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Special Issue: Multilayer Networks for Animal Sociality

How can multilayer networks expand our understanding of sexual selection and mate choice?

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Mate choice is a social behaviour that encompasses a large range of interactions, from relationships among potential partners before and after mating, through mating, fertilization, and beyond. Here we propose that new developments in multilayer network analysis can expand our ability to quantify the integration of different stages of mate choice across times and contexts to uncover the causes and consequences of mate choice. We detail many types of interactions to consider in a study of mate choice and then suggest new approaches and questions that can be addressed with multilayer network analysis. The relationship between layers can be quantified using layer overlap analysis to form a network of networks to uncover the importance of different contexts as drivers and outcomes of mate choice. Reducibility analysis can be used to uncover the biological importance of different types of interactions and determine appropriate timescales of analysis. Finally, the analysis of interconnected networks can bring together interactions of different types, such as connections between physical features in the environment and social interactions to identify modulating factors of mate choice. A multilayered approach to the study of mate choice can uncover novel dynamics of mate choice and its outcomes, opening up new biological questions and potentially revealing new ecological and evolutionary processes.

Network science has advanced the study of animal social behaviour in recent years (Webber & Vander Wal, 2019). The use of network science in animal behaviour has uncovered causes and consequences of social behaviour by providing new ways to quantify the role of individuals in a group and to describe the social structure of animal societies (Croft et al., 2008). Mate choice is a social process and our understanding of it can greatly benefit from the use of social network theory. Various approaches have been proposed for how social network methods can be used to uncover the structures of mating systems (Maldonado-Chaparro et al., 2018; G. G. McDonald & Pizzari, 2016; Safran et al., 2019; Sih et al., 2009). Here we expand on these suggestions to highlight the ways in which new developments in social network theory, multilayer network analysis (Finn et al., 2019; Silk et al., 2018), might be used to investigate the multilayered nature of mate choice and sexual selection.

Mate choice is a social phenotype: a type of nonrandom mating that arises from any property of an individual that makes it more likely to engage in sexual activity with one partner over another, whether or not gametes are exchanged (Rosenthal, 2017). Along with intrasexual competition, mate choice is a primary mechanism of sexual selection before and after mating. Historically, mate choice has been studied through the lens of how it generates directional selection on elaborate (male) display traits; but mating decisions have key consequences beyond sexual selection. Notably, mate choice serves to optimize genetic and phenotypic compatibility, such as between conspecific versus heterospecific mates indiscriminately (Rosenthal & Ryan, 2022). And mutual mate choice, where both males and females discriminate among potential mates (Schlupp, 2023), is much more widespread than previously thought.

The social environment plays a fundamental role in shaping phenotypes involved in mate choice. Before birth, and early in life, sexual imprinting shapes mating preferences for example, through learned advertisement behaviour (like learned dialects in birdsong), which shapes sexual competition (Verzijden et al., 2012). Later in life, changes in encounter rates with potential mates can have dramatic effects on how choosy individuals are (Watts et al., 2022). And the mating decisions of one individual can influence

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another through mate copying (Davies et al., 2020; B. Jones & DuVal, 2019). Here we detail how these different types of social interactions can be integrated, using a multilayer framework, to advance our understanding of mate choice.

DYADS AND BINARIES: PRENETWORK FRAMEWORKS FOR MATE CHOICE

Mate choice is often simplified both conceptually and experimentally according to communication theory, which allows us to model interactions between a single signaller and a single receiver, and perhaps an eavesdropper (Bradbury & Vehrencamp, 2011). This paradigm lends itself to sleek experiments where chooser responses are compared between two or sometimes a few alternative stimuli. The roles and relative effort that males and females each put into courting and choosing can vary across species and over time, which is why the sex-neutral terms 'courter' and 'chooser' are more apt to describe sexual interactions (Rosenthal, 2017; Fig. 1). Copying is typically studied by adding one or more 'models' to the mix, when a focal subject is eavesdropping on a simplified signal–receiver interaction. While these studies lend themselves to clean analysis, they are limited in what they can tell us about how mating outcomes happen in nature. For example, the strength of sexual selection and assortative mating are highly sensitive to the number and distribution of interactions between multiple potential mates (reviewed in Rosenthal, 2017, chapter 6). Females in a world of few males can nevertheless be relatively choosy if males can mate with many females and are not sperm-limited, or if females can afford to wait for future opportunities. At the other extreme, if females are time-constrained and have to choose among a low density of males defending breeding territories, they relax their preferences. This is the case with south American annual killifish, *Austrolebias reicherti*, where males experience higher mortality over the breeding season and females cannot defer mating (Passos et al., 2014).

NETWORKS IN THE CONTEXT OF MATE CHOICE

Network approaches push the empirical study of mate choice beyond the dyadic paradigm. Network analysis is used to examine the role of individuals in a society and the structure of the social system (Croft et al., 2008; Pinter-Wollman, 2025; Wey et al., 2008). New technologies permit simultaneous tracking of dozens of individuals in wild and complex settings (Smith & Pinter-Wollman, 2021), opening the door to testing hypotheses grounded in social network theory. In an animal social network, individuals are depicted as nodes and interactions among them are edges (Fig. 1). At the minimum, edges encode the presence or absence of an interaction (whether nodes are linked or not). In addition, edges can have a weight to indicate the strength of an interaction, the probability of a link or the number of interactions between two nodes, often graphically represented as the width of an edge (Fig. 1). In many cases, an interaction can be directed. For example, agonistic interactions can be directed from one individual to another (Fig. 2a).

