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# Conflict between the sexes and cooperation within a sex can alter classic predictions of mating systems theory

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## ABSTRACT

**Question:** How does the inclusion of conflict between the sexes alter classic predictions of mating systems theory?

**Mathematical method:** A game theoretical model of male and female behaviour was used to examine how interactions between the sexes alter the expected distribution of males and females among reproductive sites.

**Assumptions:** Male and female fitness are affected by the abundance of resources in a site, interactions within and between the sexes, expected survival, and reproductive success. I examine the possibility that interactions with males decrease female survival. Individuals are assumed to adopt the evolutionarily stable distribution strategy based on expected fitness.

**Predictions:** The inclusion of conflict between the sexes alters classic predictions of mating system theory. When the frequency of males in a site affects female survival, neither males nor females are predicted to exhibit resource matching. Furthermore, conflict between the sexes can be masked by the effect of resources and even accentuated by positive interactions among females. In general, the results reported here show that without the simultaneous consideration of how resources and interactions within and between the sexes affect fitness, one is likely to come to a false conclusion regarding the importance of resources, the extent of sexual conflict, and even the pattern of selection among sites.

*Keywords*: game theory, ideal free distribution, mating system, reproductive strategies, sexual conflict.

## INTRODUCTION

Recent research has focused on how conflict between the sexes may drive the evolution of reproductive traits in both sexes (e.g. Holland and Rice, 1998; Alonzo and Warner, 2000a; Gavrilets, 2000; Candolin and Reynolds, 2001; Chapman *et al.*, 2003; Arnqvist and Rowe, 2005; Hardling and Kaitala, 2005), while the importance of competition within a sex for access to mates or resources has long been recognized (e.g. Emlen and Oring, 1977; Dominey, 1981; Parker, 1998). However, interactions within and

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between the sexes simultaneously affect reproductive behaviours and mating systems (Davies, 1992; Hugie and Lank, 1997; Alonzo and Warner, 2000a, 2000b; Alonzo and Sinervo, 2001; Shuster and Wade, 2003). Although we have a general understanding of the individual effects of conflict between the sexes, competition within a sex, environmental conditions, and life history, there is no theory examining the combined effect of these key variables and their relative contribution to reproductive patterns (but see Lessells, 2006; Wedell *et al.*, 2006). However, a comprehensive view of mating systems must consider how interactions between these key factors affect male and female fitness and hence determine the overall mating system.

The seminal work by Emlen and Oring (1977) led to a general appreciation that ecological factors affect mating systems. However, this important variable has not been included in recent theory examining conflict between the sexes. Emlen and Oring's (1977) verbal theory predicted that females will respond to the spatial and temporal distribution of resources, whereas males mainly respond to the resulting distribution of receptive females and competition with other males. Females are predicted to respond directly to the distribution of resources, while female behaviour is argued to determine the ability of males to defend or gain access to mates. However, these predictions assume that male behaviour does not affect female fitness and therefore that females do not respond directly to the distribution of males. Yet, it is clear that conflict between the sexes affects the fitness of male and female reproductive behaviour (Arnqvist and Rowe, 2005), and hence should influence the distribution of individuals in space and time. To date, there is no theory that concurrently examines the impact of reproductive resources and conflict between the sexes.

It is often the case that we are trying to understand individual behaviour and patterns of selection. In the case of reproduction, we might be trying to understand the distribution of males and females among potential reproductive sites and understand any observed differences in mating or reproductive success. All else being equal, previous theory would predict that females and thus males should be distributed relative to differences in the abundance of reproductive resources among sites. In this paper, I examine a model that predicts the evolutionarily stable distribution of males and females among patches that vary in their abundance of resources. However, rather than assuming that females respond only to resources, the model predicts the distribution of both males and females given the effect of resources on female reproduction as well interactions within and between the sexes. Although this is an admittedly simple mating system, the situation considered here serves as a useful baseline to ask how these key factors interact to produce mating distributions. The aims of the model presented here are to examine how conflict between the sexes and interactions within a sex might cause deviations from this classic prediction, and determine to what extent ignoring these interactions might lead to an incomplete or even incorrect understanding of male and female behaviour and reproductive success.

