrained the covariance to zero for all non-genetic effects in bivariate models because extra-pair reproduction as we defined them cannot be expressed in the same individual from the male and female perspective. Initial analysis included breeding year as a random effect, but it accounted for little variation and did not change quantitative genetic estimates across multiple models. Therefore, it was removed from further analysis.

To estimate the additive genetic variance of non-Gaussian traits, we used an associated link function in the GLMM (de Villemereuil et al. 2016). We used natural log and probit link functions for male and female models, respectively, using the Poisson and threshold families in the MCMCglmm package (Hadfield, 2010). This means that the estimates are on a 'latent' scale, transformed by the link function, and no longer on the same scale of the observed data. Therefore, any variance estimates (and hence heritabilities and genetic correlation estimates) from the model will also be on the latent scale (de Villemereuil et al. 2016). Following de Villemereuil et al. (2018), it may be more appropriate to interpret heritability and genetic correlation estimates on the observed scale using back-transforming model outputs. However, due to the influence of fixed effects in estimating quantitative genetic parameters in non-Gaussian models, most studies report only the heritability of non-Gaussian traits on latent scales (latent scale quantitative genetic estimates). We used the R package QGglmm (de Villemereuil et al. 2016) to back-transform quantitative genetic variance estimates (and therefore heritability, IGEs, total heritable variation, and genetic correlations) on the observed scale. We also included both latent and observed scale estimates to aid in comparability (Table 4.2). All models were deemed to have converged when autocorrelation was less than 0.1, trace and density plots were unimodal and effective sample sizes for each effect were >1000 (Hadfield 2010). We considered heritability and variance estimates to be non-zero, to where the lower credible interval did not span zero (≥0.001).

Table 4.2: Equations used to calculate heritability and genetic correlation estimates on latent and observed scales. list of equations used to calculate heritability and genetic correlation estimates on latent and observed scales adapted from Bijma (2011), De Villemereuil *et al.* (2018), and Schroeder *et al.* (2019). Where V_p is the total phenotypic variation, V_{random} is the combined variance of the random effects, V_{fixed} is the combined variance of the fixed effects, $V_{(Xb)}$ is the variance of the linear predictor of the model, V_{Adge} is the direct genetic effects, V_{Aige} is the indirect genetic effects from the social partner, $Cov_{(VAdge * VAige)}$ is the covariance between the direct and indirect genetic effects, V_{Af} and V_{Am} are the variances of the female and male genetic effects and $Cov_{(VAf * VAm)}$ is the covariance between female and male genetic effects. Latent estimates were calculated as shown below. Estimates on the observed scale were calculated using back transformed V_A, V_P, V_{IGE}, $Cov_{(fDE * fDE)}$, V_{fA} and V_{mA} estimates using QGglmm.

Estimate	Equation	Applicable models
Latent scale fixed effect variance (V_{fixed})	$V_{fixed} = V_{(Xb)}$	All models
Total phenotypic variation (V_p)	$V_P = V_{fixed} + V_{random}$	All models
Heritability (h^2)	$h^2 = \frac{V_{Adge}}{V_P}$	1.1, 1.2, 2.1, 2.2, 5, 6
Total Heritable Variation (t^2)	$t^2 = \frac{V_{Adge} + V_{Aige}}{V_P}$	3.1, 3.2, 7
Total Heritable Variation (t^2)	$t^2 = \frac{V_{Adge} + V_{Aige} + 2Cov_{(V_{Adge}, V_{Aige})}}{V_P}$	4.1, 4.2
Genetic Correlation (r_g)	$r_g = \frac{Cov(V_{fAdge}, V_{mAdge})}{\sqrt{(V_{fAdge} \cdot V_{mAdge})}}$	5, 6
Genetic Correlation (r_g)	$r_g = \frac{Cov((V_{fAdge} + V_{fAige}), (V_{mAdge} + V_{mAige}))}{\sqrt{((V_{fAdge} + V_{fAige}) \cdot (V_{mAdge} + V_{mAige}))}}$	7

Results

Prevalence of extra-pair reproduction

We recorded 1,787 initiated broods with complete parental data, involving 776 individual house sparrows, 410 females and 366 males. The total number of offspring in the pedigree was 6,774, with 18.95% (1283) being sired by a male different from their social father. From these data, we identified 3,233 extra-pair reproduction samples for our models from the female (1721) and the social male (1512) perspectives.

Heritability and IGE models

Model outputs did not differ qualitatively between models using different priors (Tables 4.3–4.4; S4.1–4.3). Direct additive genetic variance for male and male and female extra-pair reproduction was close to zero (Table 4.3). However, the addition of social partner IGEs increased the total genetic variance available for males and females by a factor of 4.91 and 1.52, respectively (Figure 4.1).

Male and female extra-pair reproduction was mostly explained by IGEs and permanent environment, respectively (Table 4.3), accounting for 12% and 11% of total phenotypic variance (Figure 4.1; Table 4.3). All models detected high levels of residual variation for both male and female extra-pair reproduction (Table 4.3).

Table 4.3. **Model specifications for extra pair events in univariate models (1.1 - 4.2).** Random effects parameters included direct genetic effects (DGE), individual permanent environment (PE), social partner permanent environment (SE) and social partner indirect genetic effects (IGE). cov() denotes models where covariation between male and female parameters was allowed to take on any value, otherwise, covariation between male and female parameters was fixed to 0. Individual permanent environment (V_{PE}), additive genetic variance due to direct genetic effects (V_{Adge}), additive genetic variance due to indirect genetic effects ($V_{Aige)}$, social partner permanent environment (V_{SE}), observed scale heritability (h^2_{obs}), latent scale heritability (h^2_{lat}), observed scale total heritable variation (t^2_{obs}), latent scale total heritable variation (t^2_{lat}), from the posterior means of extra pair event models using prior 2. Cov() denotes where covariation between variances was measured. Heritability estimates (h^2) are derived from models 1 and 2, whilst total heritable variation estimates (t^2) are derived from models 3 and 4. Heritability, total heritable variation and variance component estimates where CIs were ≥0.001 are highlighted in bold. Fixed effect specifications are universal across all models.

Model	Random terms	V_{PE}	V_{ADGE}	V_{AIGE}	V_{SE}	Cov (V_{ADGE}, V_{AIGE})	h^2_{obs} or t^2_{obs}	h^2_{lat} or t^2_{lat}
Males as focal individuals								
1.1	male DGE + male PE	**0.699** **(0.365 - 1.123)**	0.061 (<0.001 - 0.218)	-	-	-	0.004 (<0.001 -0.014)	0.022 (<0.001 - 0.08)
2.1	male DGE + male PE + female partner PE	0.389 (<0.001-0.736)	0.106 (<0.001 - 0.36)	-	**0.625** **(0.26 - 1.016)**	-	0.007 (<0.001 -0.021)	0.034 (<0.001 -0.114)
3.1	male DGE + male PE + female partner PE + female partner IGE	0.367 (<0.001 -0.724)	0.111 (<0.001 - 0.38)	0.404 (<0.001-0.89)	0.282 (<0.001 - 0.706)	-	0.029 (<0.001 -0.056)	**0.147** **(0.001 - 0.29)**
4.1	cov(male DGE + female partner IGE) + male PE + female partner	0.315 (<0.001-0.675)	0.143 (<0.001 - 0.42)	0.428 (<0.001 - 0.086)	0.265 (<0.001 - 0.679)	-0.114 (-0.354 - 0.08)	0.02 (<0.001 -0.043)	**0.134** **(0.001 - 0.29)**

Table 4.3: continued overleaf.

Females as focal individuals								
2.1	female DGE + female PE	0.17 (0.067 - 0.286)	0.024 (<0.001 - 0.079)	-	-	-	0.013 (<0.001 -0.041)	0.02 (<0.001-0.065)
2.2	female DGE + female PE + male partner PE	**0.153 (0.033 - 0.272)**	0.03 (<0.001- 0.095)	-	0.054 (<0.001 - 0.136)	-	0.015 (<0.001 -0.047)	0.02 (<0.001 -0.065)
3.2	female DGE + female PE + male partner PE + male partner IGE	**0.151 (0.035 - 0.285)**	0.03 (<0.001 -0.098)	0.0125 (<0.001 -0.045)	0.05 (<0.001 - 0.126)	-	0.021 (<0.001 -0.059)	0.034 (<0.001 -0.095)
4.2	cov(female DGE + male partner IGE) + female PE + male partner PE	**0.15 (0.044 - 0.277)**	0.031 (<0.001 - 0.096)	0.012 (<0.001 -0.046)	0.05 (<0.001 - 0.129)	-0.0015 (-0.027 -0.018)	0.02 (<0.001 -0.057)	0.032 (<0.001 -0.092)

Table 4.4. Model specifications for bivariate covariance models (5-7). Random effects parameters included direct genetic effects (DGE), individual permanent environment (PE), social partner permanent environment (SE) and social partner indirect genetic effects (IGE). cov() denotes models where covariation between male and female parameters was allowed to take on any value, otherwise, covariation between male and female parameters was fixed to 0. Individual permanent environment (V_{PE}), additive genetic variance due to direct genetic effects (V_{ADGE}), additive genetic variance due to indirect genetic effects (V_{AIGE}), social partner permanent environment (V_{SE}), observed scale heritability (h^2_{obs}), observed scale heritability (h^2_{lat}), observed scale total heritable variation (t^2_{obs}), latent scale total heritable variation (t^2_{obs}), observed scale genetic correlation (r_{gphen}) and latent scale genetic correlations (r_{glat}) from the posterior means of extra pair event models using prior 2. Cov() denotes where covariation between variances was measured. Heritability estimates (h^2) are derived from models 5 and 6 whilst total heritable variation estimates (t^2) are derived from model 7. Heritability, total heritable variation and variance component estimates where CIs were ≥0.001 are highlighted in bold. Residual variance, intercept and fixed effect estimates can be found in Table 4.3. Fixed effect specifications are universal across all models.

Covariance models													
Model	Random terms	Male V_{ADGE}	Female V_{ADGE}	Male V_{AIGE}	Female V_{AIGE}	COV (V_{ADGE})	COV (V_{AIGE})	Male h^2_{obs} or t^2_{obs}	Male h^2_{lat} or t^2_{lat}	Female h^2_{obs} or t^2_{obs}	Female h^2_{lat} or t^2_{lat}	r_{gobs}	r_{glat}
5	cov(male DGE + female DGE) + idh(male PE + female PE)	0.063 (<0.001 – 0.227)	0.026 (<0.001 – 0.089)	-	-	0.0007 (-3.482e-02 – 0.035)	-	0.004 (<0.001 - 0.015)	0.026 (<0.001 - 0.094)	0.013 (<0.001 - 0.045)	0.021 (<0.001 - 0.072)	0.024 (-0.76 - 0.79)	0.024 (-0.76 - 0.79)
6	cov(male DGE + female DGE) + idh(male PE + female PE) + idh(female partner PE + male partner PE)	0.10 (<0.001 – 0.342)	0.028 (<0.01 – 0.096)	-	-	0.002 (-3.84e-02 – 0.046)	-	0.006 (<0.001 - 0.012)	0.041 (<0.001 - 0.14)	0.015 (<0.001 - 0.045)	0.023 (<0.001 - 0.074)	0.029 (-0.73 - 0.791)	0.029 (-0.73 - 0.791)
7	cov(male DGE + female DGE) + idh(male PE + female PE) + idh(female partner PE + male partner PE) + cov(female partner IGE + male partner IGE)												

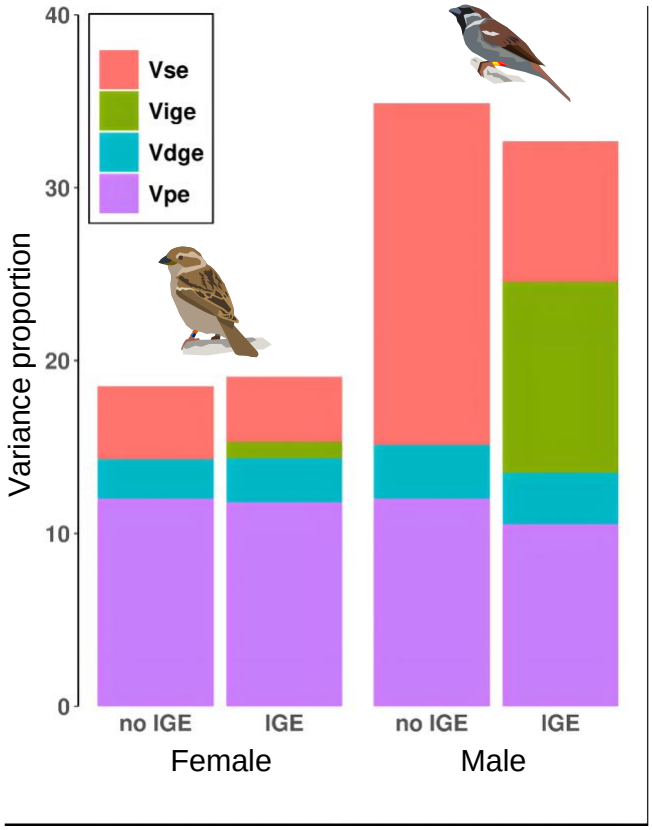

Figure 4.1. **Indirect Genetic Effects (IGEs) on the variance explained by extra-pair reproduction**. The proportion of the variance explained in male and female extra-pair reproduction by different variance components with and without the inclusion of social partner indirect genetic effects. Variance components, including social partner permanent environment variance (Vse), additive genetic variance estimated from direct genetic effects (Vdge), additive genetic variance estimated from indirect genetic effects (Vige), and permanent environment variance (Vpe). In bars without IGEs, variance proportions are estimated from Model 2.1 for females and 2.2 for males. In bars with IGEs, variance proportions are calculated from Models 3.1 for females and 3.2 for males. All variances shown were estimated on latent scales. The proportion of variance due to fixed effects is not shown here.

Male and female heritability

Both latent and observed scale heritability estimates were close to zero for male and female extra-pair reproduction (Table 4.3). Social partner IGEs slightly increased female total heritable variation estimates, but increased male total heritable variation substantially; however, CIs were still close to zero for both males and females (Table 4.3). Covariation between direct and indirect genetic effects for male and female extra-pair behaviours were both negative but overlapped 0, reducing total heritable variation estimates (Table 4.4).

Genetic correlation estimates between male and female extra-pair reproduction.

Genetic correlations between male and female extra-pair reproduction estimated from direct genetic effects were positive, but the CIs greatly overlapped zero (Table 4.4). Both models, including the addition of social IGEs, produced close to zero correlation, and CIs still overlapped zero but reduced the uncertainty in those estimates (Table 4.4). Quantitative genetic parameters did not differ between different priors, nor between univariate and bivariate models (Tables 4.3, 4.4, S4.1).

Discussion

Our results suggest that additive genetic variance and heritability for extra-pair reproduction increase with the inclusion of social partner IGEs in both sexes, but particularly in males, where total genetic variation reaches 14%. However, the addition of IGEs also increased the uncertainty in variance. Although that uncertainty may be linked to increased model complexity, simulation studies suggest (Bijma et al*.,* 2014) that 793 breeding pairs are sufficient to consider our estimates reliable. Our results support those of other systems that find marginal heritability in extra-pair reproduction with high residual variation, implying that male and female extra-pair reproduction may be inherently flexible traits (Forstmeier et al., 2011, Reid et al., 2011a; Reid et al., 2011b; Zietsch et al., 2015; Grinkov et al., 2020; Wang et al., 2020; Beck et al., 2020).

