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The evolution of strategic male mating effort in an information transfer framework

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Abstract

Sperm competition theory predicts that males should use cues indicating the risk and intensity of sperm competition to tailor their sperm investment accordingly. Rival males are an important source of social information regarding sperm competition risk. However, revealing such information may not be in the rival males' interest. Here, we use a theoretical approach based on informed and uninformed games to investigate when information transfer about sperm competition risk to competitors is beneficial for a male, and when it is not. The results show that signalling to potential future mates that a female has already mated is beneficial when the signalling male has a sperm competition disadvantage, whereas it is unfavourable when the signaller has an advantage. The reason for this counterintuitive result is that the rival males' optimal response is to reduce sperm investment when the signaller has a disadvantage and, conversely, to increase investment when the signaller has an advantage. Furthermore, we analysed scenarios where males use alternative reproductive tactics. In this situation, signalling the awareness of sperm competition risk rarely pays; instead, it is beneficial to maintain an information advantage. Thus, it may be beneficial for bourgeois males to accept cuckoldry instead of revealing their sperm competition awareness to reproductive parasites. These results provide new insight into the evolution of communication between rivals in the context of sperm competition.

Introduction

Information is a crucial component of any decision-making process (Stephens, 1989; Maynard Smith, 1999; Danchin *et al.*, 2004; Lachmann & Bergstrom, 2004; Dall *et al.*, 2005; Fawcett *et al.*, 2014). Reliable information about the environment is a prerequisite for making accurate decisions regarding a multitude of tasks such as where to breed or forage (Stephens & Krebs, 1987; Real, 1992; Grocott, 2003; McLinn & Stephens, 2010), or with whom and how to socially interact (Enquist & Leimar, 1983; Luttbeg, 1996; Mazalov *et al.*, 1996; Stevens *et al.*, 2005). In social contexts, information transfer is a complex process, as the optimal information content not only depends on the sensitivity of the receiver, but also on the benefit of the sender to provide such information (McNamara *et al.*, 1999; Lachmann & Bergstrom, 2004; Dall *et al.*, 2005). In cooperative dilemmas or conflict situations, the pay-off resulting from decisions based on available information depends on that information and on the decisions of others (McNamara & Houston, 2002; Pen & Taylor, 2005; McNamara *et al.*, 2006; McNamara & Weissing, 2010). Thus, social signal evolution depends both on the transmitter's cost-benefit ratio of providing information and on the responder's cost-benefit ratio of receiving and making use of such information.

Strategic sperm allocation is a research field in which the effect of social information about relevant parameters has been extensively studied, both by theoretical models (reviewed in Parker, 1998; Parker & Pizzari, 2010) and controlled experiments (reviewed in Wedell *et al.*, 2002; Kelly & Jennions, 2011). This research has shown, for instance, that a male should increase his current ejaculate investment if he has information about the sperm competition risk arising from rivals

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that have mated already with the same female (Parker, 1990a; Parker *et al.*, 1997), a prediction that has been confirmed experimentally in studies of a wide range of species (e.g. Gage, 1991; Nicholls *et al.*, 2001; Olsson, 2001; Evans *et al.*, 2003; Pizzari *et al.*, 2003; Zbinden *et al.*, 2003; delBarco-Trillo & Ferkin, 2004; Smith *et al.*, 2009; Kelly & Jennions, 2011). Consequently, in species where males apply alternative mating tactics, parasitic males (sneakers) usually invest relatively more than bourgeois (territorial or dominant) males in matings (Simmons *et al.*, 1999, 2007; Tomkins & Simmons, 2002; Neff *et al.*, 2003; Schütz *et al.*, 2010), as sneakers are fully informed that their sperm competes with that of others, whereas bourgeois males often have partial information only (Parker, 1990b).

