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Social and coevolutionary feedbacks between mating and parental investment

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A survey of empirical studies relating mating and parental investment reveals as many unpredicted patterns as results supporting existing hypotheses. This leaves us with individual *post hoc* explanations of observed patterns rather than an ability to make strong *a priori* predictions. I argue here that our ability to explain and predict empirical patterns can be improved by considering how social interactions and coevolutionary dynamics affect male and female reproductive traits. Recent research suggests that these social and coevolutionary feedbacks can increase our understanding of empirical patterns, while suggesting new directions of research. I also describe a social and coevolutionary dynamics modelling approach that integrates ideas from reproductive cooperation and sexual conflict to increase understanding of mating and parental investment.

Feedbacks between mating, fertilisation and parental investment

The mating system of a species can be characterised by documenting observed patterns of mating, fertilisation and parental investment (see Glossary). These three key aspects of mating systems are intrinsically connected. Explaining and predicting the evolution of any particular trait (e.g. parental care or mating behaviour) therefore requires consideration of the many ways in which the evolution and expression of reproductive traits intertwine (Figure 1). First, traits are linked within individuals as a result of phenotypic tradeoffs or genetic correlations among traits (e.g. the allocation of energy between mating effort and parental investment). Second, social interactions within and between the sexes affect both the expression of, and selection on, mating and parental investment patterns in both sexes (e.g. mating is the outcome of both male and female behaviour). Finally, multiple traits in males and females coevolve simultaneously (e.g. the parental effort and mating behaviour of one sex affects selection on the parental effort and mating behaviour of the opposite sex). Rather than representing a series of independent relationships between traits, there is increasing evidence that these connections form social (i.e. behavioural) and coevolutionary feedback loops that affect both the immediate expression and long-term evolution of multiple traits simultaneously [1–5]. Mating systems are thus an emergent property of individual reproductive traits and the social interactions that shape their expression and coevolution.

Although our understanding of mating systems and reproductive traits has increased immensely over the past decades, most research has examined how one trait interacts with another. For example, extensive research has focused on understanding the relationship between paternity and parental investment [6]. Separate research has looked at how female mate choice evolves in response to variation in male care [7,8]. Finally, conflict between the sexes over mating rate and parental care is known to affect reproductive patterns in both sexes [9]. Although each of these topics explores a single link between mating and

Glossary

Coevolution: a change in the genetic composition of one group in response to a genetic change in another group. Although often defined as reciprocal evolutionary change between species (e.g. predator–prey), coevolution also applies to reciprocal evolutionary change between groups within a species, such as between males and females.

Coevolutionary feedback: when changes in the traits of one group of individuals lead to evolutionary change in the traits of another group, which then leads to evolutionary change in the first group, forming a feedback loop of reciprocal evolutionary change.

Cooperation: an interaction that has a positive fitness effect on the receiver. This might come at a cost to the individual performing the cooperative behaviour (e.g. altruism). Alternatively, an interaction might lead to mutual fitness benefits (e.g. mutualism).

Cooperative breeding: a social system in which individuals cooperate in the care of offspring. Although classically defined as non-reproductive individuals helping to raise the offspring of others, genetic paternity analyses have revealed that many helpers sire offspring. It does, however, always involve some individuals helping to raise the offspring of others.

Mating effort: the amount of energy or other resources allocated to mate attraction and mating.

Monogamy: a social system in which one male pairs with one female. Genetic monogamy occurs when one male and female sire all of their offspring together within a reproductive bout, whereas social monogamy captures the situation where one male and female are paired but also mate and sire offspring with other individuals within a reproductive bout.

Parental care: post-copulatory parental behaviours that are likely to increase the survival and reproduction of offspring.

Parental investment: any parental expenditure (e.g. time or energy) that benefits the fitness of offspring but reduces the ability of a parent to invest in other components of fitness.

Paternity: the proportion of offspring sired by a male (typically from a single female within a reproductive bout).

Polygamy: a mating system in which multiple males and females mate and potentially sire offspring. Polygyny refers to a mating system where one male mates with multiple females, whereas polyandry refers to the situation where one female mates with multiple males.

Social feedback: when phenotypic plasticity and social interactions lead to changes in the expression and fitness of a trait or traits, which leads to change in the expression of a trait or traits in other individuals, which then leads to further change in the first trait or group, forming a feedback loop of trait expression and fitness.