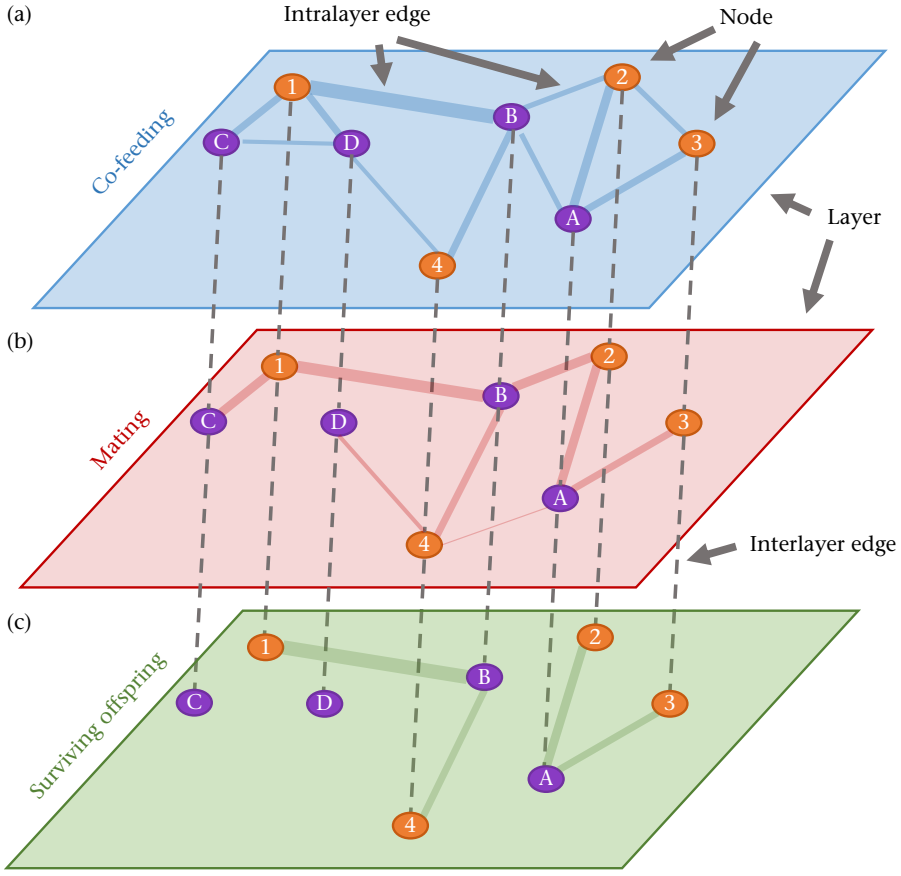

Figure 1. Introduction to multilayer networks. A hypothetical multilayer network comprising three layers (parallelograms), each depicting a different type of interaction: (a) co-feeding interactions during the nonbreeding season; (b) mating interactions; (c) co-parentage of surviving offspring. Each layer includes the same individuals, or nodes (ovals). Choosers are purple nodes (A–D) and courters are orange nodes (1–4). Edges (coloured lines) within a layer (intralayer edges) indicate interactions or relationships. The thickness of the line indicates the strength of the interaction (e.g. edge thickness increases with the number of matings (b) or with the number of shared offspring (c)). Edges across layers (dashed grey lines) connect each individual to itself in a different situation (interlayer edges).

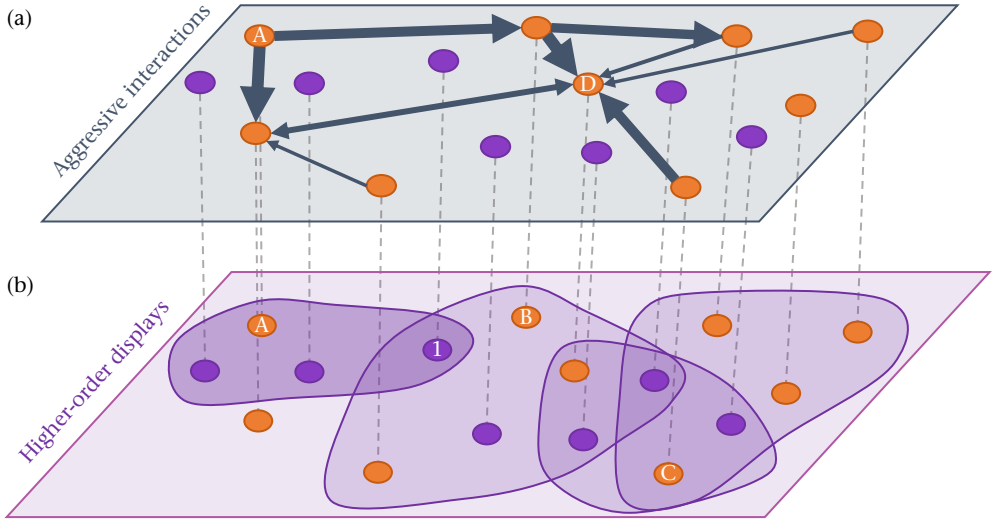

Figure 2. Different types of intralayer interactions. Interactions (edges) within a context (layer) can be directional (a) or higher-order (b). (a) When there is a clear initiator and receiver (e.g. aggression, provisioning, etc.), an interaction can be depicted as an arrow from the initiator to the receiver. The width of the line can indicate the strength of the interaction or the number of interactions. In this hypothetical example, individual 'A' aggresses two individuals with similar strength and individual 'D' is aggressed by five unique individuals, with some being more aggressive to 'D' than others. (b) Traditional network analysis does not distinguish between many dyadic interactions that occur sequentially and simultaneous higher-order interactions that occur among a group of individuals. Hypergraphs (b) can designate simultaneous interactions (denoted by the irregular shapes) as intralayer edges within a layer in a multilayer network. In this hypothetical example there are four display events by three individuals (A–C orange ovals). Three choosers (purple ovals) perceive the display of courter 'A' simultaneously and one of those choosers (1) also perceives the display by 'B' at a different time. Individual 'C' performs two displays: one display is perceived by three choosers (purple ovals) and one courter (orange oval) and the other display is perceived by two choosers (purple ovals) and three other courters (orange ovals). Nodes in both types of networks can be connected with interlayer edges (dashed light grey lines) to form a multilayer network.

Similarly, a nuptial gift can be provided from one mating partner to another. It may be important to consider the direction of an interaction, for example, to determine dominance hierarchies (Hobson, Monster, & DeDeo, 2021; D. D. McDonald & Shizuka, 2013). Furthermore, each edge in a network depicts a dyadic interaction, and in traditional network analysis, there is no way to distinguish between a simultaneous interaction among multiple individuals, referred to as a higher-order-interaction, and multiple sequential dyadic interactions (Greening et al., 2015). For example, multiple individuals simultaneously observing a single display of an individual in a lek will be depicted as many dyadic interactions between the displayer and the observers in a traditional network, losing the potentially important information that all of these interactions occurred simultaneously. Higher-order, simultaneous interactions are important to distinguish from sequential dyadic interactions, because of the difference in information transmission efficiency. In the context of mate choice, higher-order interactions can reveal eavesdropping and opportunities for mate copying. Simplicial sets, a mathematical concept from algebraic topology, and hypergraphs, a type of network generalization (Fig. 2b), can be used to quantify edges that connect multiple individuals that interact simultaneously in higher-order-interactions in the context of animal behaviour (for definitions and specific uses of these tools, see Greening et al., 2015; Iacopini et al., 2024).