If fertilization is internal, female mating status is an additional cue informing males about the risk of sperm competition, as mating with already mated females always results in sperm competition whereas mating with virgin females will do so with lower probability. Intuitively, one might think that if males mate with already mated females, they should invest more in their current ejaculate compared to matings with virgin females (see Cook & Gage, 1995; Wedell, 1998; Martin & Hosken, 2002; Friberg, 2006). However, this is frequently not the case (Linley & Hinds, 1975; Lorch *et al.*, 1993; Parker *et al.*, 1993; Baur *et al.*, 1998; Siva-Jothy & Stutt, 2003; Singh & Singh, 2004; Engqvist, 2007), which has been revealed also by meta-analyses and literature reviews (e.g. Wedell *et al.*, 2002; Kelly & Jennions, 2011). One proposed reason for this is that females that have already mated once are more likely to mate more often, and therefore, sperm competition risk and intensity are correlated (Engqvist & Reinhold, 2006). Therefore, males mating with them may benefit by *reducing* sperm investment (Parker *et al.*, 1996) to keep sperm resources for future matings. Alternatively, females subject to sperm (or seminal fluid) limitation might select for enhanced male ejaculate investment to virgin females in order to increase fertilization probability and consequently offspring number also for males (Ball & Parker, 2007).

An important assumption of previous models of optimal male sperm allocation is that males have information about female mating status and thus the likelihood of sperm competition. However, this is not necessarily the case (Parker *et al.*, 1997). A major reason why males do not respond to female mating status may be that they lack information about it, as it may not always be either in the female's or in a previous male's interest to reveal this information to future rival males. To understand strategic ejaculate expenditure in response to sperm competition cues, we must therefore ask: When is information transfer about sperm competition risk in a male's interest?

To study this question, it is important to consider the essential differences between informed and uniformed games (McNamara & Houston, 2002; McNamara *et al.*, 2006; McNamara, 2013). In an uninformed (also referred to as 'sealed bid' or 'simultaneous') game, the two players have no information regarding the decision of the other player at the time they make their own choice. This is the standard situation in evolutionary game theory (Maynard Smith, 1982; Dugatkin & Reeve, 1998; McNamara & Weissing, 2010). In an informed (also referred to as 'Stackelberg' or 'sequential') game, on the other hand, one player is informed about the other player's decision. For the two cases, the evolutionarily stable (ES) set of decisions will differ, and so will the pay-off to the two players (McNamara *et al.*, 2006). These alternative possibilities raise two interesting questions. First, if the pay-off for the player deciding about sperm allocation first is higher in an informed than in an uninformed game, it is beneficial to inform the second player of his decision and, otherwise, it is better to hide it. Thus, this pay-off comparison of the first player reveals whether providing information is beneficial or not. Second, we need to consider whether the pay-off of the second player is higher in an informed or an uninformed game. If the second player does worse in an informed game, this might imply that it should better ignore the information provided by the rival. However, this is not necessarily the case. If the first player's decision cannot be altered, it is indeed always beneficial to use the available information (McNamara & Dall, 2010). Nevertheless, if this information puts the second player at a disadvantage and if it can convincingly signal to the first player to be ignorant (e.g. by making a commitment to decide according to the uninformed ESS, see McNamara & Houston, 2002), the uninformed ESS is also the first player's best choice.

Here, we take a novel approach to study these alternative possibilities of information transfer in situations with sperm competition. Based on a modelling approach of McNamara *et al.* (2006), we ask two separate questions. First, when should a male inform rivals that they are likely to face sperm competition when mating with a female he has already mated with? Second, can this information put other males at a disadvantage compared to the uninformed situation; that is, is there scope for a 'commitment problem' (von Stackelberg, 1934; Schelling, 1960; Samuelson, 2001; McNamara & Houston, 2002)? We examine two distinct situations:

1. In the 'mating history' scenario, rival males differ in the order in which they mate with a female, and first males to mate may choose to inform potential future rivals that this particular female has already mated. Thus, we ask as follows: (i) Do males benefit by informing potential rivals about the mating status of this female, and (ii) does this information put the second male at an advantage or disadvantage compared to an uninformed situation?

2 In the ‘mating tactics’ scenario, males pursuing alternative mating tactics compete for fertilizations (see Oliveira *et al.*, 2008; Buzatto *et al.*, 2014). Typically, there is a ‘bourgeois’ tactic defending territories or nests in which females will reproduce, whereas males applying the ‘parasitic’ tactic sneak into bourgeois males’ territories to mate there with females (Taborsky, 1997, 1998). Parasitic males always experience sperm competition, whereas bourgeois males sometimes do and sometimes do not; they may only be partially informed of the current sperm competition risk, for instance by the frequency of sneaker males in the population (Parker, 1990b; Simmons *et al.*, 1999). Thus, we ask, analogously to the ‘mating history’ situation: (iii) Can it be beneficial (strictly from a sperm competition perspective) for parasitic males to inform parasitized bourgeois males about their sneaking attempt, and (iv) does this information put the bourgeois male at an advantage or disadvantage compared to the uninformed situation? Furthermore, if the bourgeois male is aware of a parasite’s sneaking attempt, (v) is it beneficial to inform the sneaker male about this awareness, and (vi) does this information put the sneaker male at an advantage or disadvantage compared to the uninformed situation?