Extra-pair reproduction may be driven by genes that control copulation and solicitation (Dixon et al., 1994; Matysioková and Remeš, 2013; Schroeder et al., 2016) and by the behaviour of neighbours (Beck et al., 2020; Beck et al., 2021). However, despite extra-pair copulations likely commonly occurring (Fossøy, Johnsen, and Lifjeld, 2006), not all copulations result in extra-pair offspring, due to mate-guarding (Forstmeier et al., 2011) and post-copulatory processes (Knief et al 2017; Girndt et al., 2019). These processes are difficult to account for in wild populations (Beck et al., 2020), and may contribute to unexplained variation in both male and female reproduction, consequently resulting in smaller additive genetic variance and heritability estimates for extra-pair reproduction (Forstmeier et al., 2014; Beck et al., 2020). This has been demonstrated in captive zebra finches *Taeniopygia* sp*.*, where the heritability of copulation behaviours is substantial (Forstmeier et al., 2011; Wang et al., 2020), but equivalent data is extremely difficult to collect in the wild (Beck et al., 2020). Also, the number of extra-pair copulations may not predict the number of extra-pair offspring produced (Girndt et al., 2018), confounding the issue further. Despite this, because these genes are only passed on to the next generation through the recruitment of extra-pair offspring, extra-pair behaviour measurements in the wild have evolutionary relevance when compared to captive systems that may miss population-scale processes. Such processes as assortative

mating may skew heritability estimates for both extra-pair copulations and successful reproduction (Reid and Wolak, 2018; Wang et al., 2020).

Between-sex genetic correlations are notoriously difficult to estimate in wild populations due to the requirement of large sample sizes (Lynch, 1999; Bonduriansky and Chenoweth 2009), resulting in uncertainty in existing estimates (Forstmeier et al., 2011; Reid and Wolak, 2018). This is likely due to the small genetic variances estimated for both male and female extra-pair reproduction (Travers et al., 2016). Estimating between-sex genetic correlations between direct measures of male and female extra-pair copulation behaviour may yield more precise estimates (Forstmeier et al., 2014). The inclusion of social IGE effects in male and female extra-pair copulation behaviour measurements may reduce uncertainty even further. However, a high degree of uncertainty may also possibly hide the existing weak positive or negative genetic correlations between female and male extra-pair reproduction (Reid and Wolak, 2018). Future work could consider simulations to aid in answering these questions (Reid and Wolak, 2018), while in field studies, sample sizes increase with subsequent generations.

Past selection on male reproductive success may also have depleted additive genetic variation in male extra-pair reproduction, and in females through positive genetic correlations with males, resulting in low heritability estimates in both male and female extra-pair reproduction and high uncertainty in genetic correlation estimates. In this case, although past correlations between male and female extra-pair reproduction might have existed in this population, we can no longer detect them. However, female extra-pair reproduction may not be maintained by positive genetic correlations with male extra-pair reproduction, even if positive between-sex genetic correlations previously existed, as partaking in extra-pair reproduction may not necessarily increase lifetime reproductive success for males. For example, in pursuit of extra-pair copulations, males may reduce mate guarding, with a gain in extra-pair offspring resulting in fewer within-pair offspring and no overall change to lifetime reproductive success (Møller and Birkhead, 1993; Møller and Ninni, 1998; Harts and Kokko, 2013; Reid and Wolak, 2018). This, combined with low extra-pair offspring fitness (Hsu et al., 2015), could result in decreased male lifetime reproductive success. It is also possible that female extra-pair reproduction persists

through additional pleiotropic effects that benefit female fecundity (Forstemier et al., 2014). Positive genetic correlations between female solicitation behaviour and female fecundity have been described in captive populations (Wang et al., 2020), but empirical evidence from wild systems is lacking.

Our study explored the genetic basis and role of the social partner on male and female extra-pair reproduction to better understand how such behaviours are maintained in socially monogamous populations. We found no support for the notion that female extra-pair reproduction is maintained in socially monogamous populations through antagonistic intersexual pleiotropy. However, we suggest that social partner IGEs can uncover hidden genetic variations, especially for males. Social partner IGEs contributed substantially more to total male extra-pair heritability, accounting for more total additive genetic variance than male direct genetic effects and explained the largest proportion of phenotypic variation. We demonstrate the importance of IGE inclusion in quantitative models that explore aspects of animal behaviour. Future studies into why female extra-pair reproduction persists in socially monogamous populations should consider the intrasexual antagonistic pleiotropy hypothesis and, where sample size allows, should include social partner IGEs when estimating heritabilities.

Chapter 5

Divorce is Linked with Extra-Pair Paternity in Monogamous Passerine

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Abstract: The question of why socially monogamous females engage in extra-pair behaviour is long-standing in evolutionary biology. Recent theoretical work has moved away from the indirect-benefits hypothesis to explain female extra-pair behaviours, instead favouring suggestions that they are the result of pleiotropic effects. That is, a trait under strong positive selection in either or both sexes are genetically linked to another, often unrelated, trait. For example, genes beneficial to female fecundity (contributing to within-pair solicitation of her social partner) are linked with extra-pair behaviour (soliciting copulations from extra-pair males). Here, we test two predictions from this hypothesis: we test the prediction that female divorce, measured by the number of social mates within a given year, is linked with (1) the number of extra-pair males and (2) the proportion of her offspring that are extra-pair. Our results suggest that females who frequently divorce social partners are more likely to produce extra-pair offspring than those who maintain social monogamy. However, in contrast, those females do not also have a higher proportion of extra-pair offspring. The number of broods initiated was also positively correlated with extra-pair males, probably through the increased opportunity for extra-pair males to sire offspring over a longer breeding season. Our results provide an empirical example of a behavioural trait beneficial to female fecundity that is also linked with extra-pair behaviour. These empirical results support the intrasexual pleiotropy hypothesis as a driver of female extra-pair behaviour.

Background

Since extra-pair paternity was first demonstrated using genetic fingerprinting to allocate parentage to a house sparrow *Passer domesticus* (hereafter sparrow, Burke, and Bruford 1987), the question of why females in socially monogamous breeding systems engage in promiscuous behaviour still presents a challenge to evolutionary biologists (Griffith, Owens, and Thuman 2022; Brouwer and Griffith 2019). Sexual selection dictates that females should choose a reproductive partner to maximize the fitness benefits he provides either directly to them, through parental care, or through a high-quality breeding territory (Møller 2000; Nakagawa et al. 2007; Brouwer and Griffith 2019). Other benefits can be incurred indirectly by providing offspring with high-quality genes from the male. However, extra-pair males, those from outside an established pair bond, can only provide indirect benefits to females. That is, extra-pair males may sire offspring without investing in costly parental care (Lebigre, Arcese, and Reid 2013; Raj Pant et al. 2022; Table 5.1). The good genes hypothesis predicts that extra-pair males should signal a better (Hamilton and Zuk 1982; Birkhead 1995; Kirkpatrick and Barton 1997), or more compatible (Blomqvist et al. 2002; Ihle, Kempenaers, and Forstmeier 2015; but also see Griffith and Immler 2009) proposition than her social partner.

However, these predictions – that offspring produced by extra-pair mating, and extra-pair males themselves are of superior quality than within-pair offspring and within-pair males, respectively – are not well supported by empirical evidence (Hsu et al. 2015; Grinkov et al. 2022). This is highlighted by multiple meta-analyses on the topic (Akçay and Roughgarden 2007; Arct, Drobniak, and Cichoń 2015), and subsequent discussion in the field (Drobniak, Arct, and Cichoń 2015; Griffith 2015; Nakagawa, Schroeder, and Burke 2015; Reid 2015; Brouwer and Griffith 2019). Further, several empirical studies have suggested costs rather than indirect benefits to extra-pair offspring (Schmoll et al. 2009; Sardell et al. 2012; Hsu et al. 2014) and to promiscuous females (Forstmeier 2007; Matysioková and Remeš 2013; Schroeder et al. 2016). Yet, females actively seek extra-pair copulations (Lifjeld and Robertson 1992; Forstmeier 2007; Girndt et al. 2018), and to date, the mechanism that drives these behaviours in females remains unresolved.

Several alternative hypotheses have sought to explain why female extra-pair behaviours persist. For example, insurance against the death (Petrie and Kempenaers 1998) or infertility (Wetton and Parkin 1991; Sheldon 1994; Vedder 2022; Table 5.1) of a social partner may motivate females to seek extra-pair copulations, maintained through indirect selection (Kempenaers and Schlicht 2010). The social environment may be another mediator of extra-pair behaviour (Maldonado-Chaparro et al. 2018; Table 5.1), where individuals with high sociality – their propensity to associate with others – likely have more opportunity to choose partners from larger pools of potential mates. Accordingly, the number (Oh and Badyaev 2010; Chapter 3) and quality (Firth and Sheldon 2016; Beck, Farine, and Kempenaers 2021) of social associations have been empirically shown to be linked to reproductive success, including extra-pair mate choice (Beck, Farine, and Kempenaers 2020). Empirical studies generally find that extra-pair partners are more likely to be close neighbours (Westneat and Sherman 1997; Schlicht, Valcu, and Kempenaers 2015; Mingju et al. 2017; Beck, Farine, and Kempenaers 2020; Beck, Valcu, and Kempenaers 2020), adding weight to the role of opportunism in extra-pair copulation (as empirically demonstrated by Fossøy, Johnsen, and Lifjeld 2006; and theoretically by Brommer et al. 2007; 2010).

Alternatively, the benefits of female extra-pair behaviour may be explained by non-adaptive hypotheses, for example, through antagonistic pleiotropy (Halliday and Arnold 1987; Arnqvist and Kirkpatrick 2005), where extra-pair behaviours are controlled by linked sets of genes and selected for in one or both sexes. The intersexual (between-sex) antagonistic pleiotropy hypothesis (Halliday and Arnold 1987; Reid and Wolak 2018; Table 5.1) posits that female extra-pair behaviours are controlled by sets of genes present in both sexes and selected where the benefit to one sex outweighs the cost to the other (Halliday and Arnold 1987; Reid and Wolak 2018; Wang et al. 2020). For example, the benefit of extra-pair copulations for males outweighs the cost of the behaviour in females who inherit the genes from their fathers. Intersexual antagonistic pleiotropy is a common driver of behavioural traits (Poissant, Wilson, and Coltman 2010). Early empirical studies into non-adaptive explanations for female extra-pair behaviour suggested a role for intersexual pleiotropy (Forstmeier et al. 2011), but subsequent work from the same

system later suggested that intrasexual (or within-sex) pleiotropic effects may better explain female extra-pair behaviour (Wang et al. 2020).

Similarly, the intrasexual antagonistic pleiotropy hypothesis posits that a trait under selection is genetically linked to another trait of the same sex, where the benefits of one trait outweigh the cost of the other trait (Halliday and Arnold 1987; Forstmeier et al. 2014; Wang et al. 2020; Table 5.1). In this case, female extra-pair behaviour could be pleiotropically linked with female fecundity. This would be the case, for example, where female responsiveness to male courtship is pleiotropically linked with increased solicitation of copulations, enhancing fertilization success also in a within-pair context, and extra-pair behaviour may persist (suggested by Wang et al. 2020; Bolund, Schielzeth, and Forstmeier 2012).

Although quantitative genetic evidence for the antagonistic pleiotropy hypotheses is described in captive experiments (Forstmeier et al. 2011; Wang et al. 2020), evidence from wild systems is scarce. Reid et al. (2018) found no relationship between genes beneficial to male reproductive success and female extra-pair behaviour (an example of intersexual antagonistic pleiotropy). Further, quantitative approaches to understanding pleiotropic effects on female extra-pair behaviours have resulted in inconclusive effect sizes, for two reasons: First, the heritability of male and female promiscuity is closely related to fitness, masking any evidence of pleiotropy effect (Reid et al. 2011; Reid 2015; Chapter 4); and second, studies with genetic pedigrees from wild populations are scarce and have few generations, resulting in inconclusive effect sizes (Reid et al. 2011; Moiron, Charmantier, and Bouwhuis 2022; Chapter 4), even where the prevalence of extra-pair behaviour is high. However, if pleiotropic effects drive female extra-pair behaviour, then the expression of two linked behaviours should be empirically—if not genetically—detectable in wild systems.

Because extra-pair behaviours are common in passerine birds (Griffith, Owens, and Thuman 2002; Cockburn 2006; Smith 1988; Forstmeier 2007), they are an excellent model system for testing hypotheses relating to sexual selection and extra-pair behaviour. Here, we used a wild house sparrow population with a twenty-year genetic pedigree to test the prediction that extra-pair behaviours are correlated with social mate choice

(suggested by Wang et al. 2020), an assumption of the intrasexual antagonistic pleiotropy hypothesis. Sparrows have high rates of extra-pair paternity (Hsu et al. 2014; Hsu et al. 2015; Girndt 2018) and are considered a model organism for studies on behaviour, life history, and sexual selection (Sánchez-Tójar, Schroeder, and Farine 2018; Hanson et al. 2020). In this study, we tested whether the female propensity to switch social partners within a breeding year (hereafter, divorce), a trait with a potential genetic basis (Germain, Wolak, and Reid 2018), and a proxy for mate choice, is linked with extra-pair behaviour. First, we tested whether divorce is linked with the number of extra-pair offspring, and then with extra-pair males. We carried out our study in a closed house sparrow system, with a near-complete genetic pedigree spanning 20 years.

Table 5.1. Hypotheses referenced in this chapter; see Brouwer and Griffith (2019) for a comprehensive review.

Referenced hypotheses	Description	References
Good genes	Extra-pair partners that signal a greater genetic proposition than the social male are sought to provide indirect benefits to her offspring.	(Hamilton and Zuk 1982; Birkhead 1995)
Fertility insurance	Extra-pair copulations are sought to protect against infertility in her own social partner, with or without phenotype cues.	(Wetton and Parkin 1991; Sheldon 1994; Vedder 2022)
Sociality as a mediator of variation in extra-pair behaviour	The social environment provides a mechanism for extra-pair behaviour through increased mate choice.	(Maldonado-Chaparro et al. 2018)
Intersexual antagonistic pleiotropy	Non-adaptive female extra-pair mating is derived from alleles where the cost of extra-pair behaviour to females is small relative to the benefit to males.	(Halliday and Arnold 1987; Forstmeier et al. 2014; Wang et al. 2020)
Intrasexual antagonistic pleiotropy	Female extra-pair behaviour is derived from alleles traits beneficial to female fecundity, for example, solicitation of social partners (considered here).	(Forstmeier et al. 2014; Wang et al. 2020)

Methods

System

We systematically monitored a population of house sparrows *Passer domesticus* on Lundy Island in the Bristol Channel, UK (51.11 N, 4.40 W) since 2000 (see Nakagawa et al. 2007; Ockendon, Griffith, and Burke 2009; Schroeder et al. 2012; Chapter 3). The sparrows on Lundy breed in nesting boxes arranged into neighborhoods broadly defined by building infrastructure or linear features. Females are socially monogamous, but genetically promiscuous (Schroeder et al. 2016), and, on Lundy, most have 2 to 3 broods of 4 or 5 eggs each per breeding season (Westneat et al. 2014).

We collected tissue samples from nestlings at the natal site and from recaptured birds post-fledging and used the DNA extracted from those to allocate paternity with the help of > 22 microsatellite loci (Dawson et al. 2012). We then constructed a near-complete genetic pedigree (see Schroeder et al. 2015), spanning 19 years, 2000 - 2019. All sparrows are fitted with a unique sequence of three coloured leg rings and a British Trust for Ornithology (BTO) coded metal ring (for details, see Simons et al. 2015), which allowed us to later identify social pairs at the nest box. Dispersal to and from Lundy Island is limited. This, and our systematic and thorough monitoring, allowed us to determine the exact age of birds in years, and to know when they died, either from the rings of birds found dead, or defined as when ringed birds were not observed for more than two years (see Simmons et al. 2015).