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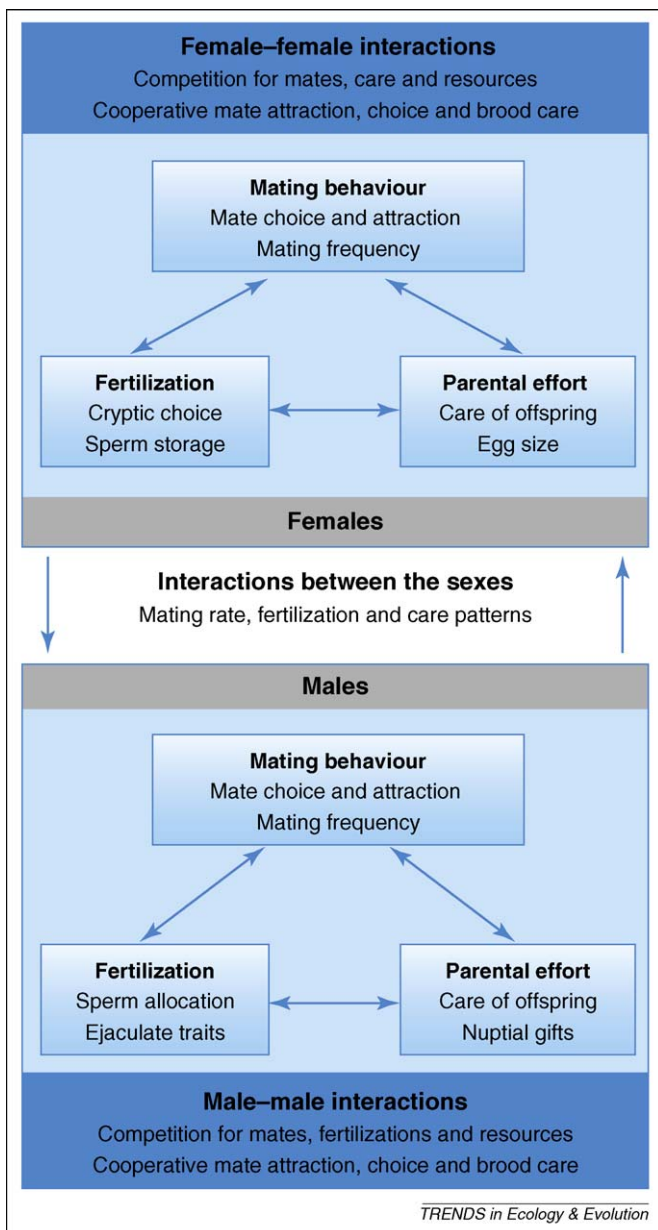
Figure 1. Mating systems are an emergent property of male and female traits that affect patterns of mating, fertilisation and parental investment. The expression of any male or female reproductive trait depends on the underlying genetic basis of the trait, social interactions, environmental conditions and interactions among these three components. Interactions between reproductive traits occur within individuals (light-blue boxes, e.g. resulting from phenotypic tradeoffs and genetic correlations), between individuals of the same sex (dark-blue boxes, e.g. competition) and between the sexes (e.g. sexual conflict and reproductive cooperation). The ability to predict the relationship between any two traits of interest in isolation (e.g. paternity and paternal care or mate choice and paternal investment) is limited by the fact that these traits will affect, and be affected by, social interactions and coevolutionary feedbacks with other traits that are driven by interactions within and between the sexes with respect to mating, fertilisation and parental investment.

parental care, they ignore the feedbacks that exist between male and female mating behaviour and parental investment. There is, however, increasing evidence that these individual interactions cannot be understood fully in isolation [1–5]. Instead, one must consider how social interactions and coevolutionary dynamics within and between the sexes affect the expression of traits related to mating, fertilisation and parental effort (Figure 1).

Here, I focus specifically on the coevolutionary and social feedback dynamics between male and female mating behaviour and parental investment. I ask how well observed patterns can be explained and predicted based on current conceptual frameworks that ignore or greatly simplify the social and coevolutionary feedbacks described above. I also show how recent research hints that a more coevolutionary approach is needed to understand observed reproductive patterns. I finish by outlining directions for future research, proposing a new modelling method that can examine social interactions and coevolutionary feedbacks, and demonstrating the potential for new insights by discussing how this approach can bring together research on reproductive cooperation and sexual conflict.

Male parental effort in response to variation in paternity
The realisation that females mate with multiple males in most species [9,10] stimulated extensive theoretical and empirical research asking how male investment in offspring is affected by variation in paternity [6,11]. Theory has examined the circumstances under which males might reduce paternal care in response to decreased paternity. Despite early disagreement, a general consensus is emerging that males are predicted to decrease parental effort with decreasing paternity if an individual male can expect higher paternity in future reproductive bouts [11–13]. This prediction is, however, based on the assumption that a tradeoff exists between current and future paternal effort and that males have information about their current paternity. By reducing investment in the current offspring, a male is assumed to invest more in future reproduction when the offspring are more likely to be his own. Between species, a positive relationship between average paternity and paternal investment is generally predicted, even in the absence of paternity cues [11–14]. Within species, males can only adjust their parental investment in response to paternity if paternity cues exist [6]. These cues can be direct indicators of relatedness (e.g. kin recognition) or indirect, in that they indicate sperm competition and multiple mating by females (e.g. the presence of other males) [15].