Traditional network analysis has been used to study mate choice. For example, network analysis has been used to show that mating is not random (Busso et al., 2022) and that individuals assort by physical attributes, such as song type, plumage and bill colour (Barou-Dagues et al., 2025; Wang et al., 2022; Zonana et al., 2019). Furthermore, who individuals mate with could be impacted by physical distance and age (Moore et al., 2015) and depends on both female choice and male rejection (Yan et al., 2024). Interactions in nonmating social situations can affect access to mates and mating outcomes. For example, mating success in rock hyrax, *Procavia capensis*, is impacted by their social interactions with competitors in the nonbreeding season (Bar Ziv et al., 2016), and prebreeding sociality affects the strength of breeding bonds in birds (Beck et al., 2021; Maldonado-Chaparro et al., 2021; G. McDonald et al., 2020). Because mate choice is a process that can be impacted by many types of social interactions, and it has varied implications for reproductive success, new developments in multilayer network analysis can further advance our ability to study how interactions in different situations affect both mate choice decisions and outcomes.

Multilayer networks bring together different types of interactions into a single framework. Layers in a multilayer network can depict different types of interactions (Figs 1–2) and/or interactions that occur at different times (Finn et al., 2019). The same individuals (or subsets of individuals) may appear in all layers of the network, and interactions within a layer are referred to as intralayer edges, which can be weighted, directed or higher-order. The connections among layers are interlayer edges, which commonly connect the same individual in different layers (Figs 1–2). Interlayer edges can sometimes be used to link different types of nodes, such as individuals to physical locations (Silk et al., 2018). Because mate choice encompasses a large range of interactions, from relationships among potential partners before and after mating, through mating, fertilization, and beyond, a multilayered approach can expand our ability to quantify how different stages of mate choice influence each other. Here we propose that new tools in multilayer network analysis can facilitate the integration of interactions that occur at different times and in different contexts to determine the causes and consequences of mate choice. Specifically, our goal is to suggest ways in which multilayer networks can help identify the relative importance of different stages in the process of mate choice for reproductive outcomes, both for individuals and at the population level. In the sections that follow, we first detail the types of interactions (or layers) one might consider in a study of mate choice, we then go on to detail some novel approaches and questions that a multilayer network analysis can bring to light. To help guide future data analysis, we provide a list of references and software in Table 1.

Table 1
Suggested references and software for implementing network analysis and multilayer network analysis

Software or paper title	Description	Source
Multilayer network analysis:		
Multilayer networks	Comprehensive review paper detailing the utility of multilayer network analysis broadly	Kivelä et al. (2014)
Multilayer networks: Analysis and visualization introduction to muxViz with R	Textbook (available as PDF online) detailing how to visualize and analyse multilayer networks. The book is linked to an extensive Github repository of R code	De Domenico (2022)
Ranking in interconnected multilayer networks reveals versatile nodes	Manuscript about multilayer network measures of individual centrality. Includes a comprehensive appendix with worked out examples as well as accompanying code for implementation	De Domenico, Sole-Ribalta, et al. (2015)
The use of multilayer network analysis in animal behaviour	A conceptual overview of how multilayer networks can be implemented to study questions in animal behaviour. Includes worked out examples	Finn et al. (2019)
muxViz	An R package to visualize and analyse multilayer network data	De Domenico, Porter, and Arenas (2015)
Using social network analysis to study animal behaviour:		
Social network analysis	An entry in the *Encyclopedia of Animal Behavior* (3rd ed.) that provides a recent introductory primer to the use of social network analysis in the field of animal behaviour with citations to helpful implementation tools	Pinter-Wollman (2025)
Conceptual representations of animal social networks: An overview	Overview of how to represent and analyse social networks in animal behaviour, includes extensive examples with accompanying R code	Silk (2023)
A guide to choosing and implementing reference models for social network analysis	A guide for statistical approaches to study animal social networks with extensive accompanying R code	Hobson, Silk, et al. (2021)
The consequences of unidentifiable individuals for the analysis of an animal social network	A commentary examining the effect of sampling effort and sample size on the accuracy of social network measures	Silk et al. (2015)
igraph	An R package to visualize and analyse network data	Csardi and Nepusz (2006)

Note that this is a partial, not comprehensive, list; there are many more helpful tools and relevant papers in the literature.

LAYERS OF MATE CHOICE

Successful sexual reproduction involves at least four different types of interactions, which occur in order: encounter, mating, fertilization and production of viable offspring. Animals encounter potential mates by sharing space and time, mate with a subset of those individuals, fertilize gametes with some of those individuals and produce viable offspring with even fewer. We can think of these fundamental interactions as constituting different layers of mate choice.

These four common interactions are shaped by a host of processes that can vary across taxa, from female responses to male advertisement calls in frogs and crickets, to sexual imprinting and mate copying in birds, to female physiological challenges to sperm in fishes (Rosenthal, 2017). Social interactions are modulated by nonsocial variables that can also be represented as layers of interactions in a multilayer network. For example, pairwise genetic relatedness, or distance between home ranges, can be depicted as interactions between individuals. In these cases, genetic relatedness or physical distance will be encoded as edge weights (more below). Layers of different types of interactions may be further decomposed into repeated time samples of the same behaviour, for example, pair-bonding networks this season and next season. In this section we detail pre-, peri- and postmating interactions that can be depicted as layers in a multilayer network. The section that follows details the multilayer approaches that could be used to integrate these layers and outlines insights that may be gleaned from such integration.