## MODELLING THE JOINT EFFECTS OF RESOURCES, COMPETITION, SURVIVAL, AND SEXUAL CONFLICT

Different modelling approaches allow one to examine different biological questions. The model described below is an extension of previous arguments based on the ideal free and despotic distribution theories (Fretwell, 1972) making a game-theoretical equilibrium approach appropriate. The model presented here examines the distribution of males and females among reproductive sites that vary in the abundance of resources important to reproduction. For consistency with Emlen and Oring's (1977) original paper, I do not consider individual differences in phenotype or competitive ability explicitly but focus instead on average expected fitness in each reproductive site. Only potentially reproductive individuals are considered. I assume an equal sex ratio of reproductive individuals and individuals can move freely with no cost between sites. The analyses presented here focus on the case where individuals distribute themselves between sites that differ in the input rate of resources (Lessells, 1995), but no other inherent differences exist between the sites. The solution of the model predicts the distribution of potentially reproductive males and females between sites. For the analyses presented here, I examine the situation where there is no inherent temporal variation in survival and reproduction and focus on predicting the relative distribution of males and females among sites. Hence the model searches for the evolutionarily stable relative distribution of males and females among sites where average expected fitness in a site determines the relative distribution of individuals among sites (Fretwell, 1972; Sih, 1998).

For simplicity, I consider a semelparous species where female survival is essential to offspring production or survival. Reproductive sites vary in the abundance of resources and the number of conspecific males and females at the site. Females settle in breeding sites, compete for resources, mate, and then produce offspring. Similarly, males come to a breeding site, compete for females, and must survive through competition to mate. Resources can affect reproductive success in a variety of ways. I assume that resources directly affect female current reproductive success. For example, more food resources may increase a female's fecundity or the provisioning of her offspring. Female average expected fecundity or reproductive success in a site is thus expected to increase with her individual share of the resources. Average male and female expected fitness in a reproductive site $i$ depend on: (1) the abundance of resources available at the site $r_i$; (2) the proportion of potentially reproductive males at the site $m_i$ (where $\Sigma_i m_i = 1$); (3) the proportion of potentially reproductive females at the site $f_i$ (where $\Sigma_i f_i = 1$); (4) male ($\tau_i$) and female ($\sigma_i$) expected survival to reproduction in the site; and (5) interactions within and between the sexes. Male and female survival will depend on the baseline expected survival to reproduction ($\tau_0$ and $\sigma_0$) and the effect of interactions within and between the sexes on individual survival. Because I do not assume settlement order effects in a site or differences among individuals in competitive ability, expected fitness is identical for both the ideal free and ideal despotic situations. For the scenario under consideration, female fitness can be represented as the product of their probability of survival and expected fecundity in a site. Assuming ideal competition, a female's average expected share of the resources will be the ratio of resources to competitors for those resources in a site. I also assume that the reproductive resources under consideration are depleted following competition so that if a female dies, her resources do not become available to other females. Assuming females compete for resources before reproduction (and before any differences in female survival among sites arise), then a female's expected share of the resources in a site is given by $r_i/f_i$. For simplicity, I assume that resources have a linear effect on female current reproduction, although other possibilities clearly exist. An asymptotically increasing relationship between resources and female fitness yields qualitatively and often quantitatively identical results. I also assume that the number of males at the mating site does not limit female reproduction and that male survival following mating does not affect female reproductive success. Then, female expected fitness $V_i$ at site $i$ will be the product of expected survival and reproductive success, which is

$$V_i = \sigma_i\left(\frac{r_i}{f_i}\right) \tag{1}$$

Male fitness depends on male survival to reproduction, competition for mates, and female fecundity. Assuming ideal competition among males for mates and that any differences in male expected survival arise before mating, then males competing for females in site *i* obtain on average $f_i/(\tau_i m_i)$ mates. Male fitness $W_i$ at site *i* is then given by the product of male expected survival to mating, the expected fecundity of their mates, and competition among the surviving males for females:

$$W_i = \tau_i\left(\frac{\sigma_i r_i}{f_i}\right)\left(\frac{f_i}{\tau_i m_i}\right) = \frac{\sigma_i r_i}{m_i} \tag{2}$$