Materials and methods

Basic model assumption

Throughout, we follow the assumptions from the ‘standard’ sperm competition models (Parker, 1998), in which fertilization success per total unit energy invested in a mating is maximized. For a male i competing with a male j, this amounts to

$$w\langle s_i, s_j\rangle = \frac{s_i}{s_i + rs_j} \cdot \frac{1}{c + s_i}. \qquad (1)$$

In this expression, w (henceforth fitness) is thus the sperm competition success (first term) per energy invested in that mating (second term), s denotes the ejaculate investment of each male, r is male j's sperm competition advantage in relation to male i (i.e. the loading factor, cf. Parker, 1990a); finally, c is the remaining nonejaculate costs of mating (i.e. the cost of achieving the mating), here expressed in the same units as the energy cost required for the production and transmission of a unit ejaculate.

Mating history scenario

We analyse a sperm competition risk game, where fertilization is internal and females mate with one or two males (see also Parker, 1990a; Parker *et al.*, 1997). Males thus either mate with a virgin or a once-mated female. This is a situation that has been analysed in great detail. Following Parker *et al.* (1997), we let q represent the probability that a female will remate. As there are twice as many matings with polyandrous females and female average mating frequency is $1 + q$, the probability that a male's ejaculate will face sperm competition (i.e. the probability that any given female will either remate in the future or has already mated in the past) is given by $p = 2q/(1 + q)$ (see also Parker *et al.*, 1997). In an uninformed game, male sperm allocation is equal regardless whether they are mating first or second, as males cannot distinguish their mating rank. The fitness function of a mutant strategy with ejaculate size s in a population of males with ejaculate size $\hat{s}$ is thus given by:

$$w(s,\hat{s}) = \left((1-p) + p\left(\frac{1}{2}\frac{s}{s+r\hat{s}} + \frac{1}{2}\frac{rs}{rs+\hat{s}}\right)\right)\frac{1}{c+s}. \qquad (2)$$

The first term $(1 - p)$ denotes the probability that there will be no sperm competition, and hence, the male will fertilize all of the female’s eggs. The second term stands for situations with sperm competition, and here, it is assumed that mating order is random so that the probability to mate first or second will both equal 0.5 for all males. Here (and throughout), we find the ES sperm allocation strategy s^* by setting

$$\left.\frac{\partial w(s,\hat{s})}{\partial s}\right|_{s=\hat{s}=s^*} = 0, \text{subject to } \left.\frac{\partial^2 w(s,\hat{s})}{\partial s^2}\right|_{s=\hat{s}=s^*} < 0.$$

In an informed game, the fitness pay-offs will be different depending on whether a male is mating with a virgin or an already mated female. In a situation where a male is mating first with a female that will eventually remate with a second male, the fitness equals

$$w_1\langle s_1|s_2^* = b\langle s_1\rangle\rangle = \left((1-q) + q\cdot\frac{s_1}{s_1 + rs_2^*}\right)\cdot\frac{1}{c+s_1}. \qquad (3)$$

Here, $s_2^* = b\langle s_1\rangle$ denotes the second male’s best response (cf. McNamara *et al.*, 2006) to the first male’s investment (which in the case of the uninformed game is the uninformed ESS s^*). Throughout, we use s_i to denote male i’s sperm investment and the vertical bar to indicate conditionality (i.e. ‘given that’). The expression above can thus be read: the fitness of a first male investing s_1 given that the second male’s investment is the optimal response to the first male’s investment. In a situation where the male is mating second, on the other hand, his fitness equals

$$w_2\langle s_2|s_1\rangle = \frac{rs_2}{rs_2 + s_1}\cdot\frac{1}{c+s_2}. \qquad (4)$$

By solving $\partial w_2/\partial s_2 = 0$, we can find a second male’s best response $(s_2^* = b\langle s_1\rangle\ )$ to s_1 (which in this case equals $\sqrt{cs_1/r}$). Inserting this in the expression for w_1 above, we can calculate a first male's optimal investment (s_1^*) by solving $\mathrm{d}w_1/\mathrm{d}s_1 = 0$. Hence, in this way we have derived the ES set of strategies $\{s_1^*, s_2^*\}$ for an informed game.