Premating

Early learning

Before sexual maturity, mating preferences are often shaped by social experience with parents or other adult models. These interactions may have positive effects on sexual preferences, as with female preferences for contemporary dialects in songbirds (Luther & Derryberry, 2012), or negative ones, as with sexual aversion in unrelated humans raised together (Lieberman & Lobel, 2012). In experimental settings, experience with a particular phenotype can have determining effects on preference, with individuals preferring or, often, avoiding experienced phenotypes when sexually active (Rosenthal, 2017). Early learning includes irreversible imprinting of preferences during a critical sensitive period (ten Cate et al., 2006). One could depict the physiological mechanisms of imprinting as a network. For example, MHC similarity (Ziegler et al., 2005) could determine the presence and weight of edges in a network to ask how strongly a physiological network affects mate choice and its outcomes.

Peer interactions

Nonsexual interactions among individuals can be considered as an extension of early learning and may shape sexual relationships later in life (Bar Ziv et al., 2016; G. McDonald et al., 2020; Oh & Badyaev, 2010). Using Fig. 1 as a hypothetical example to clarify how nonsexual interactions might relate to mate choice, individual C co-feeds with 1 and D, mates with 1, and has no viable offspring. Thus, the interactions between C and 1 when feeding before the breeding season might relate to individuals' likelihood to mate but not to their likelihood to have surviving offspring. Co-feeding during the juvenile stage could also have consequences for mate copying and cooperative displays within sexes. A multilayer approach could help link nonsexual interactions among individuals with mate choice decisions and consequences, as detailed below.

Intrasexual interactions

The social environment continues to shape mate choice leading up to intersexual interactions and mating. Intrasexual competition for access to mates is perhaps the most visible driver of sexual selection (Darwin, 1859). Intrasexual competition may serve as a

filter to restrict the pool of accessible mates, but frequently it is a dynamic process in which choosers may incite intrasexual interactions and/or base mating decisions on their outcomes (Wong & Candolin, 2005). Multiple individuals may cooperate to secure matings, as in cooperative mate guarding in lions, *Panthera leo* (Chakrabarti et al., 2020), and courtship displays in North American turkeys, *Meleagris gallopavo* (Krakauer, 2005). Network approaches have been used to characterize intrasexual interactions among courters, like agonistic interactions among male American bison, *Bison bison* (Wyman et al., 2021), and field crickets, *Gryllus campestris* (Fisher et al., 2016), and joint lek displays in longtailed manakins, *Chiroxiphia linearis* (D. D. McDonald, 2007). The use of hypergraphs or simplicial sets could improve our understanding of higher-order interactions in which multiple choosers, as well as eavesdropping courters, observe the same displays (Fig. 2b). A multilayer approach could help uncover how the relationships between intra- and intersexual interactions shape mating outcomes (Fig. 3).

Premating choice: from detection to working memory

Network analysis can inform how sensory and cognitive mechanisms shape realized mating preferences. We can start by asking which choosers are likely to detect which courter signals in the environment, and how this influences subsequent mate sampling and mate choice on the part of choosers. This is the first step towards evaluating potential mates and making mating decisions. The network of mates sampled represents an upper bound of the number of potential mates in working memory (Akre & Ryan, 2010) and constitutes a comparison set whose relationships determine perceived attractiveness (Bateson & Healy, 2005). Network approaches could be useful in understanding the real-world impacts of phenomena like the decoy effect (Lea & Ryan, 2015) and the Ebbinghaus illusion (Kelley & Endler, 2012), both of which lead to mistaken assessment of signal value based on comparison with others. Network theory gives us a framework to understand how choosers are attending to courters and comparing them in the process of choice, including distinguishing between dyadic and higher-order interactions (Fig. 2b).

Intersexual interactions

Relationships between courters and choosers can be depicted as a network to identify variation in intended recipients of courtship displays and to examine which choosers elicit the most displays. Broadcast courtship signals, like frog calls and moth pheromones, are cases in which individuals signal indiscriminately (Rosenthal & Ryan, 2022) and can be depicted as higher-order interactions (Fig. 2b).

Mate copying in which the mating decisions of one 'model' individual influences those of another, is widespread in animals (Davies et al., 2020; B. Jones & DuVal, 2019). Females typically prefer males that they have observed interacting with other females, while males prefer females with fewer mates (Wong & McCarthy, 2009). Experimental studies suggest that mate copying should be strong enough to reverse previously expressed preferences, such that choosers prefer a previously undesired mate. A recent model proposes 'inferred attractiveness' as a mechanism whereby females use copying and social context to make mating decisions (Duval et al., 2023). Network approaches may provide a powerful way to test these model predictions. Changes in the distribution of models and potential mates could have effects on expressed preferences, but current paradigms make it difficult to link experimental studies to concrete predictions for mating decisions and sexual selection in the wild.

Peri- and Postmating

Mating and remating

The mating network (Fig. 1b) is the outcome of mate choice; it describes who engages in sexual activity with whom. The mating network of who mates with whom is a representation of the 'mating system', which behavioural ecologists have historically categorized as monogamous, polyandrous (females have multiple