Surveying the empirical literature, however, yields no such consensus [6,16]. A literature search for the keywords 'paternity' and 'care' in the Web of Science found 62 papers (representing 46 different species) that examined variation in cues of paternity or genetic paternity and measures of paternal care for a single reproductive bout within a species. Male care decreased with decreased paternity in less than half of the studies (30 total, representing birds 17/36, fish 6/12, insects 1/2 and mammals 6/12), whereas the other studies found no significant effect of paternity on male behaviour. Such equivocal empirical patterns have lead to arguments in the literature about whether empirical studies can even test this theory because, when no response to paternity is found, it is difficult to determine whether reliable cues of paternity exist or if individual variation in male condition masks an underlying relationship between paternity and paternal investment [6,16]. Such caveats always offer a possible *post hoc* explanation for the lack of fit between theory and data. Thus, there is still no satisfying general explanation for observed variation (Table 1). This arises both because it is difficult to test

Table 1. Examples of the empirical relationships between paternity and paternal care[a]

Species	Pattern	Evidence for paternity affecting paternal care	Refs
Insects			
Burying beetle *Nicrophorus vespilloides*	0	Dominant males had higher paternity and provided care; no evidence that dominant males reduced care when their paternity was lower	[69]
Dung beetle *Onthophagus Taurus*	+	Dominant males decreased care when more sneaker males were present and when paternity was lower	[70]
Golden egg bug *Phyllomorpha laciniata*	0	Whether males carry offspring was independent of paternity	[71]
Fish			
Bluegill sunfish *Lepomis macrochirus*	+	Males decreased paternal care when sneaker males had been present at the nest	[72]
Pumpkinseed sunfish *Lepomis gibbosus*	+	Parental male paternity was positively correlated with the defence of eggs, but was not associated with egg fanning or the defence of hatched young	[73]
Fifteen-spined stickleback *Spinachia spinachia*	0	Males did not adjust their parental care behaviour in response to reduced paternity from sneaker males	[74]
Sand goby *Pomatoschistus minutes*	0	Paternity did not affect filial cannibalism by parental males	[75]
Ocellated wrasse *Symphodus ocellatus*	−	Certainty of paternity (e.g. lower sperm competition from sneaker males) was negatively correlated with the probability of paternal care	[35,36]
Birds			
Reed bunting *Embiriza schoeniclus*	+	One population exhibited a positive relationship whereas another had no relationship between paternity and male care	[76]
Collared flycatcher *Ficedula albicollis*	+	Males decreased paternal care when paternity was reduced	[31]
Red-winged blackbird *Agelaius phoeniceus*	+	No effect of paternity on paternal care found, although male nest defence decreased in one study as extra-pair young in the nest increased	[77]
Common yellowthroat *Geothlypis trichas*	0	Within-male comparisons found no effect of current paternity on paternal rates of feeding offspring	[78]
Western bluebird *Sialia mexicana*	0	Experimental manipulation of paternity had no effect on male provisioning of young	[79]
Pied flycatcher *Ficedula hypoleuca*	+	Paternity was positively associated with male provisioning rate	[80]
Mammals			
Barbary macaque *Macaca sylvanus*	0	Paternity had no effect on male care	[81]
Savannah baboon *Papio cynocephalus*	+	Males supported their own young more in social interactions (probably as a result of direct kin recognition)	[82]
Alpine marmot *Marmota marmota*	0	No evidence for paternity affecting care	[83]
Meerkat *Suricata suricatta*	0	Males cared for young within their social group but achieved extra paternity mainly outside the group	[84]
Human *Homo sapiens*	+	Males decreased investment in offspring with lower certainty of paternity	[85]

[a]+ (if paternity or paternity cues were positively correlated with any measure of male care); 0 (if no correlations were found); and − (if a negative relationship was found). Studies listed are representative of the existing variation in observed patterns rather than exhaustive. For information on female mating behaviour in these species, see Table 2.

the existing theory and because theory relating paternity and paternal care has ignored the effect social and coevolutionary feedbacks with female mate choice and reproductive investment on the evolution and expression of male behaviour. What remains clear is that, despite a rich body of theory and extensive empirical information, observed patterns cannot be reliably predicted even for species where the mating system and importance of parental care are well known.

Female choice for indicators of paternal investment

Interactions between mating and paternal investment have also been studied from the perspective of the female. Theory predicts that females will choose among males based on traits of the male or his territory that indicate the fitness effects of mating with that male [7] (Figure 2). These fitness effects can be divided into direct (i.e. non-genetic) and indirect (i.e. genetic). In the case of paternal effort, females are predicted to choose among males based on traits that indicate the expected quality of male care [8] (Figure 2). In some species, females choose among males based on characteristics of the breeding site directly associated with increased offspring fitness. For example, females might choose sites with low predation risk or abundant food [7]. The evolutionary dynamics of such interactions are relatively intuitive [7]. Females might also prefer
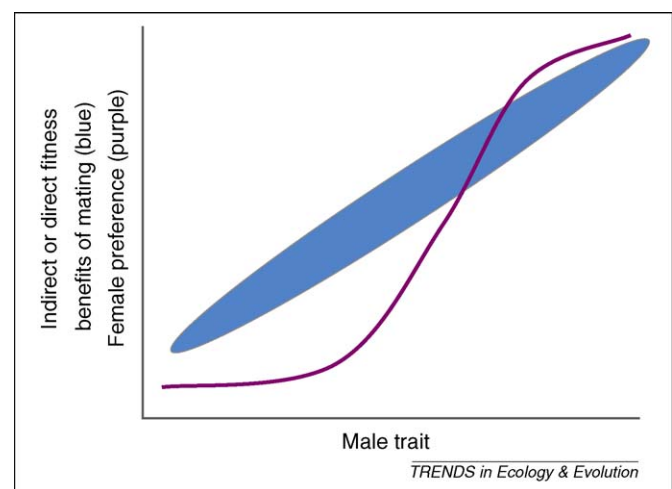
Figure 2. The evolution of female preferences for indicator traits in males. Theory examining the evolution of adaptive female choice typically considers the situation where an underlying positive relationship (blue) exists between a trait observed in males and the expected direct or indirect fitness benefits to the female. When this relationship exists, the trait is argued to indicate to the female her expected fitness benefits and a female preference for that trait (purple) is favoured by selection on females. In the case of female choice for the direct benefits of paternal care, the indicator trait is argued to predict male parental care behaviour *a priori* because mating typically precedes male care. Even when the indicator trait of the male is naturally associated with his ability to provide high-quality care (e.g. body size, age or condition), it might not necessarily reliably predict male behaviour if males decrease their paternal investment in response to certainty of paternity and additional mating opportunities.