In this scenario, any decrease in male survival ($\tau_i$) is balanced by the corresponding decrease in competition for mates. In situations where males experience a trade-off between current and future reproduction, this would not necessarily be true. Below, I describe the predicted relative distribution of males and females among sites for a number of cases that differ in the way interactions within and between the sexes affect male and female fitness.

For all of the analyses that follow, I focus on examining the general qualitative properties of the predictions by comparing them to classic theory. I focus on two comparisons. First, classic theory predicts that females will 'match' the relative distribution of resources among sites. Females are said to be matching resources when the relative abundance of females in sites *i* and *j* is equal to the relative abundance of resources in those sites (i.e. $f_i/f_j = r_i/r_j$). Females overmatch resources if more females are found in higher resource sites (and fewer females in lower resource sites) than expected by the relative distribution of resources ($f_i/f_j > r_i/r_j$ for $r_i > r_j$ and $f_i/f_j < r_i/r_j$ for $r_i < r_j$), and undermatch resources if fewer females are found in higher resource sites (and more females in lower resource sites) than expected. Classic theory also argues that males should respond to the distribution of females. Thus, I also focus on examining the case in which males are predicted to match, undermatch, or overmatch the distribution of females among sites (defined in the same way as for females above). All of the variables used in the model are summarized in Table 1.

## Case 1: No conflict between the sexes

The classic view of mating systems was that females respond to resources and males compete for females. I present this case first and use it as a baseline with which to compare all other cases. As described above, I assume ideal competition among females for resources,

**Table 1.** Parameters in the model

| | |
|---|---|
| $r_i$ | relative abundance of resources in site *i* |
| $m_i$ | proportion of males in site *i* |
| $f_i$ | proportion of females in site *i* |
| $V_i$ | expected female fitness in site *i* |
| $W_i$ | expected male fitness in site *i* |
| $\sigma_0$ | baseline expected female survival |
| $\tau_0$ | baseline expected male survival |
| $\sigma_i$ | expected female survival in site *i* |
| $\tau_i$ | expected male survival in site *i* |
| $\gamma$ | effect of males on female survival |
| $\alpha$ | effect of females on female survival |

that males compete for females, and that resources have a linear effect on female current reproduction. To find the evolutionarily stable distribution of males and females between a pair of sites *i* and *j*, we search for the conditions in which $V_i = V_j$ (given by equation 1) and $W_i = W_j$ (given by equation 2). The predicted relative distribution of males and females among two sites *i* and *j* is given by

$$\left(\frac{\sigma_i r_i}{\sigma_j r_j}\right) = \left(\frac{f_i}{f_j}\right) = \left(\frac{m_i}{m_j}\right) \tag{3}$$

Assuming no inherent differences among sites in expected female survival and in the absence of interactions within and between the sexes that lead to differences among sites in female survival ($\sigma_i = \sigma_j = \sigma_0$), male competition for access to females and female competition for resources alone determine the expected fitness of males and females. As a result, females are predicted to match (i.e. be found in proportion to) the relative distribution of resources among sites and males are predicted to match the relative distribution of both females and resources (Fig. 1A). However, it is worth noting that any inherent differences among the sites in female survival are predicted to affect both male and female behaviour and will cause deviations from perfect resource matching.