A male mating first would benefit from an informed game if

$$w_1\left\langle s_1^* \middle| s_2^* \right\rangle > w_1\langle s^*, s^* \rangle, \tag{5}$$

whereas the second male would benefit from an informed game if

$$w_2\left\langle s_2^* \middle| s_1^* \right\rangle > w_2\langle s^*, s^* \rangle. \tag{6}$$

Mating tactics scenario

Here, we model a sperm competition scenario, where the baseline assumption is that one of the males is always subject to sperm competition, whereas the other male faces sperm competition with a certain probability (Parker, 1990b). This applies to a parasitic male/bourgeois male situation; parasitic males always face sperm competition, whereas bourgeois males only sometimes do. It is irrelevant here whether these mating tactics are fixed or applied flexibly (cf., e.g. Taborsky *et al.*, 2008), such as mating with the social partner vs. extra-pair matings. It is also irrelevant whether fertilization is internal or external.

In the bourgeois-uninformed game, the fitness of a bourgeois male equals

$$w_{B^U}\left\langle s_{B^U} \middle| s_{P^U}^* \right\rangle = \left((1-p) + p \cdot \frac{s_{B^U}}{s_{B^U} + r s_{P^U}^*}\right) \cdot \frac{1}{c_B + s_{B^U}}, \tag{7}$$

and the fitness of a parasitic male equals

$$w_{P^U}\left\langle s_{P^U} \middle| s_{B^U}^* \right\rangle = \frac{r s_{P^U}}{r s_{P^U} + s_{B^U}^*} \cdot \frac{1}{c_P + s_{P^U}}. \tag{8}$$

Here, r denotes the sperm competition advantage (or disadvantage if $r < 1$) when mating in the parasitic role, generated, for example, by differences in mating sequence (Hendrickx *et al.*, 2015) or proximity to the site of fertilization (Taborsky, 1998; Stoltz & Neff, 2006). In the same expression, p is the probability of sperm competition, and c_B and c_p are the nonejaculate costs of bourgeois and parasitic matings, respectively (see also Parker, 1990b). We can find the ES set of ejaculation strategies $\left\{s_{B^U}^*, s_{P^U}^*\right\}$ by solving the equation system $\left\{\frac{\partial w_{B^U}}{\partial s_{B^U}} = 0, \frac{\partial w_{P^U}}{\partial s_{P^U}} = 0\right\}$.

If the bourgeois male is informed (and the parasitic male is aware of this circumstance), the fitness of a bourgeois male equals

$$w_{B^I}\left\langle s_{B^I} \middle| s_{P^I}^* = b\langle s_{B^I} \rangle \right\rangle = \frac{s_{B^I}}{s_{B^I} + r s_{P^I}^*} \cdot \frac{1}{c_B + s_{B^I}}, \tag{9}$$

and the fitness of a parasitic male equals

$$w_{P^I}\left\langle s_{P^I} \middle| s_{B^I} \right\rangle = \frac{r s_{P^I}}{r s_{P^I} + s_{B^I}} \cdot \frac{1}{c_P + s_{P^I}}. \tag{10}$$

Again, we find the ES set of ejaculation strategies $\left\{s_{B^I}^*, s_{P^I}^*\right\}$ by first solving the equation $\partial w_{P^I}/\partial s_{P^I} = 0$ to find $s_{P^I}^* = b\langle s_{B^I} \rangle (= \sqrt{s_{B^I} \cdot c_P/r})$. Inserting this in the expression for w_{B^I} and subsequently solving $\mathrm{d}w_{B^I}/\mathrm{d}s_{B^I} = 0$, we find the optimal investment ($s_{B^I}^*$) for a bourgeois male in an informed game. The bourgeois male would benefit from an informed game if

$$w_{B^I}\left\langle s_{B^I}^* \middle| s_{P^I}^* \right\rangle > w_{B^U}\left\langle s_{B^U}^* \middle| s_{P^U}^* \right\rangle, \tag{11}$$

whereas the parasitic male would benefit from an informed game if

$$w_{P^I}\left\langle s_{P^I}^* \middle| s_{B^I}^* \right\rangle > w_{P^U}\left\langle s_{P^U}^* \middle| s_{B^U}^* \right\rangle. \tag{12}$$