physical and behavioural traits of the male that are functionally related to the quality of parental care (e.g. large body size or nest tending) [7]. In sand gobies (*Pomatoschistus minutus*), for example, females prefer males that fan eggs at a high rate [17]. Preferred traits are also sometimes only indirectly associated with paternal care. For example, in sedge warblers (*Acrocephalus schoenobaenus*), females prefer males that have a larger song repertoire, which is correlated with the nest visitation rate of the male while feeding chicks [18]. It is unclear why male song and chick feeding are associated, although song repertoire size is associated with male condition and brain size in some species [19]. Although the traits preferred by females vary, they are generally argued to indicate (e.g. predict on average) the future behaviour of the male.

If traits exist that reliably predict male paternal care, a female preference for those traits is predicted to evolve [8] (Figure 2). Again one must ask whether empirical studies find this expected pattern. Although examples certainly

exist (e.g. sedge warblers), females in many species do not exhibit preferences for male traits associated with paternal care, and some even prefer traits negatively correlated with care (Table 2). A survey of the 206 papers identified by a Web of Science search under 'female choice' and 'care' yielded 27 species with data available on both female choice for male traits and the relationship between male paternal care or offspring survival and the preferred traits. Fourteen species exhibited female choice for a male trait associated with paternal care or offspring survival, while the 13 other species exhibited either no evidence of female choice for male indicator traits (7/13) or a negative relationship between traits preferred by females and paternal care (6/13). While females might choose males for genetic rather than direct benefits, the rarity of evidence for indirect benefits (reviewed in [7,20,21]) makes this an unlikely general explanation for such mixed results. Another possibility is that male parental care is often unpredictable. For example, recent research on sand gobies has

Table 2. Examples of patterns of female choice in species with male parental care[a]

Species name	Pattern	Evidence of female choice for indicator traits of male care	Refs
Insects			
Burying beetle *Nicrophorus vespilloides*	0	Females did not appear to prefer males with carcasses (reproductive resources) or that provided care	[86]
Dung beetle *Onthophagus Taurus*	0	No evidence for female choice among males, based on indicators of paternal care despite post-copulatory sexual selection by females	[87]
Golden egg bug *Phyllomorpha laciniata*	0	Female mate choice was independent of egg carrying	[88]
Fish			
Bluegill sunfish *Lepomis macrochirus*	0	No evidence for female choice among males based on paternal care	N/A
Pumpkinseed sunfish *Lepomis gibbosus*	0	No evidence for female choice among males based on paternal care	N/A
Fifteen-spined stickleback *Spinachia spinachia*	+	Females preferred males that fanned their nest at higher rates and that produced better nests, reflecting male condition	[89,90]
Sand goby *Pomatoschistus minutes*	+	Females preferred males that were better fathers and that constructed better nests	[75,91]
Ocellated wrasse *Symphodus ocellatus*	0	Females preferred successful males and avoided spawning with sneakers but did not prefer males based on male traits	[35,36]
Birds			
Reed bunting *Embiriza schoeniclus*	0	No evidence that females chose social mates based on indicator traits of parental care; no evidence that females benefit from extra-pair mating	[92]
Collared flycatcher *Ficedula albicollis*	−	Females exhibited context-dependent preferences for males with large forehead patches, a condition-dependent trait associated with higher male condition and lower care	[32]
Red-winged blackbird *Agelaius phoeniceus*	0	No evidence for female choice of male indicator traits of paternal care, although male care and defence was related to the mating rate for within-pair and extra-pair males	[93]
Common yellowthroat *Geothlypis trichas*	−	Males with larger ornaments were preferred as both social and extra-pair mates despite the fact that they provided less paternal care	[94]
Western bluebird *Sialia mexicana*	0	No evidence for female choice of male indicator traits of paternal care	N/A
Pied flycatcher *Ficedula hypoleuca*	0	Females preferred colourful males that produced a complex song, which was associated with territory quality but not with paternal care	[95]
Mammals			
Barbary macaque *Macaca sylvanus*	0	Dominant males had a mating and paternity advantage, but females were not more likely to mate with males that had provided care before and male care was not associated with mating and paternity	[96]
Savannah baboons *Papio cynocephalus*	0	Dominant males had greater mating and paternity success, whereas males unrelated to offspring also assisted in care and defence	[97]
Alpine marmot *Marmota marmota*	0	No evidence for mate choice among males for paternal care although females chose to breed in natal groups with related male helpers and preferred genetically different males for extra-pair mating	[98]
Meerkat *Suricata suricatta*	0	Dominant males have a paternity advantage, but there was no evidence for female choice for paternal males	[99]
Human *Homo sapiens*	0	No direct evidence for female choice of male indicator traits of paternal care, although evidence is available for female choice for wealth or status in human males	[100]