To measure female divorce, we first excluded females that only had a single brood, and thus, no opportunity to divorce their social mate. We also excluded 17 females who replaced mates following the death of their social partner, where the death of a social male occurred during the female breeding year. We removed offspring whose parents (either social or genetic) were missing or uncertain. We defined a divorce event where a female paired socially with a new male, instead of her previous social partner, between broods but within years. This resulted in 353 female breeding years. These female years represented 920 broods by 190 females, 205 social fathers, and 309 genetic sires between 2004 and 2019.

We defined a chick as extra-pair where they survived to the point of sampling on day 2 and the confirmed social father differed from the genetic father (the sire) in our pedigree. We counted the number of extra-pair offspring and the number of both social and extra-pair fathers within females within years (female years).

Models and permutations

To empirically test whether females who divorce more often were also more likely to produce extra-pair offspring, as implied by intrasexual antagonistic pleiotropy theory, we ran two GLMM models with Bayesian Markov Monte Carlo simulations, using MCMCglmm in R (Hadfield 2010; R Core Team 2023):

1) **The association of divorce with extra-pair paternity** – To examine the link between female year divorce and extra-pair paternity, and because MCMCglmm cannot easily deal with proportion data, we ran a multinomial model with the number of extra-pair and social offspring per female year as response variables (see Hadfield 2010). We fitted female divorce, measured as the number of social partners within a female year, the number of broods she initiated, to control for increased opportunity for extra-pair offspring, and her age in years since hatching to compensate for the effect of age on reproductive value (Hsu et al. 2017), as fixed effects. We also included female ID and breeding year as random effects on the intercept to account for variation within those groups.

2) **The effect of divorce on extra-pair male engagement** – To examine the link between female divorce and engagement of extra-pair partners, we used a bivariate model structure, with the number of extra-pair partners within a given female year as the response variable. We again fitted female divorce, the number of broods initiated, and her age in years since hatching as fixed effects. Female ID and breeding year were again modelled as random intercepts to account for variations within those groups. We first ran models using a Poisson distribution and logit link function, but those models failed to converge. Instead, we used a

Gaussian distribution and link function, and output estimates between the Poisson and Gaussian models were equivalent.

For all models, we used the default priors of the MCMCglmm package, and ran over 343,000 iterations, with a burn-in of 34,000, and a thinning interval of 200. We checked the posterior trace plots to ensure that autocorrelation was below 0.1 and that the effective sample sizes ranged between 1,000 and 2,000. The fixed effects were considered statistically significant when the 95% credible interval (CI) of its posterior distribution did not span zero.

To test that our results were biologically meaningful, and not the outcome of random chance, we ran a series of permutations. We removed the link between female ID and reproductive traits by building random matrices between males and females to rerun our models. First, we simulated 1000 breeding events by shuffling the number of offspring and extra-pair offspring between females while maintaining the age structure. We then repeated these steps to simulate the number of extra-pair partners for each female. For each permutation, we ran an identical GLMM model to that described above. We dropped the bottom 2.5% of the lower credible intervals, and the top 2.5% of the upper credible intervals, to leave 95% of the 1,000 credible intervals. We then extracted the minimum lower and maximum upper credible intervals and the mean estimate. We interpreted significance—that is, our results were unlikely to have occurred by chance—where the observed posterior mean fell outside the span of the permuted credible intervals.

Results

From 533 female breeding years, we identified 4,963 offspring of known social and genetic parentage, including 932 extra-pair offspring, 1.7 per female year (0–11, SD: 1.77), from 1,403 broods (2.6 per female year, SD: 0.68). Females who engaged in extra-pair behaviour had a mean of 2.5 extra-pair offspring per female year (1–11, SD: 1.6). Within female breeding years, 120 females divorced their social partners on at least one occasion (110 once, and 10 twice, 1.24 per social partners female year: sd 0.47), where 413 remained faithful to a single social partner over multiple broods within a female year.

Neither the number of social fathers nor the number of broods was significantly linked to the proportion of extra-pair offspring that hatched within a female year. However, the number of social fathers and the number of broods per female year were positively linked to the number of extra-pair partners she chose within a breeding year. The log odds of having an extra-pair partner increased by 0.43, or 1.54 extra-pair partners, per social partner, and by 0.24, or 1.27 extra-pair partners per brood, respectively (Figure 5.1). Female age was not linked to either the proportion of extra-pair offspring or the number of extra-pair sires.

Neither the number of broods nor the number of social fathers was associated with the number of extra-pair partners in our randomizations. The observed estimates all fell outside the simulated confidence intervals (Figure 5.1). Observed posterior means fell outside of simulated 95% confidence intervals for both broods (0.27, -1.29 – 0.13) and social fathers (0.81, -0.00 – 1.86), implying that our results are not the result of chance. Our results support the hypothesis that females who divorce social partners regularly also engage more extra-pair males than those who maintain social monogamy.

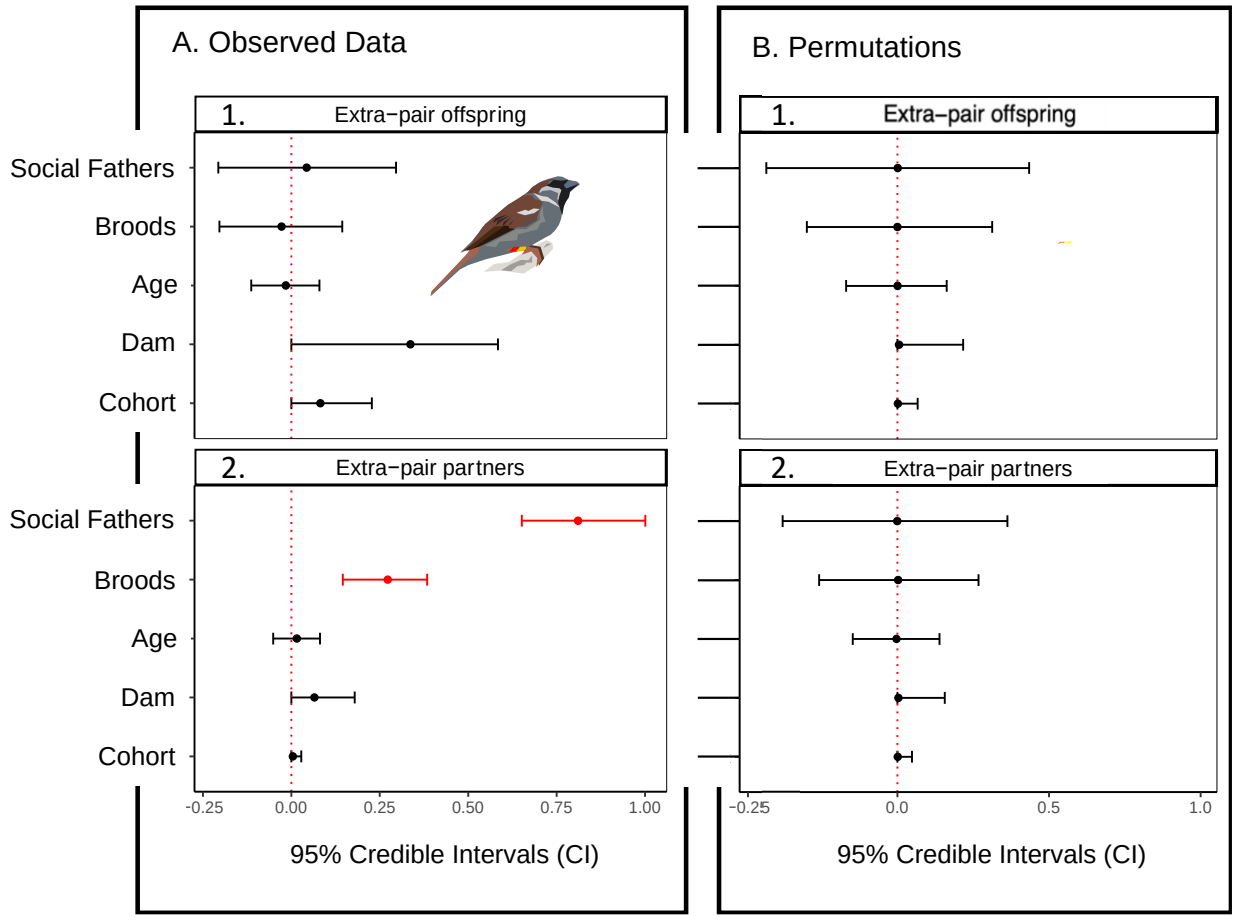

Figure 5.1. Extra-pair model outputs for observed and permuted data. We interpreted significance in GLMM model outputs where 95% credible intervals did not span zero (red bars; otherwise, black bars denote non-significant results), and points denote posterior mean. Our observed results (A1-2) suggest that female birds who divorce social partners regularly engage with more extra-pair males than those who maintain social monogamy. Likewise, the number of broods initiated also significantly predicted an increase in extra-pair males without affecting the proportion of extra-pair offspring, presumably by virtue of opportunity (A2; red bars). Simulated breeding events (B1-2), where extra-pair males and extra-pair offspring were permuted between females in our system, were not significant. Random effects are given in the shaded box (Dam and Cohort) for each model. Intercept and residuals for each model are not shown in the figure: A1, intercept -1.65 (-2.12 – -1.1), residuals 0.61 (-2.11 – 0.92); A2, intercept -1.65 (-2.11 – -1.8), residuals 0.53 (3.47 – 0.72); B1, intercept -0.5 (-8.78 – -0.14), residuals 0.81 (6.54 – 0.95); B2, intercept 1.26 (8.53 – 1.66), residuals 1.06 (9.37 – 1.2).

Discussion

We empirically tested an assumption of the intrasexual antagonistic pleiotropy hypothesis—that extra-pair behaviour is linked to another trait beneficial to female fecundity, in this case, solicitation of social partners (Halliday and Arnold 1987; Wang et al. 2020), which we measured as the rate of divorce within years. Our results suggest that female divorce is linked with females engaging more extra-pair males. However, we found no effect of divorce on the proportion of extra-pair offspring. We also found a link between the number of broods initiated and female engagement of extra-pair males, which we consider a by-product of the opportunity for more extra-pair paternity over a longer breeding period.

Opportunity has been demonstrated to increase extra-pair behaviour in several systems (see Maldonado-Chaparro et al. 2018), including empirical studies suggesting that extra-pair copulations may be obligate, where they are facilitated by opportunity (Fossøy, Johnsen, and Lifjeld 2006). Liker, Freckleton, and Székely (2014) suggest that the sex ratio of the wider social environment also influences the divorce rate, driven by female-biased sex ratios and infidelity, by male-biased sex ratios (but also Culina, Hinde, and Sheldon 2015). However, opportunity cannot explain what drives extra-pair decision making; instead, that must come from selective advantage to those who engage in extra-pair copulations. Our results support the suggestion by Wang et al. (2020) that female social solicitation behaviours are linked with extra-pair mate solicitation, and therefore, support intrasexual antagonistic pleiotropy as a mechanism for female extra-pair behaviour. However, we suggest that other, probably post-copulatory, processes control the proportion of extra-pair offspring born to females within a breeding year. Equivalent attention has also been given to intersexual pleiotropic effects, where female extra-pair behaviour may be linked with a trait that benefits male reproductive success. These studies have found little support in captivity (Wang et al. 2020), or in wild populations (Zietsch et al. 2015; Reid and Wolak 2018). Where quantitative genetic studies have sought to demonstrate a heritable basis for male extra-pair behaviour required for intersexual pleiotropy to drive female extra-pair behaviour, estimates are

low (Reid et al. 2011; Reid and Wolak 2018; Grinkov et al. 2020). However, in Chapter 4, we found that the inclusion of social partner indirect genetic effects (those derived from the behaviour of another) improved model fit for the heritability of both male and female extra-pair behaviour, implying a role for the wider social environment in the plasticity of extra-pair behaviour.

We used divorce rate within a female breeding year, between multiple broods, as a measure of solicitation, but not between breeding years—more akin to a classic definition of divorce behaviour. Divorce is more broadly defined as where both partners are alive, and at least one of them has been paired with a new social partner (Black and Hulme 1996; but also see Culina, Radersma, and Sheldon 2015). However, the motivations for female sparrows to divorce social partners between broods may be like those described elsewhere for divorce, which has been demonstrated to represent an adaptive strategy between sexes across monogamous birds (Choudhury 1995; Culina, Radersma, and Sheldon 2015; Mercier, Yoccoz, and Descamps 2021; Wilson, Nguyen, and Burley 2022). Previous works have also considered divorce and extra-pair behaviours as linked traits in the context of indirect benefits (Cezilly and Nager 1995; Choudhury 1995); that is, both provide females with a mechanism to improve the quality of their social partner by divorcing or cuckolding lesser quality males. However, empirical evidence for indirect benefits derived from extra-pair behaviours is scarce (Akçay and Roughgarden 2007; Arct, Drobniak, and Cichoń 2015), and multi-paternity broods were not linked to the divorce rate (Ramsay et al. 2000).

Although we consider our data to be near complete, our phenotypic study is still subject to some bias (Hadfield 2008). For example, we sampled chicks for paternity at day two (see Chapter 3), but this may still exclude an invisible fraction of those pairs, females (Kidd et al. 2015) or eggs (Yuta et al. 2018; Assersohn et al. 2021) that fail early. As a result, our study measures extra-pair paternity, and not extra-pair copulations, which could be more frequent than is reflected in paternity analysis (Fossøy, Johnsen, and Lifjeld 2006; Girndt 2018). Females that exhibit extra-pair behaviours may not always produce extra-pair offspring, but their within-pair offspring will inherit their genes, which may determine the extra-pair behaviour. Future work may support intrasexual pleiotropy

as a mechanism for female extra-pair behaviour by either including measures of copulation attempts (rather than paternity) or through further quantitative genetic methods. Further, future work may also seek to repeat the study we present here but incorporating some measure of fitness in order to do this, such a study must first establish the fitness consequences of divorce by comparing divorced with non-divorced groups and while accounting for the age and identity of individuals involved. Such an analysis is beyond the scope of this study, in which we sought to establish an empirical link between two types of mate switching, within- and extra-pair.

We demonstrate that females who swap mates more frequently within breeding years engage more extra-pair males but do not have greater proportions of extra-pair offspring. Our study contributes an empirical example to the growing body of research that supports non-adaptive phenomena as mechanisms for why females engage in extra-pair behaviours.

Chapter 6

Animal Social Networks and Female Extra-Pair Paternity: A Summary of Findings and Future Research Direction

Publication statement: This chapter has not been submitted for publication at the time of writing (December 2023)

Summary of core findings

The theme of this thesis relates to the influence of sociality on life history, split into two parts. The first part, Chapters 2 and 3, relates to how social associations may be defined, particularly in gregarious systems, and how those social associations influence individual fitness. The second half of this thesis, Chapters 4 and 5, relate to how social behaviour can be applied to the question of female extra-pair paternity. In the first part of this thesis, we demonstrated that a social association should be defined in the context of the ecology of the study system. Then, that social behaviour has fitness consequences for the individual over the short term. In the second part, we applied principles from the first two research chapters to test hypotheses explaining female extra-pair paternity. We tested two ideas proposed by Maldonado-Chaparro et al. (2018); in Chapter 4, we demonstrated that the inclusion of indirect genetic effects in extra-paternity models increases the heritable variance of extra-pair behaviour for both males and females, suggesting a role for the social preference of the partner and wider social environment. In Chapter 5, we tested an assumption of the intrasexual pleiotropy hypothesis for female extra-pair behaviour, that female extra-pair paternity is linked to another trait beneficial to female fecundity. Below, we review the aims and objectives for each chapter, set out in the introduction, and suggest avenues for future research.

Review of aims.

Aim 1: To test the suitability of existing definitions for social associations between animals and their influence on the structure of a social network (Chapter 2).