In this mating tactic game, we consider a further dimension of information transfer. If the bourgeois male has acquired information (intentionally or unintentionally) regarding the sneaking attempt, we analyse whether it is beneficial to inform the parasitic male of this awareness, and whether this information puts the parasitic male at a disadvantage. If the bourgeois male is informed (and the parasitic male is unaware of this circumstance), the fitness of a bourgeois male equals

$$w_{B^{IU}}\left\langle s_{B^{IU}} \middle| s_{P^U}^* \right\rangle = \frac{s_{B^{IU}}}{s_{B^{IU}} + r s_{P^U}^*} \cdot \frac{1}{c_B + s_{B^{IU}}}, \tag{13}$$

and the fitness of a parasitic male equals

$$w_{P^{IU}}\left\langle s_{P^U}^* \middle| s_{B^{IU}}^* = b\langle s_{P^U}^* \rangle \right\rangle = \frac{r s_{P^U}^*}{r s_{P^U}^* + s_{B^{IU}}^*} \cdot \frac{1}{c_P + s_{P^U}^*}. \tag{14}$$

We find the bourgeois ES strategies $\left(s_{B^{IU}}^*\right)$ by solving the equation $\mathrm{d}w_{B^{IU}}/\mathrm{d}s_{B^{IU}} = 0$. The bourgeois male would benefit from informing the sneaker if

$$w_{B^I}\left\langle s_{B^I}^* \middle| s_{P^I}^* \right\rangle > w_{B^{IU}}\left\langle s_{B^{IU}} \middle| s_{P^U}^* \right\rangle \tag{15}$$

whereas the parasitic male would benefit from being uninformed if

$$w_{P^{IU}}\left\langle s_{P^U}^* \middle| s_{B^{IU}}^* \right\rangle > w_{P^I}\left\langle s_{P^I}^* \middle| s_{B^I}^* \right\rangle \tag{16}$$

Note, however, that as $s_{P^U}^*$ is not the parasitic male's best response to $s_{B^{IU}}^*$, inequality 16 is unlikely to ever hold. We nevertheless analysed this situation for the sake of completeness.

Results

Although closed-form solutions are available, they are unwieldy and not very informative. Throughout, we

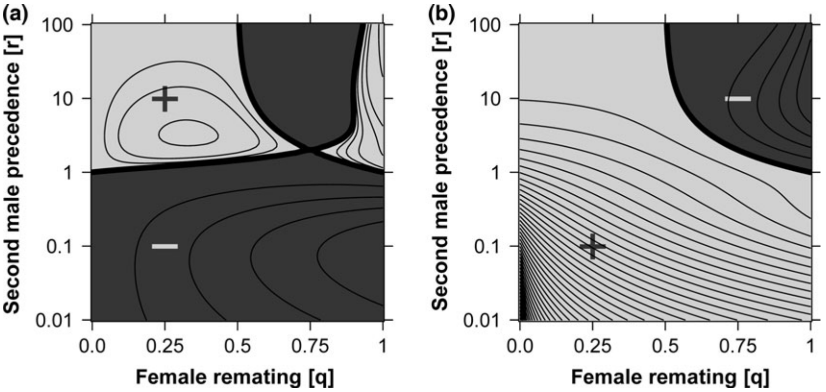

Fig. 1 Fitness advantage from being informed vs. uninformed in the 'mating history' scenario for (a) the first male to mate (i.e. ineq. 5) and (b) the second male to mate (i.e. ineq. 6), in relation to the female remating probability (q) and the second male sperm precedence (r). Lighter areas denoted with '+' indicate parameter values for which the informed game is more beneficial for the focal male than the uninformed game; darker areas denoted with '−' indicate parameter values for which the uninformed game is more beneficial. Each line indicates a 0.1 increment/decline in the value of $\log(w_I/w_U)$, which roughly represents a 10% relative fitness change of the two games. The result is independent of the value of c.

therefore present the results numerically as $\log(w_I/w_U)$, which if positive will favour an informed game and if negative will favour an uninformed game.