[a]The species represented are the same as in Table 1 and all exhibit male care that is important to female fitness. Studies are categorised as supporting (+); negating (−); or finding no direct evidence (0) of female choice for traits of the male associated with paternal care. These examples (and the references within) are illustrative rather than exhaustive.

shown that males increase their fanning rate in the presence of a new female [17]. Although fanning in the presence of a female might still indicate the quality of paternal care, these results demonstrate that even current parental care behaviours do not have to be reliable indicators of future care. For both sexes, the future behaviour of their mate might be unpredictable. Predicting the evolution of mate choice and indicator traits will hence often require incorporating behavioural plasticity in response to social interactions within and between the sexes, while also considering how these traits coevolve with other traits affecting fertilisation and parental investment in both sexes.

Paternal investment and the cost of promiscuity

Research on sexual conflict over mating has begun to explore how parental investment affects selection on mating behaviour [22]. Based on the assumption that multiple mating causes reduced paternal investment, researchers have argued that it is surprising that females mate with multiple males in most species, including many with male care (e.g. all species in Tables 1 and 2). Four main explanations have been given for this pattern [22]: first, females could remate to increase indirect benefits despite a loss of paternal care [23]. Second, male care might not have a large effect on female fitness [24]. Third, multiple mating by females can be driven by sexual conflict over mating rather than by female choice [3,25]. Fourth, female multiple mating might confuse paternity, thereby reducing the risk of infanticide or leading to care from multiple males [26]. The survey above suggests the additional explanation that males do not necessarily decrease parental effort in response to multiple mating by females.

Recent meta-analyses of data from socially monogamous birds (such as song sparrows, *Melospiza melodia*) estimated selection on females as a result of extra-pair young and found that indirect selection (i.e. owing to genetic benefits through extra-pair young) did not balance direct selection against extra-pair mating resulting from reduced male care [27,28]. The authors argued that the observed extra-pair paternity is best explained by conflict between the sexes over mating (which males are 'winning'). Selection on females for fertility assurance could, however, also favour extra-pair paternity in these species [29]. In contrast another study found that polygynous avian species (such as dunnocks, *Prunella modularis*) exhibit lower multiple paternity than do monogamous species, and argued that this is consistent with female choice driving the patterns of paternity among species of birds [30] (for further taxonomic variation, see Box 1).

Thus, there is no clear support for any single hypothesis to explain multiple mating by females. In reality, the evolution and expression of female promiscuity will depend on all of these factors in combination. In addition, the proximate factors influencing mating and fertilisation, and how these mechanisms evolve, needs to be understood more fully to distinguish between male effects and female effects on fertilisation and fecundity and the degree to which each sex determines the outcome of a mating interaction. Therefore, reliably predicting female mating patterns will require considering the coevolutionary and social feedbacks between male and female mate choice, fertility and parental investment.

Recent research hints at social and coevolutionary feedbacks

Although there is extensive theoretical and empirical information on male and female parental investment and mating behaviour, the discussion above illustrates that there are as many unexpected patterns as support for general predictions. Observed patterns of mating and parental investment are typically explained after the fact, which does not lead to rigorous tests of theory or the development of a general predictive framework (Box 2). I argue that much of the disagreement between expected and observed patterns arises because the social and coevolutionary feedbacks between mating, fertilisation and parental investment have not been addressed. Here, I highlight three species that demonstrate the importance of addressing how male and female mating behaviours and

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Box 1. Additional unexplained diversity yielded by comparative studies

Synthesis within and between taxonomic groups highlights the diversity of interactions that exist between mating and parental care. In birds, paternity tends to be positively correlated with paternal care, and extra-pair paternity is higher when the indirect genetic benefits of multiple mating are high or the costs of losing male care are low for females [24,27,28,30]. In birds, variation in extra-pair paternity exists that can only be explained by considering interactions within and between the sexes in the context of the ecological and social environment [25].

In mammals, female multiple mating might have evolved to reduce infanticide [26] (but see [46]) and in response to group living [47,48]. Male care is typically associated with either monogamous or cooperative breeding in mammals, although these mating systems are not associated with higher certainty of paternity [10,47]. Unlike in birds, paternal care is not typically explained by paternity or female mating behaviour [10,26,47].