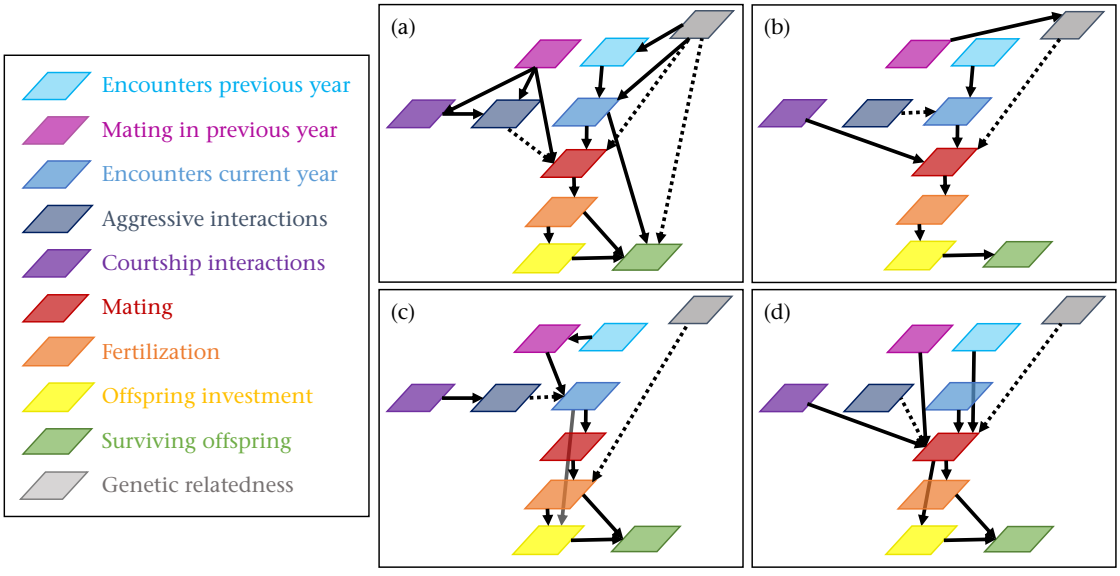

Figure 3. Network of networks. Interactions related to mate choice, detailed in the text, can be connected as layers in a multilayer network. Here, each type of interaction (or layer in a multilayer network) is a node (parallelograms) in a 'network of networks'. Layers are connected using directed edges that indicate hypothetical direction of influence. Solid arrows indicate a positive impact from the origin to the destination of the arrow, and dashed arrows indicate a negative impact. The directed edges shown here are hypothetical and do not represent specific study systems. Edges can either be specified by the researcher, based on knowledge of the system, or be generated from information about each layer (see legend on left), as detailed in the text and in Fig. 4. Note that layers are indicated as nodes in a 'network of networks' and the connections between them (edges in the 'network of networks') can represent a relationship that pertains to all, or some, of the elements in each layer, defined based on the study question, see examples. (a–d) These four hypothetical examples serve to illustrate systems that differ in the relationship among layers, or alternative hypotheses for the network of networks in a single system. For example, in (a–c), the mating network directly influences only fertilization, but in (d), it also influences offspring investment.

mates), polygynous (males have multiple mates) or polygynandrous (or promiscuous). These categories are useful for roughly characterizing social mating systems, but parentage analyses have revealed that nearly all species are promiscuous to some degree. Nevertheless, populations can exhibit extreme reproductive skew, from all females mating with one or two males, to extreme polygynandry in which males and females both mate multiply with one another (A. Jones & Ratterman, 2009).

Networks can consider remating during a reproductive period and beyond. Mating partners may persist year after year, forming long-term relationships in which mating interactions in one year are directly linked with mating interactions in the following year. These networks offer a fresh look at mating systems, perhaps addressing controversies regarding how to measure the intensity of sexual selection, for example using reducibility analysis (see below) of multiyear mating interactions.

Mate choice between mating and fertilization

Mate choice can continue during the time between mating and fertilization. For example, there can be variation among individuals in the amount of sperm that is transferred during mating. Sperm competition and cryptic mate choice (mate choice by females during and after mating), from sperm ejection to the egg prosoma (Eberhard, 1996), further shape fertilization outcomes, which can differ from what would be predicted based only on observed matings. These types of interactions are more challenging to measure directly than premating behaviour, but some systems may lend themselves to measuring these networks.

External fertilizers (including plants) lend themselves well to crossed experiments where fertilization success is compared across all possible pairs of multiple individuals (Aguirre et al., 2016), an approach that could be extended to interactions between sperm and female reproductive fluid (Gasparini et al., 2020). More generally, network theory offers an indirect approach to quantify these hidden relationships by comparing networks of mating with networks of reproductive outcomes (Fisher et al., 2016) to quantify how postmating interactions reinforce, or counteract, premating choice (see below).

Postfertilization

Parentage analysis allows us to determine which individuals share offspring that have survived to a particular stage (birth, fledging, sexual maturity). In many systems, partners may continue to interact directly or indirectly through investment in offspring, like allocation of nutrients and hormones to embryos, egg and offspring, potentially into adulthood. Such postfertilization investment can extend to grandoffspring (Weiss et al., 2023), impacting differential reproductive success for generations and potentially impacting their mating success.

Modulating factors

Other modulating factors can further impact mate choice. For example, spatially explicit environmental and landscape features can influence which individuals can come into contact with one another and mate. Genetic relatedness (which can be depicted as edge weights representing relatedness likelihoods) can influence premating avoidance of sexual contact with kin (Dorsey & Rosenthal, 2023).

HOW CAN MULTILAYER NETWORK ANALYSIS ADVANCE THE STUDY OF MATE CHOICE?

Multilayer network analysis allows us to integrate the layers of mate choice into a single framework that can be used to determine how the ways in which networks interact with one another impact the dynamics of mate choice and its outcomes, opening up many biological questions. In the sections below, we detail some of the multilayer network tools that may help investigate novel biological questions. For example, it might be possible to predict the structure of a mating network (e.g. the degree of reproductive skew) from premating interactions within and between the sexes by examining layer overlap. A multilayer network allows us to connect physiological, intrasexual and intersexual networks to determine their impact on mating choices and outcomes, for example by linking layers in a network of networks. Such integration is important because it allows us to quantify the role of chooser agency in structuring reproductive outcomes. For example, an intersexual network that quantifies how choosers sample courters can be linked (as detailed below) to an intrasexual network of competition among courters to ask whether choosers benefit or suffer from this competition filter and how much mating decisions depend on public information. By linking behaviour to environmental features, multilayer networks can help uncover how choosers sample courters spatially as well as the interplay between sampling potential mates and avoiding harassment, by integrating modulating factors. Furthermore, intersexual mating biases are dynamic, with preferences frequently shifting as a function of mate sampling and mate copying. Multilayer networks can help uncover how sensitive mating encounters are to the order in which courters and choosers encounter each other and how networks of intersexual courtship map onto intrasexual interactions among choosers, for example using reducibility analysis.

Network of Networks

To uncover the ways in which different layers are connected, one can study a network of networks. Multilayer networks are traditionally depicted as a stack of networks, one on top of another (e.g. Fig. 1), suggesting there is a linear transition between one layer and the next. Such an assumption might be appropriate if layers describe interactions that occur at sequential time points, and interactions at one time point influence interactions only in the next time point (Gahm et al., 2026). However, in cases where each layer depicts a different context, there could be many ways in which layers are connected (Fig. 3). Mate choice is a mixture of processes that occur sequentially, with clear linear ordering (e.g. fertilization after mating), and processes that may act in parallel, at varying times and with varying impact on one another, depending on the study system. For example, mating might be influenced by other encounters in the current year, such as co-feeding, while fertilization might be impacted independently by genetic relatedness (Fig. 3c).