Mating history scenario

Figure 1a reveals that an informed game is beneficial for the first male to mate especially at large values of r (where second males have a sperm competition advantage), and at low values of q (where females rarely remate). Second males, on the other hand, always benefit from an informed game, except for the combination of high female remating probability (q) and second male sperm precedence (r) (Fig. 1b).

Mating tactics scenario

The analysis revealed that for a sneaker male it is always beneficial to play an uninformed game (i.e. ineq. 12 never holds). Thus, from a sperm competition perspective, it is never beneficial to inform the bourgeois male about the current elevation in sperm competition risk. An uninformed game can also be beneficial for the bourgeois male. This is more likely to hold (see Fig. 2) when the bourgeois male has an advantage in sperm competition (small r), sneaker events are frequent (large p), and the relative nonejaculate costs of parasitic matings are relatively low (low c_p/c_B). As males should invest more in attaining high fertilization

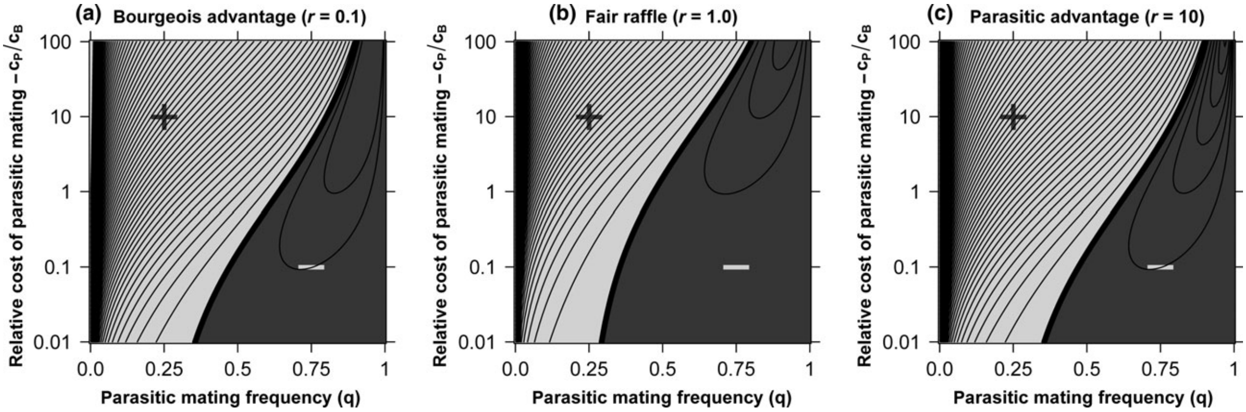

Fig. 2 Fitness advantage from being informed vs. uninformed for bourgeois males in the 'mating tactic' scenario (i.e. ineq. 11), in relation to the probability (p) and relative costs (c_P/c_B) of parasitic matings. In (a), bourgeois males have a sperm competition advantage ($r = 0.1$); in (b), there is a fair raffle ($r = 1$); and in (c), bourgeois males have a disadvantage ($r = 10$) in sperm competition. Lighter areas denoted with '+' indicate parameter values for which the informed game is more beneficial for the bourgeois male than the uninformed game; darker areas denoted with '−' indicate parameter values for which the uninformed game is more beneficial. Each line indicates a 0.1 increment/decline in the value of $\log(w_I/w_U)$, which roughly represents a 10% relative fitness change of the two games.

success if the cost of achieving matings is high (Tazzyman *et al.*, 2009), the last point signifies situations in which parasitic males make a relatively small ejaculate investment in each mating.

If bourgeois males are aware of a sneaking attempt, it is never beneficial to communicate this information to the sneaker male. In other words, inequality 15 never holds and the bourgeois males always benefit from a second-order uninformed game. As we already suspected, inequality 16 never holds, and thus, the parasitic male always benefits from being informed that the bourgeois male is aware of the sneaking attempt.

Discussion

Theoretical analyses of sperm competition games predict how males should allocate ejaculates across matings (Parker & Pizzari, 2010). An underlying assumption of these analyses is that males have information on the current level of sperm competition. Here, we have taken a different approach and examined under which circumstances information transmission between males regarding the expected sperm competition risk is likely to evolve.