In Chapter 2, we described the current systems by which most social systems are defined, that is, either by interaction networks or through association (Krause, Lusseau, and James 2009). Where social interactions are discrete, defined by observed behaviours (Wey et al. 2008; Krause, Lusseau, and James 2009), associations are more ephemeral, often defined by proximity or membership of a group (Franks, Ruxton, and James 2010; Psorakis et al. 2012; Webber et al. 2022). However, poorly defined definitions of behaviour or association may limit the comparability of networks and subsequent hypothesis testing (Castles et al. 2014; Farine and Whitehead 2015). In social birds, associations are often defined between individuals visiting a resource (for example, Aplin et al. 2012; Sánchez-Tójar et al. 2017; Ferreira et al. 2020; Beck, Farine, and Kempenaers 2020), but this in itself may introduce bias, because an association must be defined separately from random aggregation at a bird feeder. This can be achieved through experimental design, for example, by siting more feeders at which birds can be recorded or limiting access to a feeder. However, in most cases, groups are defined by proximity in time—the time window approach or using statistical methods—the GMM approach (Psorakis et al. 2012, 2015). The time window simply links birds who are present in a given space within *t* seconds of each other (Farine 2015). The GMM approach defines a flock (or foraging event) based on activity at a bird feeder—where birds are recorded after a period of absence, before leaving again—and links all individuals within that foraging event as socially associated. This approach has been widely applied across bird systems using the asnipe R package (Farine 2017; Team 2023), but how universally suitable it is remains untested. We compared three commonly applied methods to define an association in flocks of birds and developed a third (which we then also used in Chapter 3): the sliding-time window (Psorakis et al. 2012; Plaza et al. 2019), the GMM approach (Psorakis et al. 2012, 2015) and a third definition based on arrival time to a resource.

In Chapter 2, we introduced the arrival time definition of a social association to compensate for the gregarious ecology of our sparrow system on Lundy Island. Previous works have also found that the GMM may not represent social associations in highly gregarious systems (Ferreira et al. 2020), probably by virtue of increased tolerance to feeding together in flocking species. Rather than assuming that birds that feed together are socially associated, using arrival time, we instead assumed that birds who arrived together were together before they arrived at the feeder. The time birds spent at the feeder, and the other birds that they overlapped with while feeding, were then ignored.

We then used four study systems to extract social networks from foraging birds but using three definitions of social association (time window, GMM, and arrival time). We compared the resulting social networks within the four study systems but between definitions. We demonstrated that despite their specific definition of a social association, differences in network structures were small, and thus, robust to differences in system ecology. Tests for reputability and similarity indices were significant within systems, but, where small differences existed, networks were most similar between systems with similar ecologies (i.e., gregarious systems like house sparrows and sociable weavers were more similar than the great tit system with its nomadic social groups).

In this first research chapter, we presented the argument for using an association definition that aligns with the ecology of the study system, for example, in our system of gregarious house sparrow, time-window or GMM approaches may misrepresent co-incidental overlap at a bird feeder as social association. We suggest that future researchers into the social behaviour of wild animals, particularly in gregarious flocks of birds, choose an association definition that reflects the study system, but also should justify how associations are defined in published work.

Network comparisons are an important tool in animal behaviour, but comparing networks of different types (i.e., social and reproductive networks) or networks of the same type but containing different individuals (i.e., collected over different time frames) still present a challenge (Croft, James, and Krause 2008; Castles et al. 2014; Silk 2023). Here, we used similarity indices (Jaccard and Mantel tests) as well as repeatability analyses (Nakagawa and Schielzeth 2013; Magnani, Rossi, and Vega 2021), but accessible statistical

approaches that encompass network layers (see Silk 2023) would be beneficial to future research (although see Hart et al. 2021, 2022).

Aim 2: To test the link between social traits and fitness at the annual and lifetime scales (Chapter 3).

In Chapter 3, we tested the relationship between sociality and annual and long-term fitness. Previous works have demonstrated the fitness consequences of sociality, often over short-term timescales (McDonald 2007; Oh and Badyaev 2010), but how these consequences accumulate to influence lifetime fitness is poorly resolved. We used principles developed in Chapter 2 to extract association data for two non-breeding years in the Lundy sparrow system, defining an association between birds that arrived together at an RFID bird feeder. We defined fitness following Alif (2022), in which we found that genetic recruits and de-lifed fitness were significantly correlated with realised reproductive value. We extracted fitness data at the annual scale (for the breeding period following the year of the non-breeding social network), and over the lifetime for all birds for which we had social data, life-history data, and ultimately a year of death. We demonstrated that some aspects of individual sociality are clearly beneficial on the annual scale. Opposite-sex degree, the number of opposite-sex social associations a bird holds, was beneficial to both sexes, probably by virtue of an increased pool of potential mates in the pre-breeding period. This result was also corroborated by similar results from a blue tit system, where the number of potential partners increased breeding success in the short term (Beck, Farine, and Kempenaers 2020). However, over a lifetime, individuals with the highest fitness had sociality equivalent to the population average, thereby stabilizing selection, rather than favouring those at the social extremes.

Previous studies have suggested links between sociality and short-term measures of reproductive success (Culina, Hinde, and Sheldon 2015; Firth and Sheldon 2016; Beck, Valcu, and Kempenaers 2020), but few have tracked how these benefits translate to longer-term fitness. Likewise, social networks tend to be static, measured within a short window (Farine 2018). This assumes that social behaviours are repeatable over time. In

this chapter, we demonstrated that social behaviours are repeatable over multiple weeks (and for four systems in Chapter 2), and repeatability of social traits is well described in the context of animal personality (Krause, James, and Croft 2010; Aplin, Firth, et al. 2015; Aplin et al. 2014; Proops et al. 2021). Few studies have addressed changes to individual social behaviour over the long term, particularly in response to the physical or social environment (Voelkl, Firth, and Sheldon 2016; Firth et al. 2017; Culina, Firth, and Hinde 2020). Future work should consider the plasticity of individual social behaviour in the context of the social environment at differing scales, as social lability has been demonstrated to optimize reproductive advantage (McDonald 2007; Oh and Badyaev 2010).

Aim 3: To apply concepts from Chapters 2 and 3 to test whether the inclusion of the social environment in quantitative behaviour models improves heritability for female extra-pair behaviour (Chapter 4).

In Chapter 4, we introduced the conundrum of female extra-pair paternity—'why females cheat'—and how considering the social environment in these long-standing questions may provide new avenues of research (following Maldonado-Chaparro et al. 2018). We also introduced the concept of indirect genetic effects, which describe the effect of one individual's genes on the behavioural expression of another (Wolf et al. 1998; Bijma 2011). For example, when a male sparrow invests in guarding his mate during the breeding season, she may be unable to engage in extra-pair copulation with other males (Maldonado-Chaparro et al. 2018). Another example is how individuals mediate parental care in response to their social partner (Schroeder et al. 2019); they are driven to provision offspring by their own genes—a direct genetic effect—but the expressed behaviour is ultimately mediated by the genes of another. In this chapter, we argued that extra-pair behaviours have the potential to include up to four individuals that influence the way extra-pair behaviours are expressed: the focal individual, the social partner, the extra-pair partner and their social partner. We tested for indirect genetic effects on the between-sex correlation and within-sex heritability of extra-pair reproduction, an inherent

assumption of non-adaptive hypotheses to explain female extra-pair paternity (Forstmeier et al. 2014; Wang et al. 2020).

We found that although additive genetic variance was close to zero for both male and female extra-pair behaviour, the addition of social partner IGEs increased the genetic variance for both sexes. Likewise, social partner IGEs significantly increased the total heritable variance for males, but also for females to a lesser extent. The inclusion of IGEs also increased uncertainty in variance, which may be linked to model complexity (Bijma 2014). Our work may corroborate previous studies that found low heritability but high residual variance in extra-pair reproduction, implying some plasticity in trait expression (Beck, Valcu, and Kempenaers 2020; Grinkov et al. 2020; Reid et al. 2011; Wang et al. 2020), but that did not include a variable capturing indirect genetic effects.

Despite our results, empirical evidence for why females specifically engage in extra-pair behaviour is still lacking, but indirect genetic effects have been demonstrated to affect female behaviour. For example, male parental care is reduced in response to infidelity (Dixon et al. 1994; Schroeder et al. 2016), or in response to the wider social environment (Beck, Farine, and Kempenaers 2021). Our results mean that this study is unable to support intersexual pleiotropy as a driver of extra-pair behaviour but cannot rule out intrasexual drivers. If extra-pair behaviour is a pleiotropic trait, controlled by genes for mate choice, solicitation, or copulation (Halliday and Arnold 1987; Forstmeier et al. 2014; Wang et al. 2020), then empirical work from wild populations is still lacking—although such processes have been demonstrated in captivity (Wang et al. 2020). However, between-sex correlation—required for pleiotropic effects to drive extra-pair behaviours—is difficult to demonstrate in the wild, and the large sample sizes required may result in large uncertainty in estimates (Forstmeier et al. 2011; Reid and Wolak 2018). Future work should then focus on intrasexual drivers of extra-pair behaviour in the wild (Wang et al. 2020), either through an empirical study of linked behaviours or, where sample sizes allow, a quantitative genetic study including indirect genetic effects.

Aim 4: Building on Aim 3, to identify empirical evidence for a pleiotropic driver of female extra-pair behaviour (traits beneficial to female fecundity, linked to extra-pair solicitation, Chapter 5)

In Chapter 5, we described the prevalence of extra-pair behaviour in the Lundy system and tested a hypothesis supporting intrasexual pleiotropy as a driver for female (specific) extra-pair behaviour—that genes beneficial to female fecundity are correlated with extra-pair behaviour (Wang et al. 2020). We used female mate-switching as a proxy for solicitation, which could explain female extra-pair behaviour (Wang et al. 2020), in other words, genes which drive soliciting copulations from within-pair partners are the same as those that drive extra-pair copulations. Using an empirical data set spanning 20 years, we demonstrated that female sparrows who switched social mates more frequently also engaged more extra-pair partners than monogamous females. However, frequent mate-switchers did not have a higher proportion of extra-pair young females when compared with more monogamous females. Although this in and of itself does not support the intrasexual pleiotropy hypothesis as the central driver of female extra-pair paternity, it does support a central tenet of that hypothesis—that a trait, or traits beneficial to female fecundity, are linked with extra-pair behaviour. Future work could develop the ideas presented in this chapter in the context of fitness consequences of divorce, for example, recent studies have found fitness advantages to mate-switching (Sacchi et al. 2023; Zhang et al. 2023). Such work should consider the motivation for mate-switching behaviours from the two sexes separately to reflect differing reproductive strategies, while accounting for age and partner identity, for example see Chen et al. (2023), who reported a significant advantage for males (but not females) involved in frequent mate-switching.

General conclusions and future research

In this thesis, we have tested hypotheses to explain the drivers of social behaviours, and female extra-pair behaviour, in the context of the social environment. We have demonstrated that the methods we have used to define social non-breeding behaviours are robust, that social preference has consequences for reproductive fitness, that the social preference of others has the potential to influence the expression of female extra-pair paternity, and that females who switch social mates often are also more likely to engage extra-pair males than those that maintain monogamy.

A central principle, implied by good genes hypotheses (described in Table 5.1) is that females choose an extra-pair partner based on some social information (which may or may not be an honest reflection of fitness), as opposed to blindly soliciting extra-pair copulation from males regardless of their genes (Maldonado-Chaparro et al. 2018). And then, by extension, female birds are able to differentiate between within and extra-pair copulation.

Although the question of why females engage in extra-pair behaviours at all remains unresolved, the body of research presented here suggests that extra-pair behaviour is common and seemingly random, perhaps controlled by genes beneficial to female fecundity (suggested by Wang et al. 2020) - that is, there is little or no consideration for the genes of the extra-pair males in the Lundy system (also suggested in other systems by Fossøy, Johnsen, and Lifjeld 2006; Brommer et al. 2007). This argument, against good genes as a driver of female engagement in extra-pair behaviours, is also supported across study systems by multiple meta-analyses (Akçay and Roughgarden 2007; Arct, Drobniak, and Cichoń 2015), discussion in the field (Drobniak, Arct, and Cichoń 2015; Griffith 2015; Nakagawa, Schroeder, and Burke 2015; Reid 2015; Brouwer and Griffith 2019), and a systematic review of costs associated with extra-pair paternity, mostly experienced by the female (Søraker and Dunning 2023).

These studies describe the circumstances under which female extra-pair behaviours take place, but scarcely do they suggest a driver - that is, a fitness benefit to females

when they solicit extra-pair copulation upon which selection can act (Endler 1986). Yet, female extra-pair copulation persists in the wild, suggesting an alternative driver.

Recent suggestions as to alternative drivers to good genes include non-adaptive hypotheses (Halliday and Arnold 1987; Forstmeier et al. 2014; Wang et al. 2020), or perhaps fertility insurance, which still cannot be dismissed as a driver of female extra-pair copulation (Wetton and Parkin 1991; Sheldon 1994), and still finds support in contemporary research (Santema, Teltscher, and Kempenaers 2020). In the case of the latter, a female must be able to distinguish between within- and extra-pair copulations in order to insure against infertility of her social partner, but the genes of the extra-pair male may still be irrelevant. However, in the former, extra-pair mating may be an indirect result of some other benefit to either sex. In either case, future work which is able to test if females can distinguish between with and extra-pair copulations would be beneficial to the study of female extra-pair paternity, perhaps by moving paired females between aviaries in captivity. Wang et al. (2020) suggested that extra-pair behaviours could be linked to a trait beneficial to female fecundity, contrary to a previous study by the same research team (Forstmeier et al. 2014). They suggest that this benefit may be linked to solicitation, and in chapter 5 of this thesis we also suggest a mechanism for this, but that mechanism may still be that females receive fertility insurance from extra-pair copulations. Further, a review of potential drivers of female extra-pair paternity (similar to Maldonado-Chaparro et al. 2018) but broken down into the implicit assumptions of each may also be beneficial to facilitate more specific empirical research.

Our results in combination suggest that the social environment is a powerful force in shaping life history and should be accounted for in studies in behavioural ecology. We demonstrated this in Chapters 3 and 4, where we show that social connections directly influence fitness and, the inclusion of indirect genetic effects reduced uncertainty in our models. However, we also demonstrated in Chapter 2 that defining what a social connection is, and thus, inferring the structure of the wider social environment is a challenge to researchers and should be considered in the context of the study system. Although we find evidence that female sparrows who switch social mates (divorce) more

frequently also are more likely to engage more extra-pair males than monogamous birds, possibly supporting a non-adaptive driver of female extra-pair paternity, the question remains unresolved.

Future works should focus on the role of the fine-scale social environment, in particular the influence of indirect genetic effects on individual decision-making. Likewise, partitioning the consequences of extra-pair behaviours into costs as well as benefits at the fine scale. For example, although we found evidence for non-adaptive phenomena, future work could also continue to explore the consequences of fertility insurance for females.