How to Connect Layers in a Network of Networks?

There are two approaches to linking different types of interactions in a multilayer network. Interlayer interactions can be explicitly specified by the researcher based on observations, or they can be inferred, for example, from the similarity across layers. Which approach to use depends on the research question, the study system and the data available.

Biological processes and observations can be used to connect layers explicitly. For example, there can be no surviving offspring without fertilization, and therefore, biologically, there should always be a link directed from fertilization to surviving offspring (Fig. 3). In addition to indicating whether a link is present or not, one might further be interested in its strength, or weight. The weight of a link between mating and fertilization layers can differ across systems if, for example, it depicts the population-level

average of fertilization success. Furthermore, interlayer edges between fertilization and successful offspring can differ among individuals, based on their relative contribution to fertilization and their relative contribution to surviving offspring (discussed below). This interindividual variation in interlayer edges can be translated to interlayer link weights using summary statistics (e.g. difference or sum of averages, difference in standard deviations, etc.). The relationships among layers can be directional and/or carry opposite weights. For example, courtship interactions between individuals usually increase the likelihood of two individuals mating, while prior aggressive interactions with intrasexual rivals might tend to reduce it (Fig. 3d). Decisions about the directionality of links between layers should be informed by their biological representation.

When the strength of influence between layers is not known, the goal of the research could be to uncover the weights of interlayer interactions. For example, one could use the similarity among layers to determine the weight of interlayer relationships. Layers that are more similar, or have more overlap with one another, can be more strongly connected. The relationship between layers can be quantified based on the amount of overlap in a variety of network elements, including nodes, edges (De Domenico, 2022) and degree (Nicosia & Latora, 2015) (Fig. 4). Some network similarity measures take into account the heterogeneity among individuals in their degree and strength within each layer (Gemmetto & Garlaschelli, 2015). For example, individuals may vary both in their ability to transfer sperm and in the tendency of their sperm to produce viable offspring. In seed beetles (Bilde et al., 2009), males with high fertilization rates produce offspring with lower survivorship and therefore do not necessarily sire a high number of offspring (e.g. Fig. 4a–c). Multilayer measures can be used to quantify the relationship among such nested layers by examining layer overlap. Basing layer overlap on similarity in nodes (Fig. 4d) can be used to examine changes in population composition and social participation across time or contexts. Shared edges (Fig. 4e) can be used to indicate similarity in social relationships across time and contexts. Overlap based on shortest paths (Fig. 4f) can be used to examine similarity in