Comparative studies of parental care evolution in fish have shown that male territoriality and the evolution of paternal care are often associated [49]. A recent comparative study of cichlids, however, found increased sexual selection on males preceded the evolutionary loss of male care from a state of biparental care [50]. Yet, male-only care is common in other fishes and is often associated with female choice among males.

Although true paternal care is rare in insects, males often exhibit paternal investment in the form of nuptial gifts and spermatophores [51]. In the few insects with exclusive male care, females prefer males that provide care [52]. In insects, unlike in birds and cichlids, sexual selection (resulting from female choice) favours paternal investment.

Parental care is also rare in reptiles. However, males of some species allow only their genetic offspring within their home ranges, which could represent a direct cost of promiscuity for females [53]. Yet, multiple paternity is common in reptiles and is probably the outcome of both mate encounter rates and conflict between the sexes with respect to mating [54].

This brief overview demonstrates that mammals, reptiles, insects, fish and even birds all exhibit complex interactions between mating behaviour and paternal investment not captured by existing theory. These comparative studies also highlight that one cannot expect interactions between mating and parental investment to be explained fully by simple correlations. Instead, coevolutionary and social feedbacks between mating and parental investment patterns exist across taxonomic groups [10,25,53,54].

Box 2. A social and coevolutionary dynamics modelling approach

Surprisingly little theory has examined the coevolution of male and female traits (for exceptions see [5,13,55–58]), and no theory has considered the evolution of mating behaviour and parental investment in both sexes simultaneously. Interactions between the sexes are typically modelled using quantitative genetics or game theory.

Quantitative genetic models examine social interactions by allowing the phenotype of one individual z_i to be influenced by the phenotype of others z'_j [58,59] (Figure I). Using the multivariate breeders equation (Eqn I), the expected change (Δz_i) in traits is predicted from selection on each trait (β_i), heritability (G_{ii}) and the between-trait genetic correlations (G_{ij} for traits i and j) such that for two traits

$$\begin{bmatrix} \Delta z_1 \\ \Delta z_2 \end{bmatrix} = \begin{bmatrix} G_{11} & G_{21} \\ G_{12} & G_{22} \end{bmatrix} \begin{bmatrix} \beta_1 \\ \beta_2 \end{bmatrix} \qquad \text{[Eqn 1]}$$

Recently extended to examine sexual conflict [58], these methods offer a way to model the coevolutionary dynamics of male and female traits. β_i is usually, however, a relatively simple function. For example, in a recent model of sexual conflict over mating [58], fitness was a fixed function of mating rate, such that it could examine the consequence of sexual conflict rather than asking whether the interaction leads to conflict (or cooperation, Figure II).
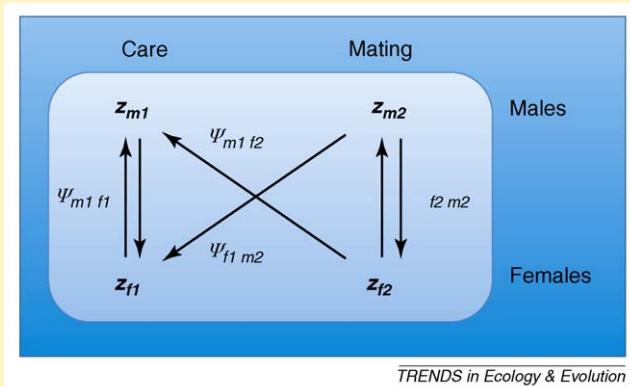
The essence of game theory is the realisation that the fitness of a trait depends on interactions with other individuals [e.g. $W(z,z')$]. Recent game theoretical models have examined the coevolution of male and female parental investment [5,11,13,60], but without allowing mating behaviour to coevolve. Although game theory allows fitness to arise from social interactions, it does not explicitly address the genetic basis of traits, which are often necessary to capture sexual selection, especially the genetic benefits of mating [61].

To include social interactions, coevolutionary feedbacks and sexual selection within one framework, I propose an approach that combines quantitative genetics and game theory.

Expected fitness $W(z, z')$ for males and females can be derived as a function of individual phenotype z and the phenotype of other individuals in the population z' using game theory. Fitness functions determine selection on both sexes [where $\beta_i = (\delta W / \delta z_i)/\overline{W}$], which within a quantitative genetic framework (or more generally using the Price Equation [62]) predicts coevolutionary social dynamics. Although the proposed method makes simplifying assumptions, this blend of game theory and quantitative genetics enables models to examine the social and coevolutionary dynamics of male and female mating and parental investment.
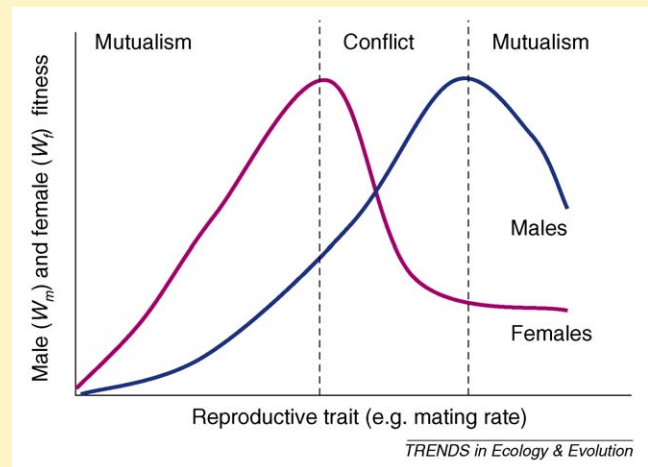