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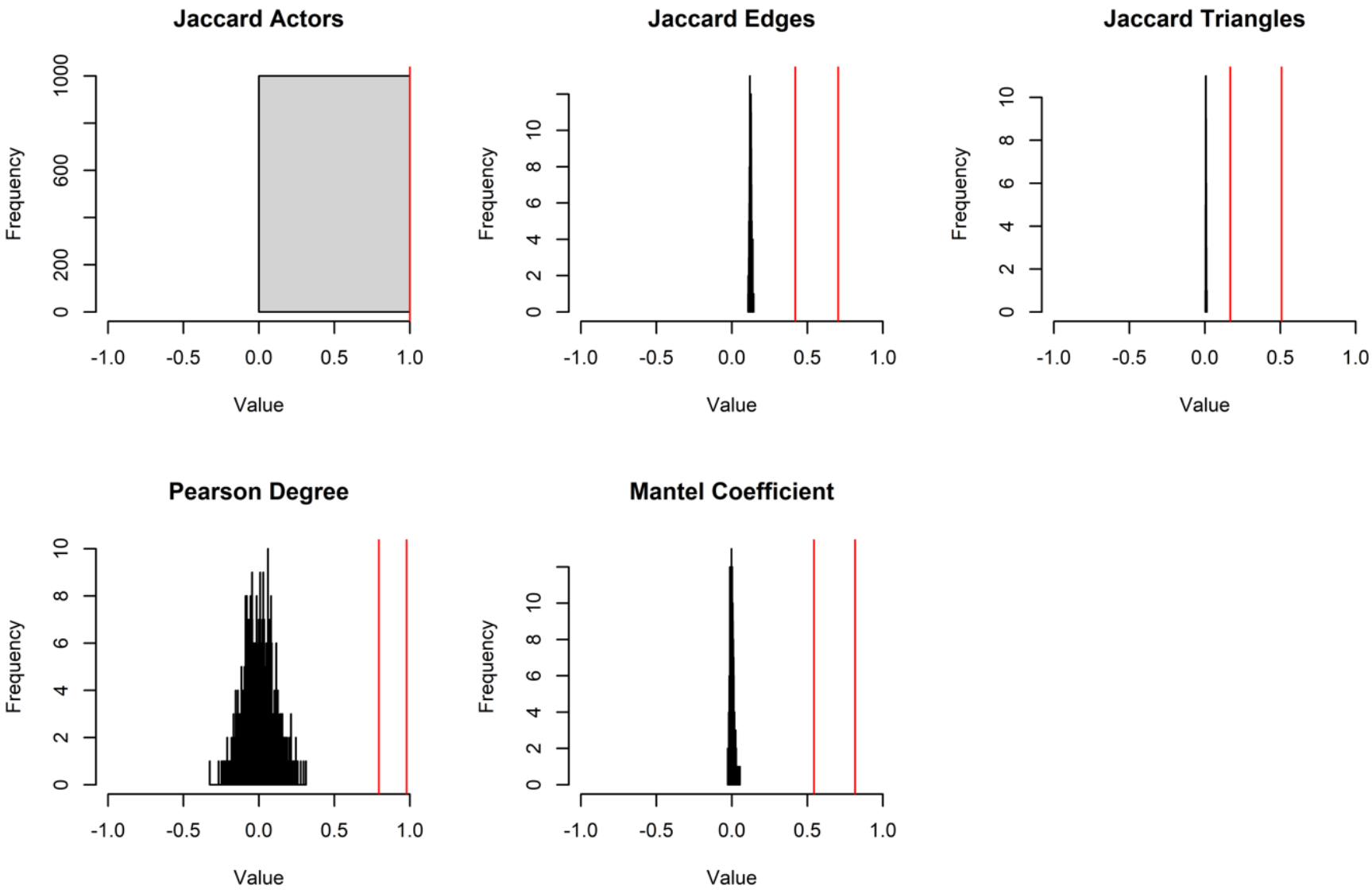
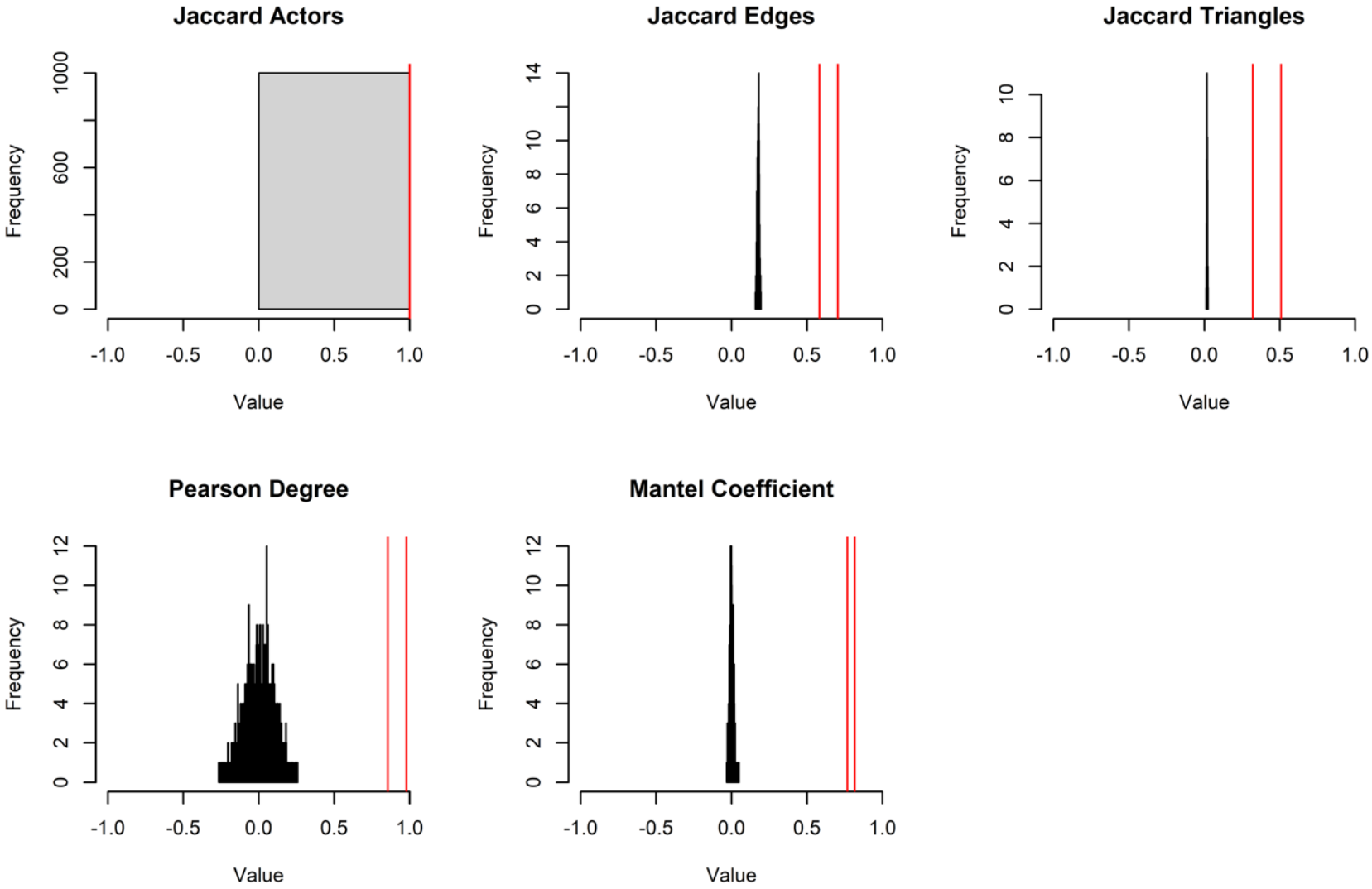
viii. Appendix