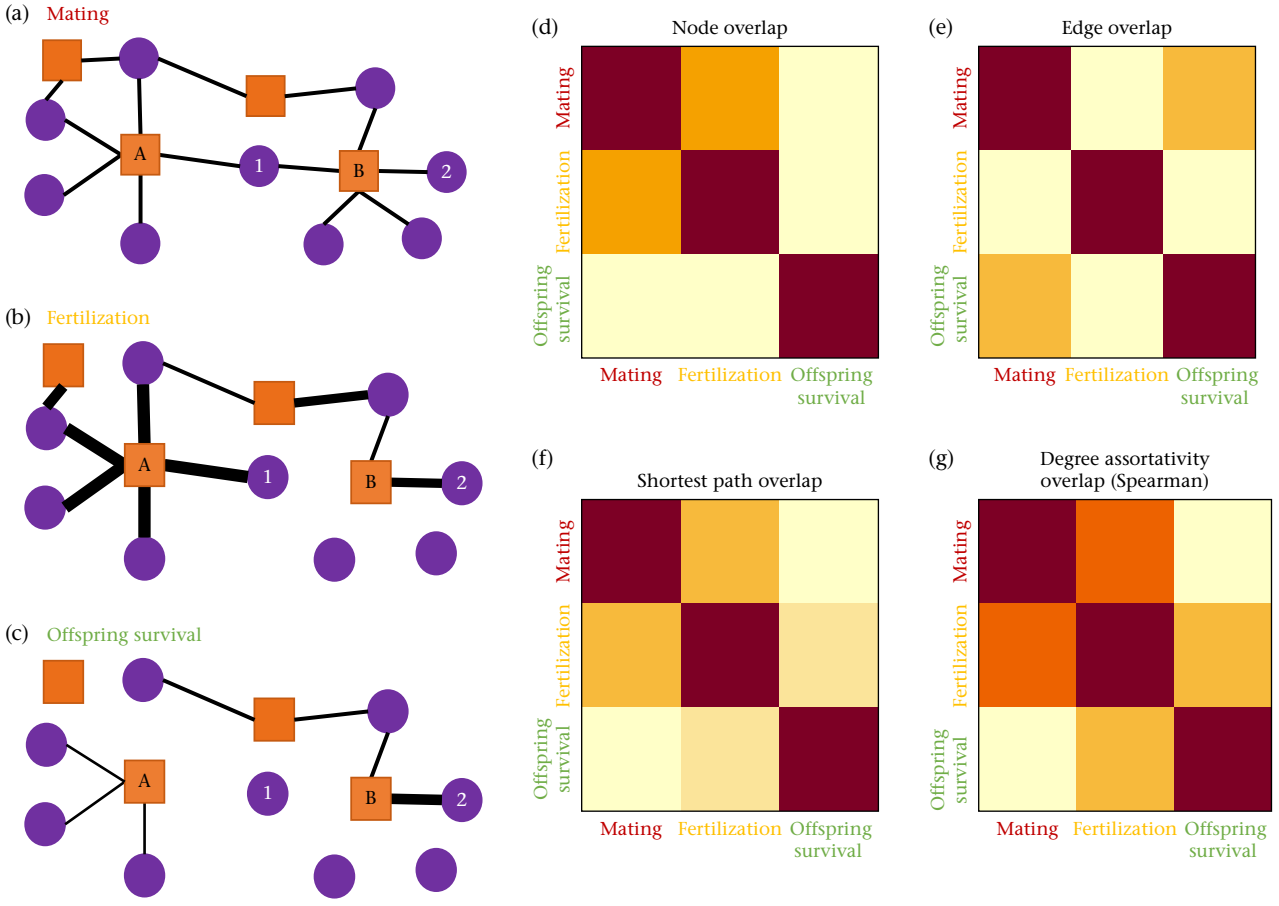

Figure 4. Hypothetical multilayer network and layer overlap analysis. In this hypothetical network (inspired by Bilde et al., 2009), offspring survival is not linearly related to fertilization rate. (a) In this example, two males (A and B orange squares) mated with the same number of females (purple circles). (b) Male 'A' has higher fertilization rates: he fertilizes more females (higher degree) and transfers more sperm (greater edge strengths, as shown by the width of the lines) in each mating compared to male 'B'. (c) However, due to postmating competition, male 'A' sires fewer offspring (lower strength in (c)) relative to his fertilization (high strength in (b)). On the other hand, the number of offspring that male 'B' sires is in direct proportion to his fertilization effort. From the female perspective, by mating with individual 'A', female 1 ends up with no offspring because male A's competitive sperm overwhelm male B's and male A's progeny have higher mortality (following the work by Bilde et al., 2009). Female 2 on the other hand mates only with male B, resulting in surviving offspring. A multilayer network analysis of layer–layer similarity (De Domenico, 2022) depicts different types of relationships among the layers. (d–g) Each row and each column in the heatmaps represent a layer, and colour indicates layer similarity based on overlap in (d) nodes, (e) edges, (f) shortest paths and (g) assortativity by degree. Darker colours indicate higher similarity. Note that when calculating layer overlap using (d) node, (f) shortest path and (g) degree assortativity, the mating and fertilization layers are more similar to one another than they are to the surviving offspring layer. The biological interpretation of this similarity is that individuals that mate with one another are more likely to fertilize each other's gametes, but less likely to co-parent surviving offspring. However, when using (e) edge overlap, mating and offspring survival are more similar to one another compared to fertilization (note that this overlap measure takes into account edge weight). Biologically, this means that interaction strength in mating (e.g. number of mating events) is a better predictor of offspring survival than fertilization rate. R code to produce components of this figure is provided as a Supplementary Material.

community cohesiveness. Finally, assortativity overlap (Fig. 4g) can be used to infer similar processes that shape sociality. Each measure of similarity may show a different relationship among layers (Fig. 4f, g). Which approach to use when linking layers would have to be informed by the biological question addressed and the biological meaning of the measures used.

Once layers are connected, one can apply traditional social network analysis to a network of networks, which is in itself a monolayer network (De Domenico et al., 2013). For example, measures such as degree and strength can be used to determine the centrality of the mating network (red node in Fig. 3), or of other types of interactions in the system. The mating network in Fig. 3 (red node) is directly impacted (measured with 'in degree', the number of arrows pointing to a node) by a different number of situations in each panel. The 'in degree' of the mating network is four in Fig. 3a, three in Fig. 3b, one in Fig 3c and six in Fig. 3d, showing that mating outcomes in the four hypothetical populations depicted in Fig. 3 emerge from and are impacted by very different processes. Similarly, the outcomes of matings can differ (or be the same) across systems. For example, in Fig. 3a–c, the mating network directly influences only fertilization, but in Fig. 3d, it also influences offspring investment. Comparisons across populations or species can unravel how pre-, peri- and postmating processes interact to shape fitness outcomes, population structures and sexual selection.

Reducibility Analysis

Reducibility analysis is used to determine which layers are redundant in a multilayer network. Layers can provide similar, potentially redundant, information and therefore determining which layers provide the most unique information can help inform which types of interactions to focus research efforts on and what is the timescale over which meaningful changes occur. Such a reducibility analysis can both save resources by focusing research on where it is most beneficial and reduce the potential for overfitting models with redundant information. Multilayer reducibility analysis first determines the similarity among all layers using the Jensen–Shannon divergence index, which is a statistical measure from information theory that quantifies the similarity between two distributions by essentially comparing them to the average distribution of the two (De Domenico, Nicosia, et al., 2015). It then begins aggregating the layers based on their similarity (combining the most similar layers first) and compares the combinations to a fully aggregated network in which all layers are added. The comparison asks how much information is lost in the aggregation process. The more similar the aggregated layers, the less information is lost. Such an analysis can uncover which social situations are most (or least) informative for predicting mating interactions. For example, if aggregating feeding interactions and display interactions does not result in lost information, then these layers provide redundant information. Identifying such redundancy can provide both biological and logistical insights. Biologically, such redundancy means that the two social contexts are highly related to one another and that individuals feeding and displaying have similar social connections. Logistically, such similarity suggests that if one behaviour is easier to observe, or quantify, than the other, then it is sufficient to examine only one of the two behaviours to save time and resources.

In addition to identifying redundant types of interactions, reducibility analysis can further be used to determine the timescale over which important social dynamics occur. From ontogeny through multiple reproductive seasons, an individual's phenotype changes and its social network changes on a timescale of a lifetime, season, or a few days. Empirically, both affiliative (Firth et al., 2018) and agonistic (Bierbach et al., 2014) interactions change throughout the prebreeding season, and as affiliative interactions with eventual mating partners accumulate, there is an increase in access to mates during the breeding season (Firth et al., 2018). Social encounters that are aggregated on a timescale of a season can impact partnerships when the breeding season starts (G. McDonald et al., 2020). Finally, social interactions over longer timescales, throughout ontogeny, can improve the social position of individuals and increase their access to potential mates. The social position of males in manakin leks improves over their lifetime, leading to increased reproductive success (D. D. McDonald, 2007; Ryder et al., 2008).