Figure I. Interactions within and between the sexes affect trait expression. Here, I illustrate the potential interactions between two male (z_{m1} and z_{m2}) and female (z_{f1} and z_{f2}) traits that affect mating and parental care, respectively. For simplicity, all possible interactions are not shown. The expression of any individual trait, z_i, will depend on the traits of other individuals in the population. For example, let z_i represent a reproductive trait in individual i who is interacting with another individual j with phenotype z'_j (where the prime represents the fact that the environment and trait of individual j can differ from z_i). Using the quantitative genetics 'interacting phenotypes' approach [58,59], the trait of individual i will depend on the additive genetic basis of the trait (a_i), the non-social environment in which it is expressed (e_i) and the influence (ψ_{ij}) of a trait z'_j in individual j on the focal individual i. These multiple effects can be represented as $z_i = a_i + e_i + \psi_{ij}(z'_j)$ where $z'_j = a'_j + e'_j + \psi_{jk}(z''_k)$. This general effect of social interactions can be extended to examine social interactions within and between the sexes where trait expression can depend on a variety of interactions between the sexes as shown here [58].

Figure II. Sexual conflict and mutualism can arise with respect to mating. In the example shown here, the fitness of an individual female W_f is maximised at a lower mating rate than is the fitness of an individual male W_m. Whereas total male and female reproductive success at the population level and mating rate will be constrained by self-consistency, differences between the sexes as a result of individual fitness can lead to sexually antagonistic selection on any particular reproductive trait. Therefore, anywhere between the optimal female mating rate and male mating rate, conflict between the sexes will exist with respect to mating because differences in the direction of selection on mating rate exist between the sexes (e.g. $\beta_f < 0$ and $\beta_m > 0$, where $\beta_f = (\delta W_f/\delta z_f)/\overline{W}$ and $\beta_m = (\delta W_m/\delta z_m)/\overline{W}$). For mating rates below the optimal for females, both sexes will experience selection for increased mating rate ($\beta_f > 0$ and $\beta_m > 0$, and thus experience a mutual fitness benefit of increased mating rate and cooperation with respect to mating); above the male optimum, both sexes will experience selection for decreased mating rates ($\beta_f < 0$ and $\beta_m < 0$, and thus experience a mutual fitness benefit of decreased mating). Yet, the effect of mating rate on fitness is not fixed (as shown here) but instead arises out of social interactions and coevolutionary dynamics within and between the sexes. This implies that male and female fitness functions shift as traits change in expression as a result of social interactions and coevolve over time in both sexes. As a result, regions of conflict and cooperation will change or even appear and disappear as a result of these social interactions and coevolutionary dynamics.

parental investment are the outcome of social interactions and coevolution.

Mutual mate choice in the collared flycatcher

The collared flycatcher (*Ficedula albicollis*) was one of the first species in which experiments demonstrated the expected reduction in male care with decreased paternity [31]. Yet, it remains unclear what drives observed variation in extra-pair paternity. Although females are known to choose among males based on male secondary sexual traits (e.g. forehead patch size), mate choice and its fitness effects are context dependent [32]. Recent studies have

found that extra-pair paternity is explained by female size, but not by the traits of her social mate or genetic benefit to her offspring [33]. Females do, however, exhibit sexually selected traits (e.g. egg colour [34]). Understanding patterns of extra-pair paternity in this species will require consideration of the social dynamics of mutual mate choice for both social and extra-pair mates, and the effect of these mating opportunities on the parental investment of both sexes. An interesting experiment would be to examine how females that vary in size and sexually selected traits respond to opportunities for extra-pair mating, and how this affects male and female parental investment, future mate choice and fitness.

Mate choice and paternal care in the ocellated wrasse

In the ocellated wrasse (*Symphodus ocellatus*) large, colourful nesting males defend territories, court females and provide parental care. Yet, there is no evidence that females choose among these males based on behavioural or physical traits. Instead, females prefer to spawn where other females have spawned, and these nesting males provide parental care despite high sperm competition from sneaker males [35,36]. Although these patterns are not predicted by current theory, they can be explained by considering how behavioural interactions within and between the sexes affect mating success and paternal care. In this species, the best indicator trait of male parental care is the mating behaviour of other females because successful males are more likely to provide parental care [36]. This explains female choice for successful nesting males. Sneaker males are attracted to successful nests for the mating opportunities. Consequently, a few nesting males have high mating success, high sperm competition and low paternity, and these males are preferred by females and sneakers and provide parental care [35,36]. To understand the evolutionary persistence of exclusive paternal care and the absence of females' choice for male traits in this species requires considering not only the coevolutionary dynamics of mating and care, but also the social feedbacks that exist in this species between females, nesting males and sneaker males [4,36].