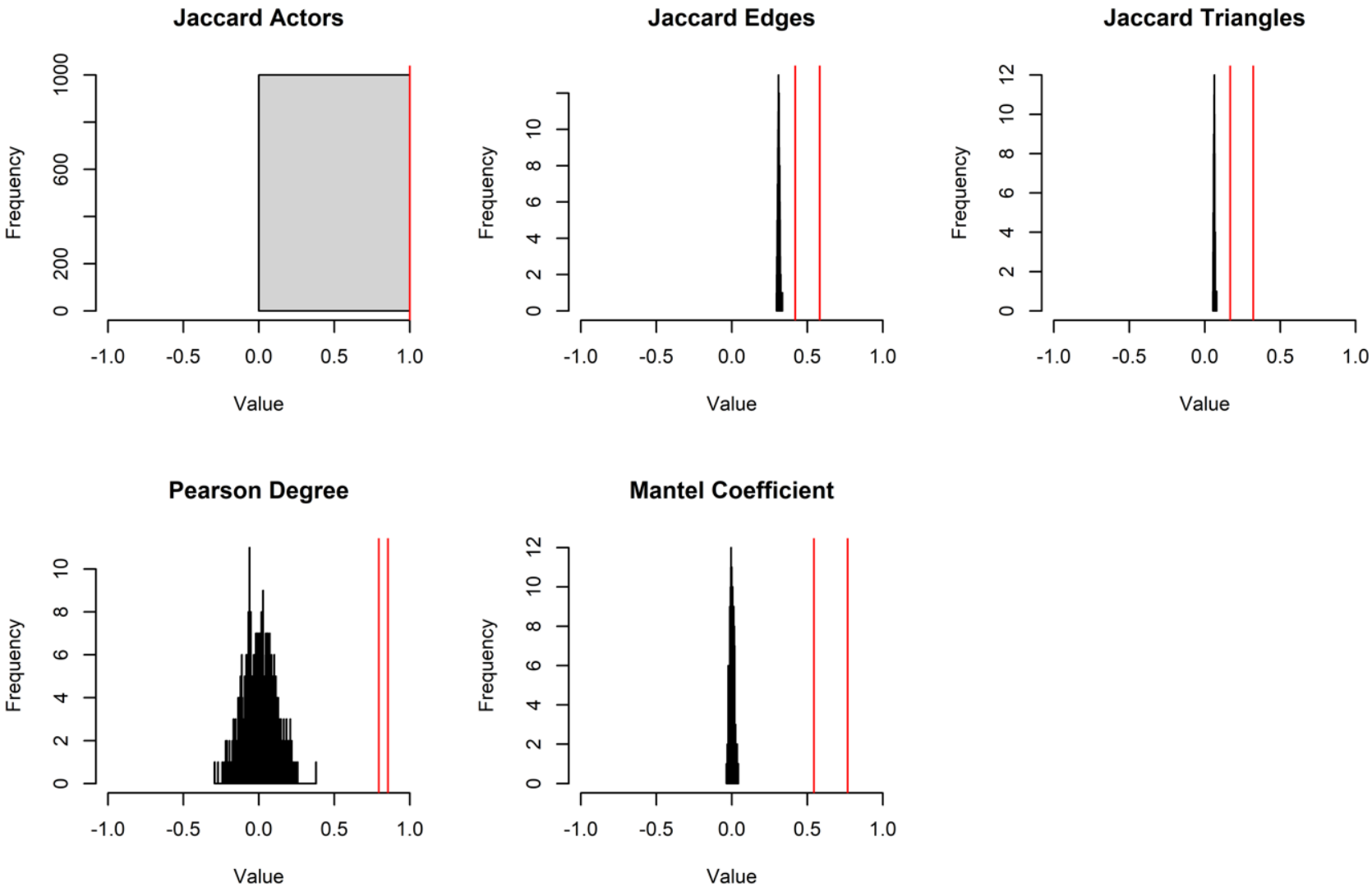
Lundy Island - Time-window



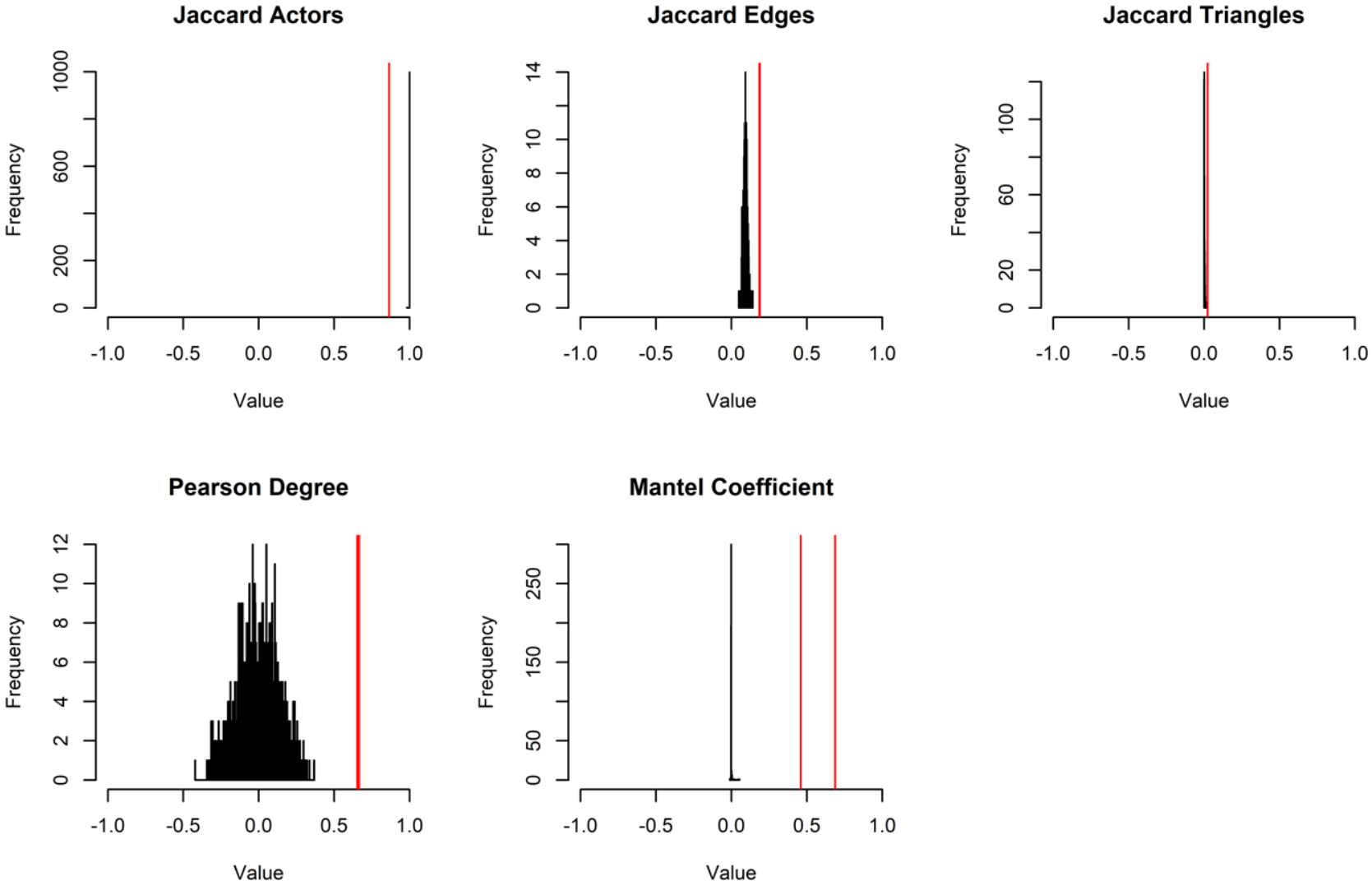
Lundy Island - GMM



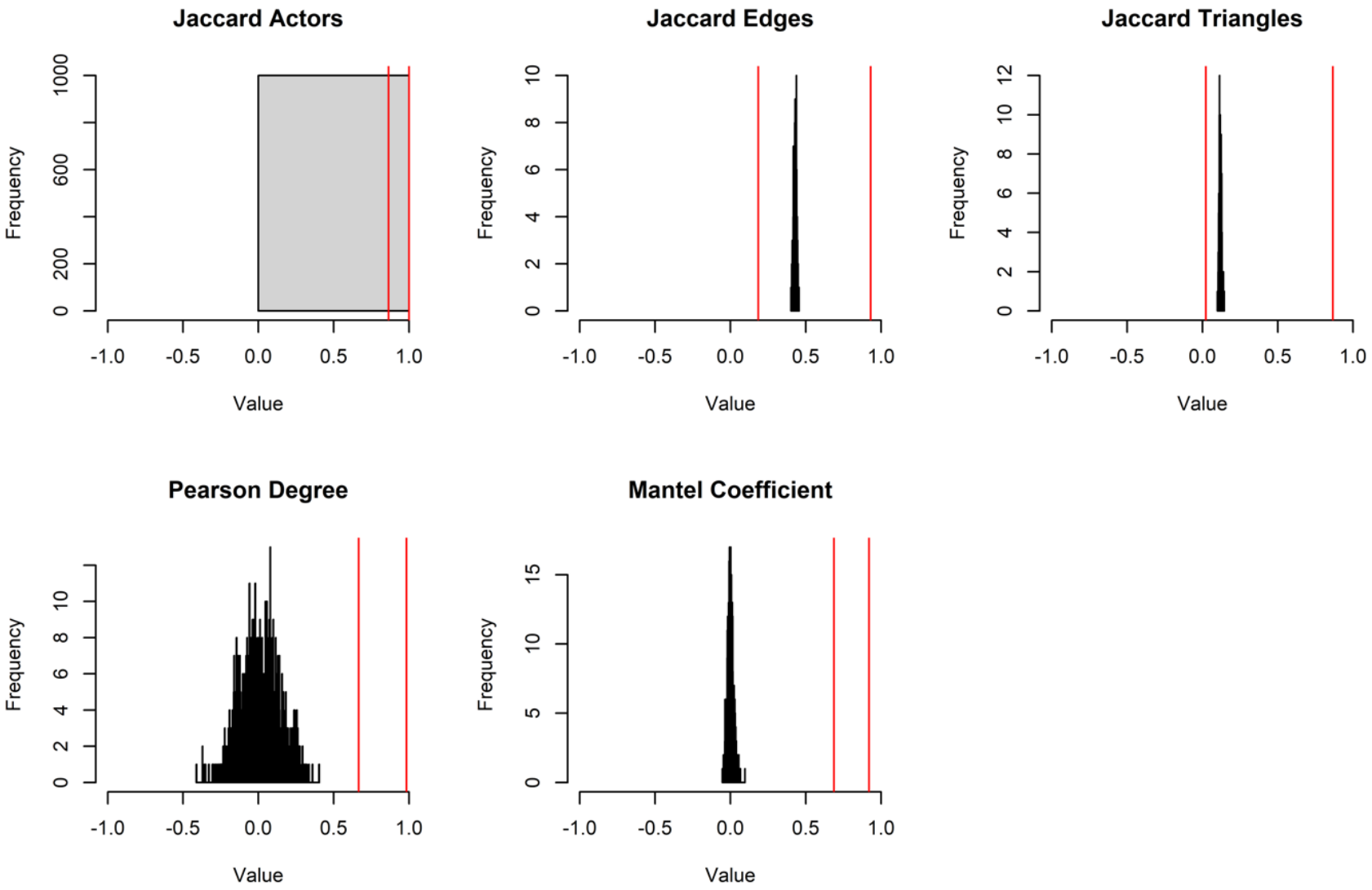
Lundy Island - Arrival

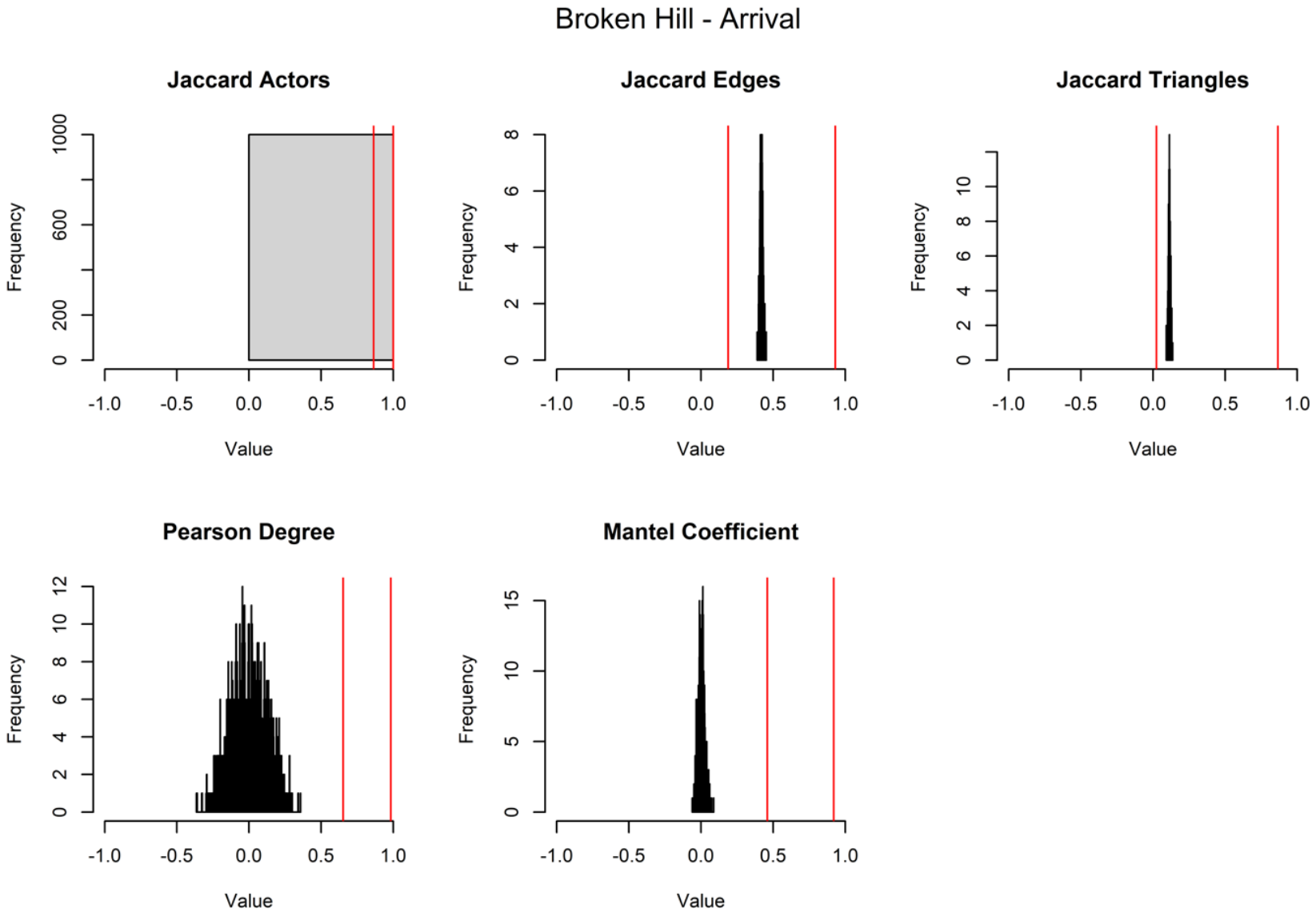


Broken Hill - Time-window



Broken Hill - GMM




Broken Hill - Arrival
Jaccard Actors
Frequency
0
200
600
1000
-1.0
-0.5
0.0
0.5
1.0
Value
Jaccard Edges
Frequency
0
2
4
6
8
-1.0
-0.5
0.0
0.5
1.0
Value
Jaccard Triangles
Frequency
0
2
4
6
8
10
-1.0
-0.5
0.0
0.5
1.0
Value
Pearson Degree
Frequency
0
2
4
6
8
10
12
-1.0
-0.5
0.0
0.5
1.0
Value
Mantel Coefficient
Frequency
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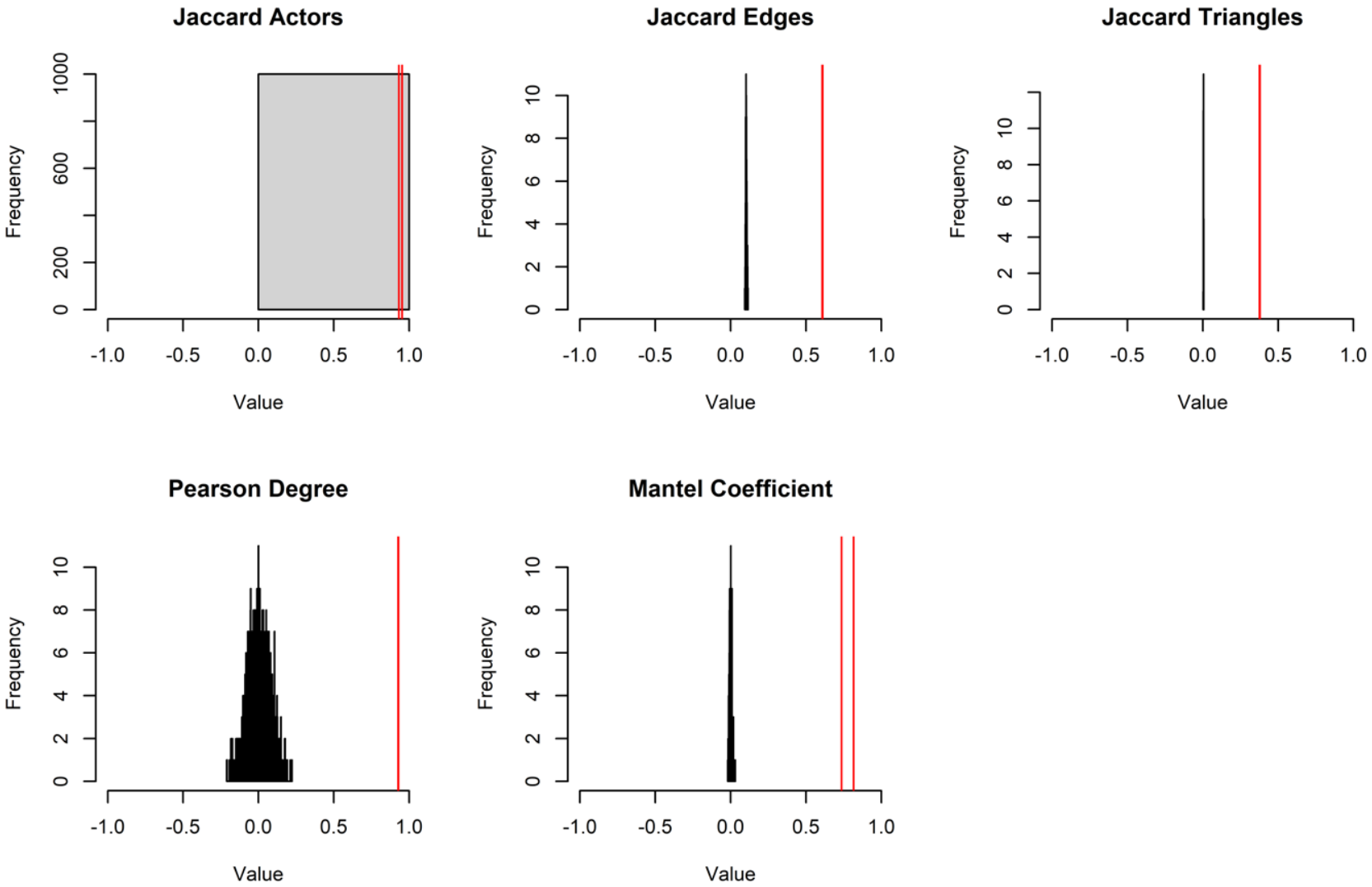
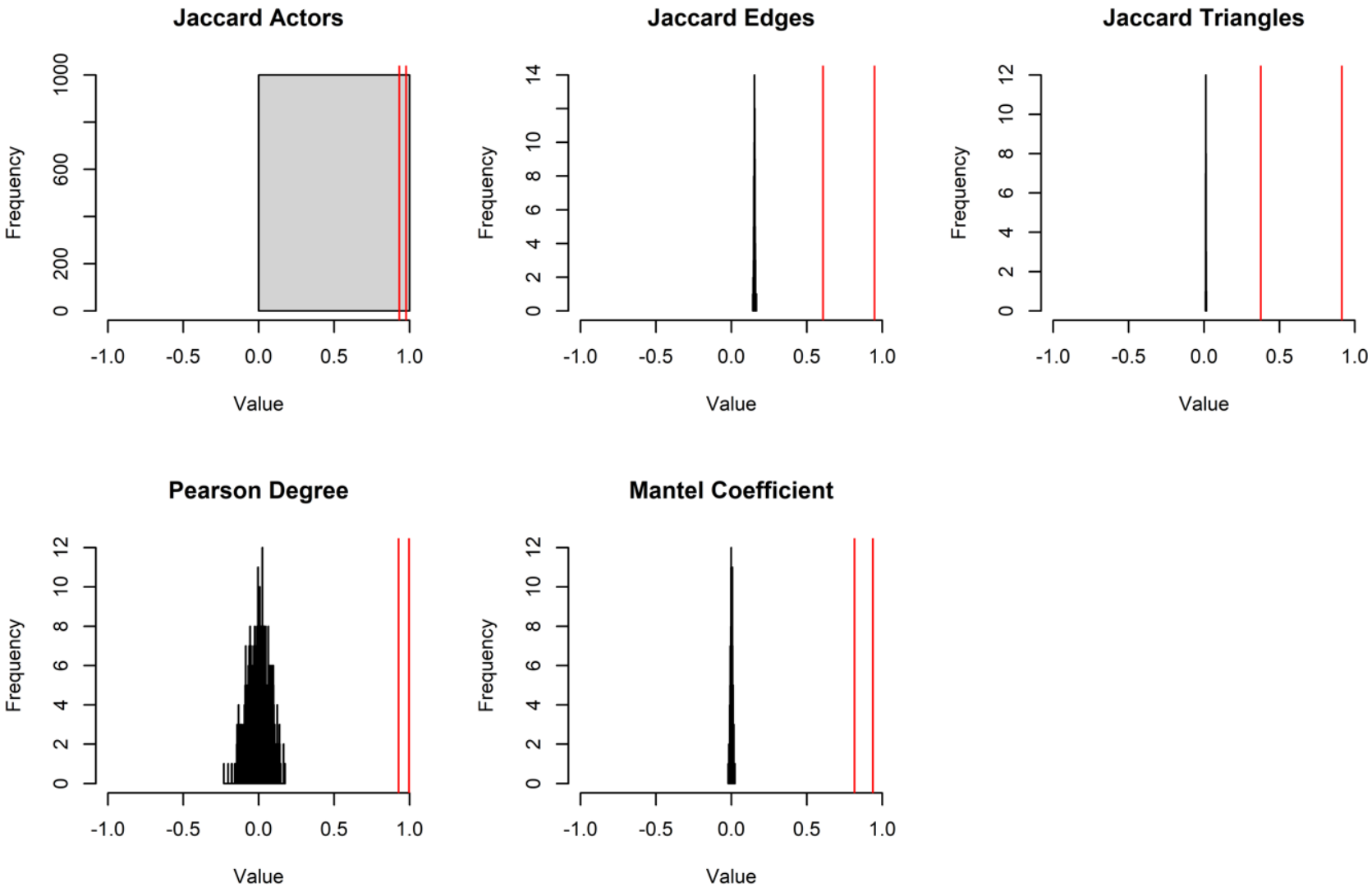
5
10
15
-1.0
-0.5
0.0
0.5
1.0
Value