Interactions at one time point can affect interactions at another time point and these influences of interactions can occur at short and long timescales. Multilayer network analysis can reveal social dynamics that are hidden when interactions are aggregated over timescales that are too long (Fig. 5). If each layer in a multilayer network depicts interactions that are aggregated over a different time window, then reducibility analysis may help determine the biologically appropriate window over which to aggregate interactions, as well as the duration over which interactions should be observed to gain the most information about social dynamics (Gahm et al., 2026). Once multiple layers of a single time window

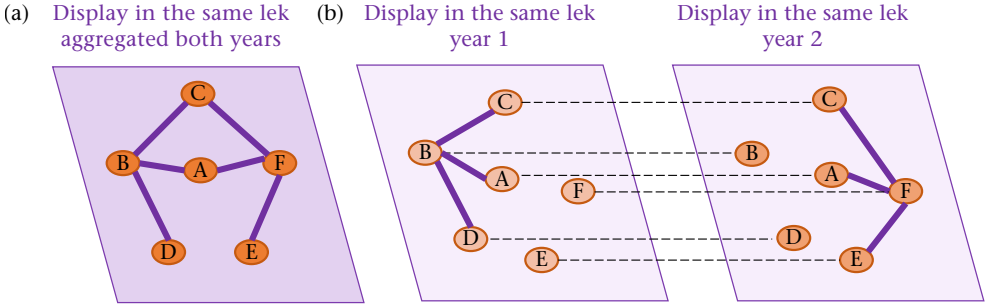

Figure 5. Different considerations of time alter the quantification of individual centrality. Hypothetical example in which six males (nodes) display in a lek. Purple edges connect males that display together. In this hypothetical example, displaying with more unique individuals (greater degree) increases the intrasexual dominance rank of an individual and therefore its potential mating opportunities. (a) An aggregate network that shows the co-display interactions over two years combined. (b) A multilayer network in which co-display networks are shown for two consecutive years with interlayer edges (dashed black lines) connecting the same individuals across the two years. An analysis of the aggregate network would conclude that individuals B and F share the highest rank because they have the greatest degree (both connected to the most unique individuals). An analysis of year 1 only would conclude that individual B is the highest ranking, and analysis of year 2 only would conclude that individual F is the highest ranking because they each have the greatest degree in each of those years, respectively. However, an analysis of the multilayer network, which takes into account that individuals A and C connect two distinct groups across years, would conclude that individuals A and C share the highest rank because they both have the highest 'versatility' (a multilayer equivalent of 'degree'; for details, see Sharma et al., 2022; Smith-Aguilar et al., 2019). Which quantification of centrality is most informative would depend on the study system, biological questions, and potentially on links to other traits, such as reproductive success. This figure reproduces an example from (De Domenico, Sole-Ribalta, et al., 2015).

are created, they can be put together in a multilayer network and reducibility analysis can be used to provide information about how many layers of the particular window size are needed to provide nonredundant information. Shorter window sizes might each provide more unique information than layers that are aggregated over a large time window. Each layer based on a short time window might be sparse but as part of a multilayer network, it may provide more meaningful information than an aggregate of all layers into a single network (Fig. 5).

Integrating Modulating Factors: From Landscapes to Pleiotropy

In addition to connecting stages and mechanisms of mate choice, multilayer networks offer an opportunity to connect different types of networks, such as geographical distances with social interactions (Silk et al., 2018). Many studies of animal social networks ask whether animals interact 'at random'; i.e. do interactions happen by chance or because animals choose to interact with specific individuals and have a social preference? This question is key to the study of mate choice. Randomization is often used to produce reference networks that are compared with observed interactions to determine whether observed interactions emerge from social preference or from other processes (Gahm et al., 2024; Hobson, Silk, et al., 2021). For example, individuals might interact because they are attracted to the same resource, such as a water hole, rather than because they want to meet each other. Randomization procedures developed to study whether or not social interactions are intentional or incidental (Gahm et al., 2025, in press) can be expanded to study mate choice. For example, the comparison of an observed network of sleepy lizards, *Tiliqua rugosa*, to reference networks revealed that male–female interactions are stronger than what would be expected by chance based only on individuals' movement patterns (Spiegel et al., 2018).

Multilayer networks can link social behaviour with relationships between physical locations, such as distances between nest sites, leks, territories and food sources. If nodes in one layer represent physical features that facilitate social interactions and another layer depicts interacting individuals, then interlayer edges can connect individuals to the locations they visit (Silk et al., 2018). In the context of mate choice, signals from courters are part of the environment because broadcast information (e.g. birdsong) becomes part of the environment and may impact many individuals simultaneously in a higher-order interaction (Fig. 2b). Such signalling networks can become additional environmental layers in a multilayer network. Linking social networks with environmental networks can then reveal opportunities of interactions by applying community detection analysis that aggregates individuals into social communities based on different types of layers (Kinsley et al., 2020). An analysis of interconnected multilayer networks that link different types of nodes can reveal constraints on who might be able to encounter whom based on their spatial distribution, potential constraints on movements and ability (physiological or physical) to perceive relevant signals. Such integration is important for mate choice because, for example, if a chooser can only encounter or perceive courters who are all worse than average at parental care, they will do worse than those with access to just a handful of courters that are relatively good parents.

Finally, network science can be used to create phenotypic networks that describe within-individual relationships among traits. Wilkins et al. (2015) used phenotypic networks of multiple male courtship traits according to their co-occurrence within individuals. These phenotypic networks were then used to show that some phenotypic components affect reproductive success while others shape the spatial structure of the population, providing a more holistic view of multiple traits simultaneously. A multilayer network approach could expand this approach to focus on the relationship between social interactions and connectivity of traits, in a trait network, to reveal social communities that potentially assort by courter traits and chooser preferences. Uncovering such communities that are driven by trait similarity can have important implications for the study of the evolution of mate choice and speciation, in particular for the evolution of species in close sympatry.

Conclusions

Much of the challenge in understanding sexual selection and mate choice lies in connecting individual phenotypes, like mating decisions, with population-level processes like sexual selection and assortative mating. Networks address this challenge by embracing the fact that mate choice and sexual selection involve groups of dynamically interacting individuals. Multilayer network analysis provides a framework for integrating not only interactions among individuals at naturalistic scales, but also for quantitatively understanding the relationships among stages, across reproductive seasons and across generations. How these interactions map on to estimates of reproductive skew and assortative mating may open a window to uncover real-world mechanisms of sexual selection.

Author Contributions

Noa Pinter-Wollman: Writing – review & editing, Writing – original draft, Visualization, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Gil Rosenthal:** Writing – review & editing, Writing – original draft, Visualization, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

Data Availability

The R code for this study is available as Supplementary Material.

Declaration of Interest

None.

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Supplementary Material

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The Supplementary Material has not been copy-edited and the content, formatting and file functionality are the sole responsibility of the author(s).

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