We first considered a scenario where males mate with females sequentially. We found that when the male mating first is at a disadvantage ($r > 1$), or when sperm competition risk is low, the first male should signal to potential future males that this female has mated already (Fig. 1a). At first, this may seem counterintuitive. However, the knowledge that the female has already mated reduces the second male′s optimal sperm investment (Parker *et al.*, 1997), as he will fertilize most of the female′s eggs anyway, and this reduction is to the first male′s advantage. Thus, by 'marking' females as mated, the male mating first will benefit, as the male eventually mating second will as a consequence downgrade the value of these matings (cf. Schütz *et al.*, 2017). When there is first male sperm precedence ($r < 1$), on the other hand, the second male's knowledge increases his optimal sperm investment to compensate for this disadvantage (Parker *et al.*, 1997), and this is to the first male′s disadvantage.

An informed game is mostly to the second male′s advantage, except when he has a sperm competition advantage and remating risk is high (Fig. 1b). As this parameter space mostly coincides with the zone where the first male also benefits from an uninformed game, the potential for a commitment issue is limited. Furthermore, as males in this scenario do not need to actually meet, we may assume that the male communication channel is mainly via cues that are transmitted, for instance, by a manipulation of the mated female′s pheromonal profile, behaviour or genital tract (e.g. Siva-Jothy & Stutt, 2003; Friberg, 2006; Larsdotter-Mellström & Wiklund, 2009). In this case, there is no credible way in which males could signal to previous males that they will commit themselves to the uninformed ESS. Nevertheless, there are many situations where males have conflicting fitness interests regarding information transfer, namely when first males are selected to hide the information that females have mated, yet second males would benefit from this information. This happens mainly when there is first male sperm precedence (cf. Fig. 1). In this case, it is not straightforward to tell whether cues indicating female mating status will evolve or not. Mating males should benefit from extracting any available information regarding female previous mating history, whereas they are expected to conceal such cues to potential future males, resulting in an evolutionary 'hide-and-seek' arms race. The least constrained situation for male information transfer of female mating status is thus when there is second male sperm precedence and female remating rate is relatively low. Here, males mating in both roles would benefit from an informed game.

These results highlight that an uninformed game may be beneficial for one or even both males. Thus, an additional reason why males may appear not to respond sensitively to female mating status (cf. Engqvist & Reinhold, 2006; Ball & Parker, 2007) is that selection will not always favour the evolution of male discrimination of female mating status. An interesting target of future research might be to disentangle the evolution of apparent 'tags' of female mating status from the evolution of specialized sensory abilities enabling males to detect female mating status. For instance, male cabbage butterflies (*Pieris napi*) seem to mark their female mating partners with special pheromones that help future males to assess mating status (Larsdotter-Mellström & Wiklund, 2009; Larsdotter-Mellström *et al.*, 2016). In contrast, male bedbugs (*Cimex lectularius*) have chemoreceptors on their intromittent organ enabling them to detect whether females have recently mated (Siva-Jothy & Stutt, 2003). It seems possible that the routes towards male detection of female mating status in these examples have followed different evolutionary trajectories – one favouring active signalling of mating events and the other favouring novel and more sensitive detection abilities. The theory presented here identifies when signalling vs. detection of female mating status is likely to evolve in males. Yet, the females' ability to adapt to this male–male competition might modify the conditions (Alonzo, 2008; Alonzo & Pizzari, 2013). Females themselves might be selected to conceal or advertise their mating status, and this can affect the evolutionary outcome. For instance, female fecundity may be affected by nuptial gifts received during mating (Vahed, 1998). If male provisioning is affected by female mating status (e.g. Simmons *et al.*, 1993), female reproductive success will be influenced by the mating males' perception of their mating status. The evolution of communication strategies in this three-way interaction is an intriguing avenue for future research.