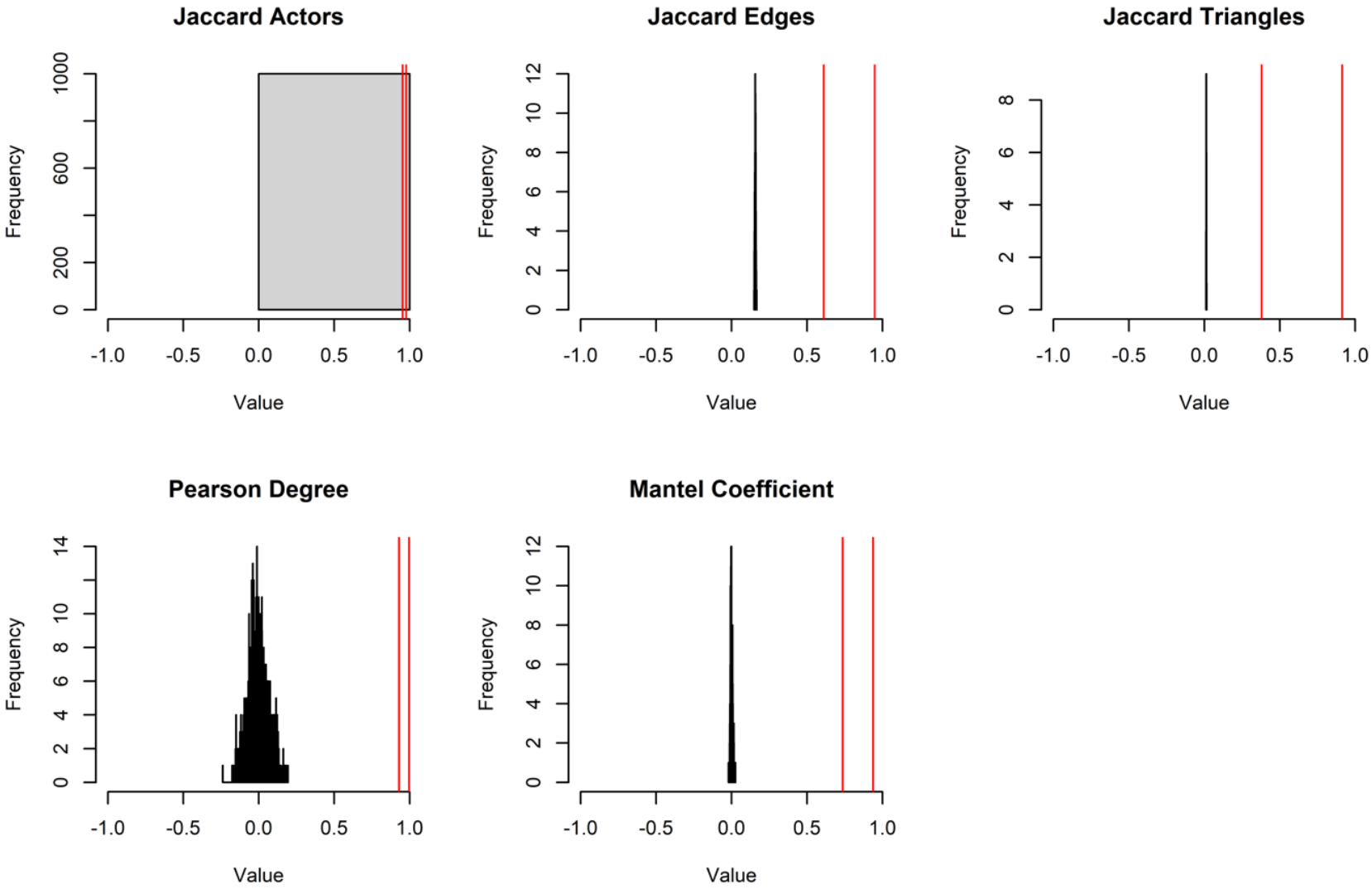
Wytham Woods - Time-window



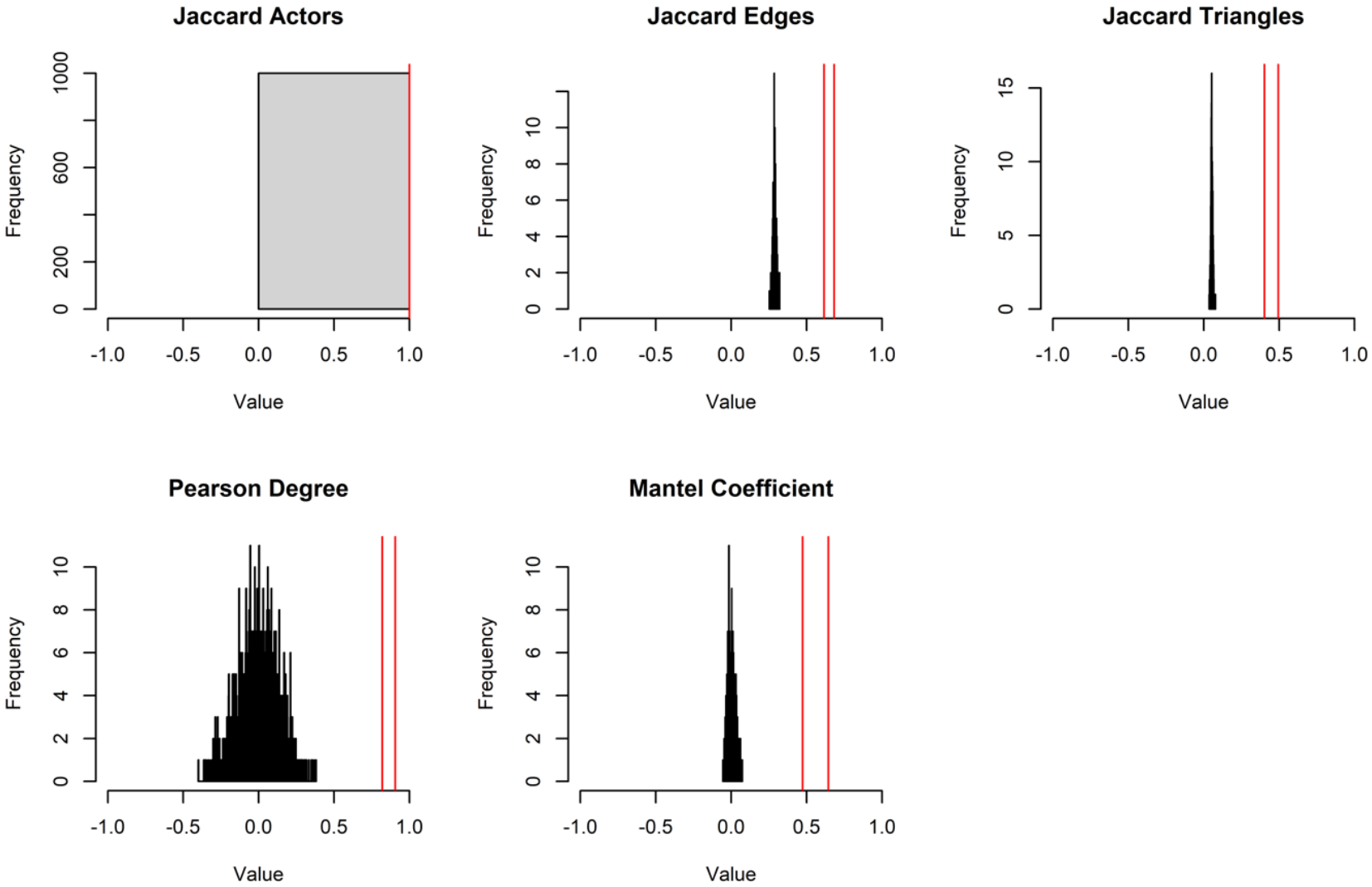
Wytham Woods - GMM

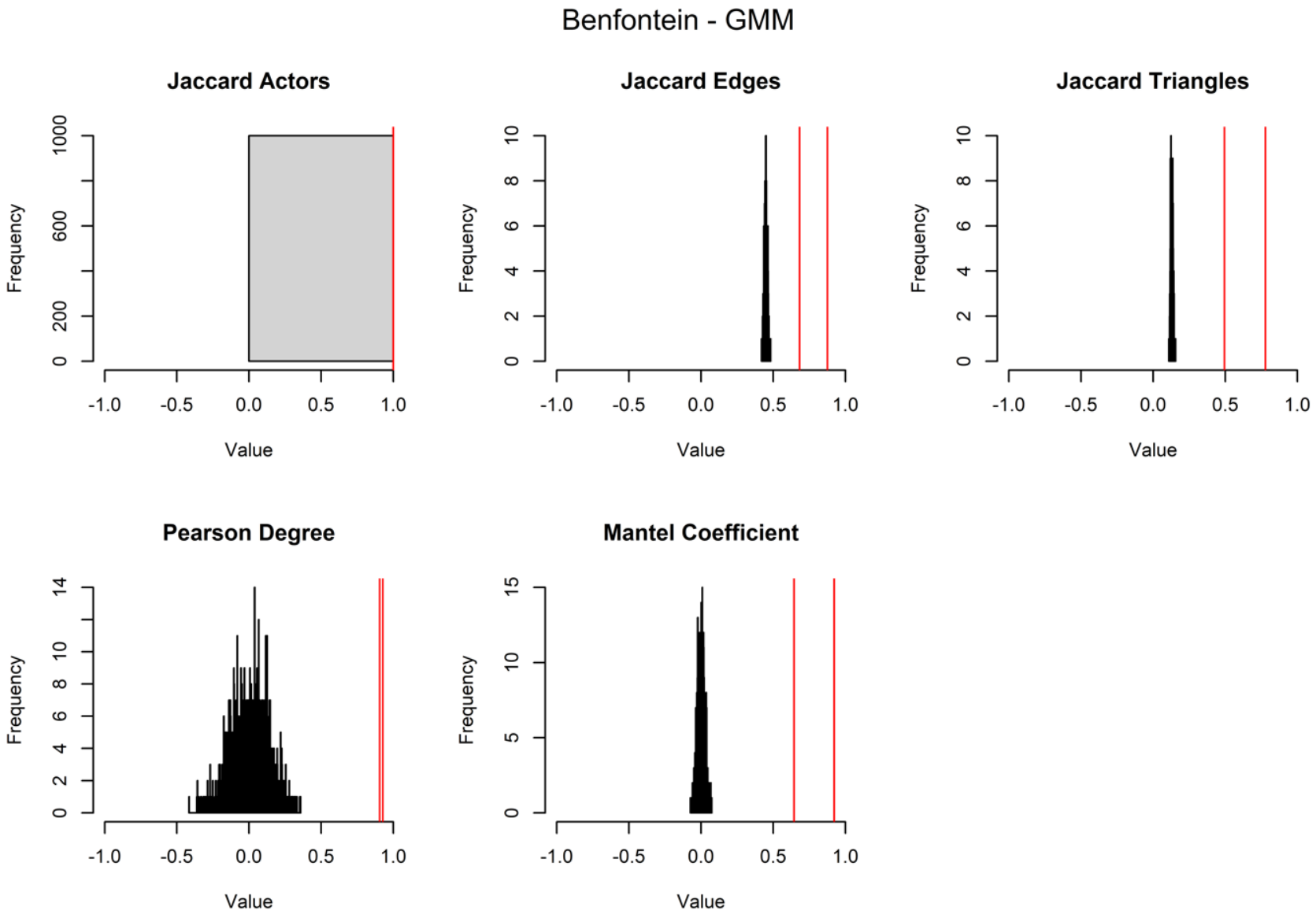


Wytham Woods - Arrival



Benfontein - Time-window




Benfontein - GMM
Jaccard Actors
Jaccard Edges
Jaccard Triangles
Pearson Degree
Mantel Coefficient
Frequency
Value
0
200
600
1000
2
4
6
8
10
5
15
-1.0
-0.5
0.0
0.5
1.0

Benfontein - Arrival

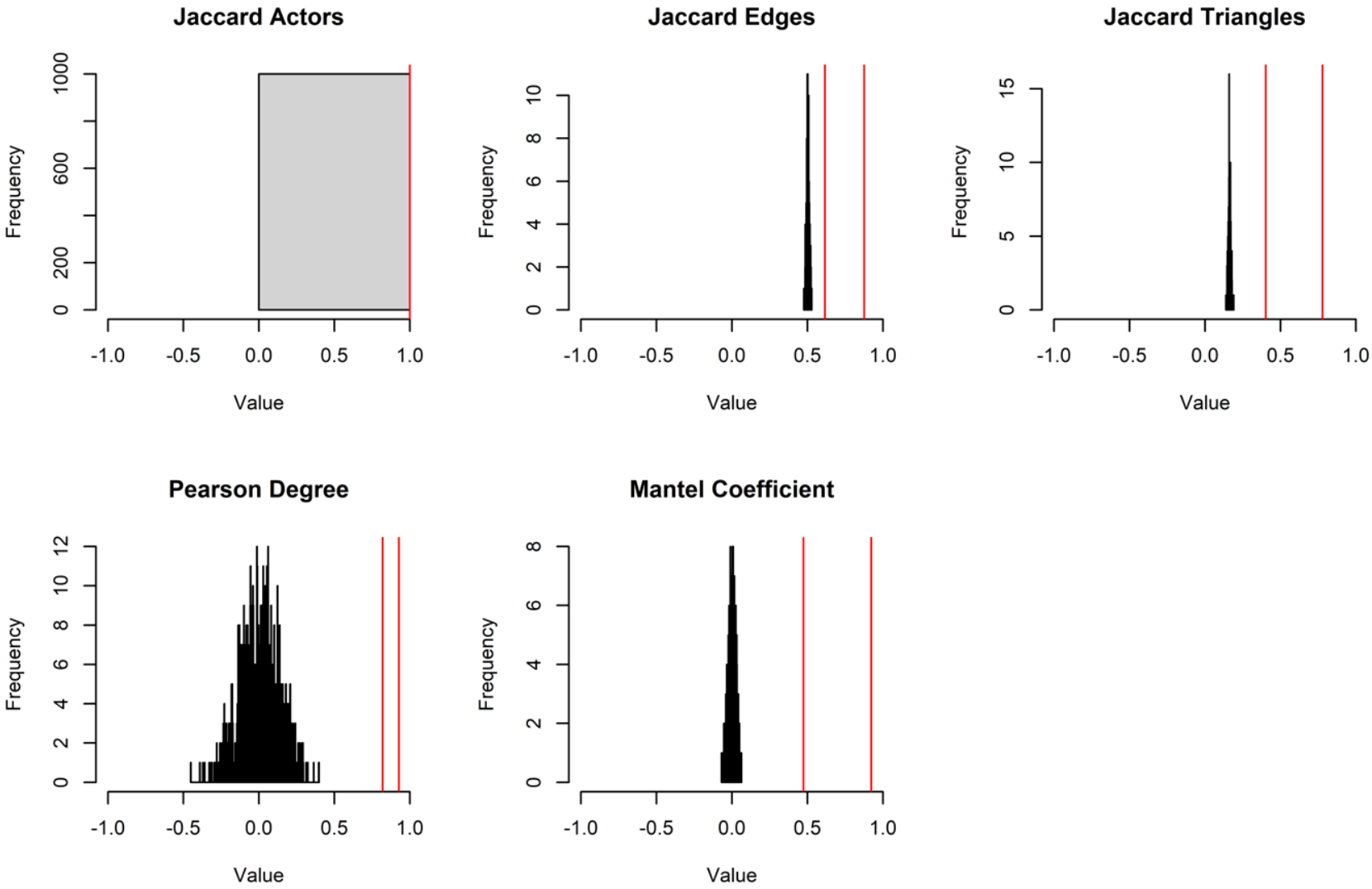


Figure S1.1: Network comparison – permutation summary results. Distribution of network comparison metrics obtained from 1000 network permutations for 3 association definitions across 4 study systems compared with actual comparison values. Metrics include Jaccard actors (shared nodes), Jaccard edges (shared edges), Jaccard triangles (shared triangles), pearson degree (correlation of degree) and Mantel coefficient (correlation of adjacency matrices). For each network built by each association definition, we did 1000 permutations by shuffling the edge list with replacement, then calculating the network comparison metric against a non-shuffled network (arrival, co-occurrence, proximity). Actual values of network comparison reported in the main text are shown in red.

Chapter 3

Figure S3.1. Annual and lifetime model outputs – permutation summary results. Model outputs derived of a node-permutation null-model, randomizing bird identity against arrival time, without replacement, before constructing new networks and calculating mode network centrality measures from 1000 randomized permutations.