The coevolution of parental care and mating in a burying beetle

In a species of burying beetle (*Nicrophorus vespoilloides*) small mammal carcasses are important for provisioning young and attracting mates [37]. Dominant males often provide parental care, whereas satellite males do not, despite having sired offspring [37,38]. Recent research estimated the genetic basis of, and selection on, male and female parental care behaviour and found that observed sex differences in parental care behaviours can be explained by differences between the sexes in selection on direct (feeding) versus indirect (carcass tending) parental care, and the existence of negative genetic correlations between these behaviours [38]. Selection on direct care by females appears, through correlated evolution, to favour indirect care by males. A separate study found evidence for the correlated evolution of male and female mating behaviour as a result of strong selection on males to increase paternity through repeated mating and little

selection against mating in females [39]. Together, this research suggests the potential for the coevolution of mating behaviour and parental care in both sexes. However, these studies did not consider the effect of social dynamics on patterns of parental care, which probably also influences interactions between mating and care in this species. Experimental evolution could test specifically whether selection on one trait (e.g. female remating) drives predictable changes in the social and coevolutionary dynamics of male and female mating behaviour and parental care.

Future directions: where do we go from here?

Given how much there is to learn about traits in isolation, one might argue that things are made unnecessarily complex by considering the coevolution of multiple male and female traits. Yet, our current understanding of mating systems is based predominantly on *post hoc* explanations of individual patterns, despite the existence of thousands of papers on reproductive traits that examine pairs of traits or single interactions in isolation. I argue that new theory examining the coevolutionary and social feedbacks of multiple male and female reproductive traits simultaneously is needed to increase our ability to make *a priori* predictions that can capture the diversity of empirical patterns (Box 2). Moving from *post hoc* explanations to *a priori* tests of theory will also require empirical approaches that can directly examine the effect of social and coevolutionary feedbacks on patterns of mating and parental care.

I suggest three empirical approaches to examine feedbacks between mating and parental investment. First, further comparative phylogenetic analyses are needed that examine the correlated evolution of multiple male and female reproductive traits [40]. While phylogenetic methods always leave open questions, as they are by their nature correlative, a powerful approach would be to combine information on correlated evolution with detailed data on current selection and social interactions within species.

Second, experiments within species are needed that explore specifically how changes in the expression of a trait in one sex affect the expression (owing to social interactions) and fitness of multiple traits in both sexes. One promising way to examine the effect of social interactions on coevolutionary dynamics would be to use the ever-increasing understanding of the proximate mechanisms underlying behaviour [41–43] to conduct phenotypic manipulations of social behaviour. I suggest that this would enable researchers to examine how induced changes in the behaviour of one individual affect the expression of and selection on male and female reproductive traits. For example, one could manipulate female choosiness at a proximate level and then examine the cascade of consequences for social interactions, mating and parental care and selection on all of these traits.

Finally, coevolutionary dynamics should be examined directly in species where quantitative genetic studies or experimental evolution are possible. The research described above on the burying beetles illustrates that examining both the genetic basis of traits and selection on male and female reproductive traits has the potential to examine directly how male and female traits such as

mating and care coevolve. Research should also examine coevolutionary dynamics in the wild. For species where long-term pedigree and phenotypic data are available, the 'animal model' approach can been used to estimate the genetic basis of traits and selection on individual traits [44,45]. If combined with data on multiple reproductive traits and the effect of social interactions on behaviour and fitness, this approach has the potential to examine social feedbacks and coevolutionary dynamics directly.

Conclusions: moving from *post hoc* to *a priori* understanding

Mating behaviour and parental investment in both sexes will affect and be affected by social interactions and coevolutionary dynamics within and between the sexes. Ignoring these feedbacks limits our ability to explain and predict observed patterns. To move forward, there must first be a stronger connection between empirical and theoretical research. At present, many empirical studies test only the most general theoretical predictions (e.g. whether paternity and parental care are correlated). Theoretical papers also frequently fail to make concrete predictions testable in wild populations. Without a better integration between theory and data, *post hoc* explanations of individual patterns will predominate. In addition, greater synthesis is needed across topics now studied in isolation. For example, I argue that bringing ideas from cooperative breeding and sexual conflict together would help researchers to understand patterns of mating and care in general [22,26,63–68,74]. While we tend to think of cooperative breeding and sexual conflict as separate topics, both examine the direct and indirect fitness benefits of mating and providing care for offspring [26,56,58]. Understanding the factors that favour caring for unrelated offspring will increase our general understanding of the benefits of parental care. In species with cooperative breeding, females are argued to be freed from the costs of promiscuity. However, paternity confusion and multiple male paternity might also be favoured if this increases parental care. An integration of ideas from cooperative breeding, social evolution and sexual selection would yield new insights into each of these fields in exciting and likely unexpected ways. While the equivocal empirical patterns reported here illustrate a failure of our current understanding, they also promising possibilities for future research if one is willing to embrace the complexity these patterns represent.

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