In the mating tactics scenario, we found that it is never beneficial for a parasitic male to inform the bourgeois competitor of his sneaking attempt. The reason is that the bourgeois male's best response to this information is always to increase sperm investment (Parker, 1990b), which is disadvantageous to the parasite. This adds to another drawback such information transfer typically entails: bourgeois males aware of sperm competition risk by parasites try to chase off the latter to avoid sneaking attempts altogether (see, e.g. Taborsky *et al.*, 1987). Thus, for the parasitic male it is always preferable if the bourgeois male is unaware of his sneaking attempt. This provides an additional explanation for the fact that, to our knowledge, there is no described biological system in which males applying a parasitic tactic do not try to remain undetected (see, e.g. Taborsky, 2008). Obviously, parasitic males should avoid bourgeois male aggression and eventual eviction, but here, we have shown that they also have a sperm competition advantage by promoting an information asymmetry regarding the expected sperm competition risk. If the bourgeois male has detected the sneaking attempt, however, the parasitic male should be aware of this; the worst outcome for the parasite is not being aware that his sneaking attempt has been spotted.

Regarding the fitness effects on bourgeois males, several intriguing results have emerged. First of all, the informed game is not always advantageous for them compared to the uninformed game. This is especially true when bourgeois males have an advantage in sperm competition (small r), sneaking events are frequent (large p) and parasitic males invest relatively little in each mating (low c_p/c_B) (see Fig. 2). Conversely, this illustrates that an informed game benefits the bourgeois male especially when the information asymmetry puts him at a strong disadvantage, that is when parasitic males invest heavily in matings, have a sperm competition advantage and are apparently rare (so that bourgeois males do not expect them). Similar to the mating history scenario, in the region of parameter space where bourgeois males do better at the uninformed ESS, the parasitic males also benefit from an uninformed game (as they always do), so there is no real conflict of interest generating a commitment issue.

It is important to note, however, that the previous comparison contrasts the 'both informed' with the 'both uninformed' situations. As it is never beneficial for a parasitic male to inform the bourgeois male of his sneaking attempt, the parasitic male can be uninformed about the awareness of the bourgeois rival. Thus, there is potential for a 'second-order' information asymmetry – the bourgeois male is aware of the sneaking attempt, but the parasitic male does not know this. This situation is always favourable for the bourgeois male, as he can consequently adjust his ejaculation strategy, and unfavourable for the parasite, as he is unaware of this response. Thus, the bourgeois male may face a dilemma when being aware of the sneaking risk. An attempt to defend and monopolize the female, and thereby avoid sperm competition altogether, is certainly beneficial if this defence is cost-effective and successful. If the bourgeois male cannot deter the sneaking attempt, however, his defensive action will give away his information advantage. Thus, in this situation the bourgeois male will be better off by accepting cuckoldry and maintaining the information asymmetry. This may provide an intriguing explanation why males sometimes seem to tolerate or even ignore potential sperm competition from nearby rival males (see Taborsky, 1994). For example, in the dwarf surfperch *Micrometus minimus*, small parasitic males seem to be completely ignored by the larger territory owners (Warner & Harlan, 1982). In other fish species, there are varying degrees of tolerance; parasitic males are often aggressively pursued yet tolerated at the edge of territories (e.g. Ross & Reed, 1978; Ross, 1983; Kodric-Brown, 1986). Sometimes, rival males are completely tolerated during spawning (e.g. in catostomid fishes; Reighard, 1920; Page & Johnston, 1990). It has been suggested that it may be energetically more costly to expel sneakers than to accept the loss of fertilizations (Kodric-Brown, 1977; Dominey, 1980). Losing an information advantage could add to this cost, and may put an additional constraint on males' capacity to avoid sperm competition. This argument is equally valid for a male's incentive to avoid extra-pair matings by their social partner, as occur in many bird species (see Petrie & Kempenaers, 1998).

Concluding remarks

It is evident that males in many species use cues indicating the level of sperm competition to adaptively adjust their ejaculate investment (Wedell *et al.*, 2002; Kelly & Jennions, 2011). Nevertheless, when potential rival males can provide or withhold this information, there is a potential conflict of interest. We have analysed the fitness pay-offs resulting from uninformed and informed sperm competition games to reveal under which circumstances signals indicating sperm competition risk are likely to evolve. Our analyses showed that it is sometimes beneficial for males to disclose signs of female mating status to future potential mates, specifically when the first male has a sperm competition disadvantage. We further showed that males parasitizing the reproductive effort of other males should always behave surreptitiously, and our results provide an explanation as to why males may apparently tolerate being cuckolded.

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