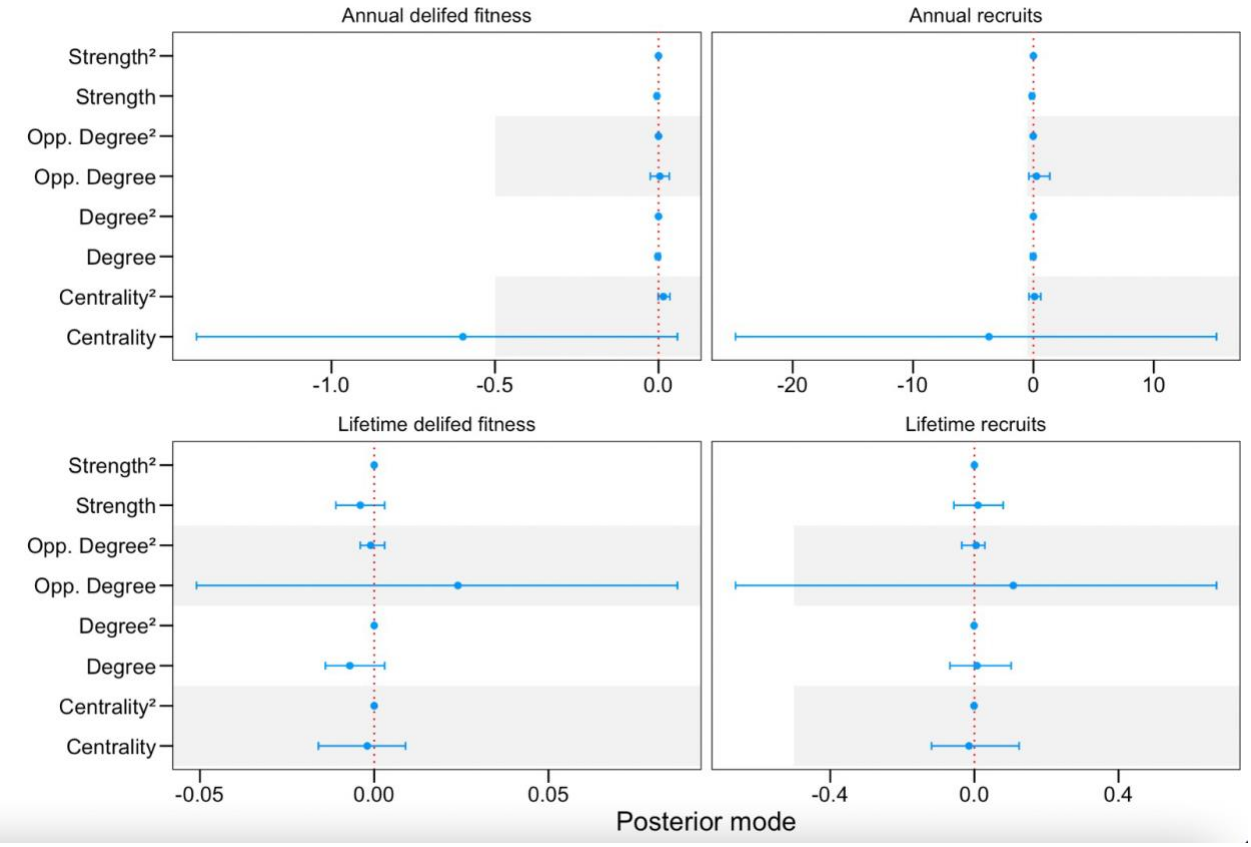


Table S3.1. Correlations between social measures. showing the correlation between each social measure, but also same-sex degree and frequency of visit to the feeder. Note that frequency is not strongly correlated with sociality measures. Also, the three measures of degree are closely correlated, suggesting that sparrows with more associations of either sex, are also more likely to have more opposite sex friends, however, only opposite sex associations are linked with fitness – suggesting a role in mate choice.

	Degree	Centrality	Strength	Op_Degree	Same_Degree	Freq
Degree	-	-	-	-	-	-
Centrality	0.776	-	-	-	-	-
Strength	0.456	0.867	-	-	-	-
Op_Degree	0.962	0.753	0.434	-	-	-
Same_Degree	0.964	0.743	0.445	0.857	-	-
Freq	0.364	0.612	0.591	0.374	0.328	-
						0.131
ELO	0.13	0.13	0.141	0.116	0134	

Table S3.2. **Comparisons between social variables.** Model outputs from GLMMs for each of our four sociality measures (Degree, Strength, Centrality and Opposite-sex degree shown in Figure 2), against delifed fitness (Gaussian) at two scales in the Lundy house sparrow system. We inferred significance where the 95%CI do not span zero, positive effects on the response variable are highlighted in red, and negative in blue. Social variables are shown in Figure 2.

Annual delifed fitness	Posterior mode, 95% credible intervals (lower – upper)			
Variable	Degree	Strength	Centrality	Opposite sex degree
Fixed term				
(Intercept)	-0.02 -0.05—0.03	-0.01 -0.04—0.03	-0.01 -0.04—0.03	-0.01 -0.05—0.03
Sex (male)	-0.02 -0.04—0	-0.01 -0.04—0	-0.02 -0.04—0	-0.02 -0.04—0
Age	0.03 0—0.05	0.03 0—0.04	0.03 0—0.04	0.03 0—0.05
Age^2	0 -0—-0	0 -0—-0	0 -0—-0	0 -0—-0
Age*Sex (male)	0 -0—0.01	0 -0—0.01	0 -0—0.01	0 -0—0.01
Random effects				
*Bird ID	0 0—0	0 0—0	0 0—0	0 0—0.001
*Cohort	0 0—0	0 0—0	0 0—0	0 0—0.002
Residuals	0 0—0	0 0—0	0 0—0	0 0—0.001

Table S3.2 – continued overleaf.

Lifetime delifed fitness	Posterior mode, 95% credible intervals (lower – upper)			
Variable	Degree	Strength	Centrality	Opposite sex degree
Fixed term				
(Intercept)	0.02 -0.05—0.07	0.01 -0.05—0.07	0.01 -0.05—0.08	-0.02 -0.06—0.05
Sex (male)	0.03 -0.04—0.09	0.03 -0.05—0.08	0.03 -0.03—0.08	0.02 -0.03—0.09
†Age	0.01 -0—0.02	0.01 -0—0.01	0.01 -0—0.01	0.01 -0—0.02
†Age*Sex (male)	-0.01 -0.02—0	0 -0.01—0.01	0 -0.01—0	-0.01 -0.02—0
Random effects				
*Cohort	0 0—0	NA 0—0	0 0—0	0 0—0
Residuals	0 0—0	NA 0—0	0 0—0	0 0—0

Chapter 4

Table S4.1. Model Specifications. Structure of priors, number of iterations, thin and burnin specified for each MCMCglmm model. G and R represent G- structure and R-structure respectively

Model	Prior 1		Prior 2		nitt	thin	burnin
	G	R	G	R			
1.1	V = 1, nu = 1, alpha.mu = 0, alpha.V = 1	V = 1, nu = 1	V = 0.01, nu = 1, alpha.mu = 0, alpha.V = 1000	V = 1, nu = 1	205000	200	5000
1.2	V = 1, nu = 1, alpha.mu = 0, alpha.V = 1	V = 1, fix = 1	V = 0.01, nu = 1, alpha.mu = 0, alpha.V = 1000	V = 1, fix = 1	310000	200	10000
2.1	V = 1, nu = 1, alpha.mu = 0, alpha.V = 1	V = 1, nu = 1	V = 0.01, nu = 1, alpha.mu = 0, alpha.V = 1000	V = 1, nu = 1	505000	500	5000
2.2	V = 1, nu = 1, alpha.mu = 0, alpha.V = 1	V = 1, fix = 1	V = 0.01, nu = 1, alpha.mu = 0, alpha.V = 1000	V = 1, fix = 1	1055000	1000	5000
3.1	V = 1, nu = 1, alpha.mu = 0, alpha.V = 1	V = 1, nu = 1	V = 0.01, nu = 1, alpha.mu = 0, alpha.V = 1000	V = 1, nu = 1	1055000	1000	5000
3.2	V = 1, nu = 1, alpha.mu = 0, alpha.V = 1	V = 1, fix = 1	V = 0.01, nu = 1, alpha.mu = 0, alpha.V = 1000	V = 1, fix = 1	2555000	2000	5000
4.1	V = 1, nu = 1, alpha.mu = 0, alpha.V = 1	V = 1, nu = 1	V = 0.01, nu = 1, alpha.mu = 0, alpha.V = 1000	V = 1, nu = 1	6055000	3000	5000
4.2	V = 1, nu = 1, alpha.mu = 0, alpha.V = 1	V = 1, fix = 1	V = 0.01, nu = 1, alpha.mu = 0, alpha.V = 1000	V = 1, fix = 1	6055000	3000	5000
5	V=diag(2), nu= 2, alpha.mu = c(0, 0), alpha.V = diag(2)	V = diag(2), nu = 1.002, fix = 2	V = diag(2)*0.02, nu = 3, alpha.mu = c(0, 0), alpha.V = diag(2)*1000	V = diag(2), nu = 1.002, fix = 2	755000	500	5000
6	V=diag(2), nu= 2, alpha.mu = c(0, 0), alpha.V = diag(2)	V = diag(2), nu = 1.002, fix = 2	V = diag(2)*0.02, nu = 3, alpha.mu = c(0, 0), alpha.V = diag(2)*1000	V = diag(2), nu = 1.002, fix = 2	505000	500	5000

7	V=diag(2), nu= 2, alpha.mu = c(0, 0), alpha.V = diag(2)	V = diag(2), nu = 1.002, fix = 2	V = diag(2)*0.02, nu = 3, alpha.mu = c(0, 0), alpha.V = diag(2)*1000	V = diag(2), nu = 1.002, fix = 2	2555000	2000	5000

Table S4.2. Observed h^2 and Effect of Year on H^2 and Vg_{lat}. Observed scale heritability estimates (h^2) and genetic correlation estimates (Vg_{lat})) + 95% credible intervals between univariate and bivariate models with year as a random effect vs without year as a random effect.

Model	**With Year**	**No Year**
1.1	h^2: 0.004 (<0.001 –0.016)	h^2: 0.004 **(<**0.001 – 0.016)
1.2	h^2: 0.007(<0.001 – 0.022)	h^2: 0.007 (<0.001 – 0.023)
2.1	h^2: 0.007 (<0.001 – 0.02)	h^2: 0.006 (<0.001 – 0.02)
2.2	h^2: 0.009 (<0.001 – 0.029)	h^2: 0.008 (<0.001 – 0.025)
5	Male h^2: 0.004 (<0.001 – 0.015) Female h^2: 0.007 (<0.001 – 0.025) Vg: 0.04(- 0.8 - 0.8)	Male h^2: 0.003 (<0.001 – 0.011) Female h^2: 0.007 (<0.001 – 0.024) Vg: 0.09 (-0.84 - 0.94)
6	Male h^2: 0.004(<0.001 – 0.013) Female h^2: 0.008(<0.001 – 0.024) Vg_{lat}: 0.01 (-0.7 – 0.9)	Male h^2**:** 0.006 (<0.01 – 0.02) Female h^2: 0.008(<0.001 – 0.026) Vg_{lat}**:** 0.045 (-0.81 – 097)

Table S4.3: Intercept, Fixed effect and residual effect estimates for univariate and bivariate MCMCglmm models.

model	Intercept/ Age		Residual Effects	
	Prior 1	**Prior 2**	**Prior 1**	**Prior 2**
1.1	Intercept: -3.046(-3.46 - -2.68) pMCMC: <0.001 *** Age: 0.312 (0.21 - 0.423) pMCMC: <0.001 ***	Intercept: -3.049(-3.46 - -2.655) pMCMC: <0.001*** Age: 0.312(0.19 - 0.41) pMCMC: <0.001***	1.49 (1.075 - 2)	1.49 (1.07 - 1.97)
1.2	Intercept: -0.222(-0.35 - -0.063) PMCMC: 0.0027*** Age: -0.011(-0.067 - 0.044) pMCMC: 0.7	Intercept: -0.222(-0.363 - -0.08) pMCMC: 0.00533** Age: -0.012(-0.071 - 0.043) pMCMC: 0.68	1	1
2.1	Intercept: -3.14 (-3.57- -2.72) pMCMC: <0.001 *** Age: 0.359 (0.24 - 0.48) pMCMC: <0.001***	Intercept: -3.14(-3.56 - -2.73) pMCMC: <0.001 Age: 0.3562(0.23 - 0.47) pMCMC: <0.001***	1.15 (0.8 - 1.6)	1.14 (0.79- 1.62)
2.2	Intercept: -0.227(-0.361 - -0.059) pMCMC: 0.0117*** Age: -0.01(-0.067 - - 0.0467) pMCMC: 0.72	Intercept: -0.226(-0.376 - -0.067) pMCMC: 0.00333 *** Age: -0.01(-0.066 --0.045) pMCMC: 0.71	1	1
3.1	Intercept: -3.16(-3.65 - -2.72) pMCMC: <0.001*** Age: 0.369 (0.26- 0.51) pMCMC: <0.001***	Intercept: -3.18 (-3.7 - -2.7) pMCMC: <0.001 *** Age: 0.37 (0.25 - 0.5) pMCMC: <0.001***	1.163 (0.74- 1.58)	1.158 (0.73 - 1.35)
3.2	Intercept: -0.22(-0.38 - -0.061) pMCMC: 0.001** Age: -0.01(-0.067 - 0.04) pMCMC: 0.757	Intercept: -0.226(-0.39 - -0.067) pMCMC: 0.002*** Age: -0.009(-0.068- 0.046) pMCMC: 0.776	1	1
4.1	Intercept: -3.15(-3.62 - -2.74) pMCMC: <0.001***	Intercept: -3.155(-3.6 - -2.7244) pMCMC: <0.001***	1.159 (0.75 - 1.56)	1.162 (0.76- 1.57)

	Age: 0.37 (0.256-0.49) pMCMC: <0.001 ***	Age: 0.37(0.25 - 0.48) pMCMC: <0.001 ***		
4.2	Intercept: -0.23(-0.39 - - 0.067) pMCMC: 0.005** Age: -0.01(-0.068 - 0.045) pMCMC: 0.728	Intercept: -0.226(- 0.38 - -0.065) pMCMC: 0.005** Age: -0.01(-0.068 - 0.05) pMCMC: 0.71	1	1
5	Male Intercept: -3.24 (-3.7 - -2.84) pMCMC: <0.001*** Male:Age: 0.328 (0.2 - 0.44) pMCMC: <0.001** Female Intercept: -0.217(-0.35 - -0.07) pMCMC: <0.002** Female:Age: -0.01(-0.07 - 0.04) pMCMC: 0.64	Male Intercept: -3.051(-3.45- -2.67) pMCMC: <0.001*** Male Age: 0.31(0.2 - 0.42) pMCMC: <0.001 *** Female Intercept: -0.22(-0.365- -0.06) pMCMC: 0.004** Female Age: -0.012(-0.06 - 0.047) pMCMC: 0.688	Male: 1.952 (1.4 - 2.5) Female: 1	Male: 1.47 (1.075-1.92) Female: 1
6	Male Intercept: -3.16(-3.57 - -2.73) pMCMC: <0.001 *** Male Age: 0.358 (0.23- 0.47) pMCMC: <0.001 ** Female Intercept: -0.23(-0.39 - -0.08) pMCMC: 0.005 *** Female Age: 0.01(-0.07 - 0.04) pMCMC: 0.64	Male Intercept: -3.16(-3.56 - -2.71) pMCMC: <0.001*** Male Age: 0.358(0.251 - 0.49) pMCMC: <0.001*** Female Intercept: -0.226(-0.38 - -0.067) pMCMC: 0.004 **** Female Age: -0.01(-0.066 - 0.047) pMCMC: 0.747	Male: 1.165 (0.78 - 1.58) Female: 1	Male: 1.15 (0.71 - 1.55) Female: 1
7	Male Intercept: -3.17 (-3.65 - -2.67) pMCMC: <0.001 *** Male Age: 0.369 (0.243 - 0.48) pMCMC: <0.001 *** Female Intercept: -0.231 (-0.37 - -0.067) pMCMC: <0.001		Male: 1.178 (0.76 - 1.632) Female: 1	Male: Female: 1

	Female Age: -0.009 (-0.068 - 0.04) pMCMC: 0.74			