### Case 2: Conflict between the sexes over mating costs

In many species, interactions with males can have negative consequences for females. Male harassment could decrease a female's energy available for survival, could lead to an increased risk of predation, or could decrease a female's time available for feeding. Furthermore, re-mating frequency has been shown to decrease female survival and future reproduction in some species (Andersson and Iwasa, 1996). For example, toxic seminal fluids involved in sperm competition decrease female survival in *Drosophila* (Chapman and Patridge, 1996; Rice, 1996). Male harassment could depend on the amount of competition among males for females in the site, in which case $m_i/f_i$ would affect female survival. If the ratio of males to females determines male harassment, then female survival can be represented by the function

$$\sigma_i = \frac{\sigma_0}{1 + \gamma\left(\frac{m_i}{f_i}\right)} \tag{4}$$

where $\gamma$ represents the strength of the effect of males on female survival (and $\gamma \geq 0$). Alternatively, if the frequency of male harassment depends on the number of males in a site, then female survival will decrease with the proportion of males $m_i$ in a site *i*. This might be the case if all males attempt to mate with every female present in a site (i.e. more males means more interactions with males), and mating or interacting with males is costly. Similarly, if females visit potential reproductive locations (such as territories, leks, or oviposition sites) sequentially, then male harassment should depend directly on the frequency of males. For this case, the effect of males on female survival $\sigma_i$ can be represented by the function

$$\sigma_i = \frac{\sigma_0}{1 + \gamma m_i} \tag{5}$$

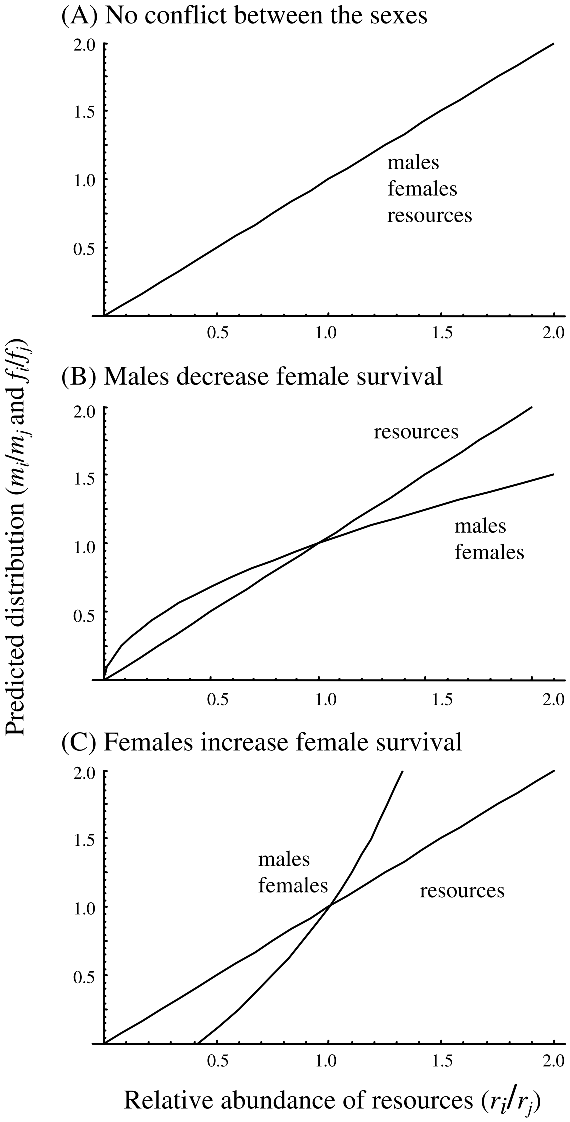

**Fig. 1.** The predicted relative distribution of males and females among patches that vary in their resource abundance. See the Appendix for additional details of the calculations that allow this graphical representation of the results. Each panel has the relative distribution of resources ($r_i/r_j$) on the horizontal axis and gives the relative distribution of females ($f_i/f_j$) and males ($m_i/m_j$) on the vertical axis. The line of perfect resource matching ($r_i/r_j = m_i/m_j$ or $f_i/f_j$) is also shown for comparison. (A) Case 1: Both males and females are predicted to exhibit resource matching in the absence of conflict between the sexes (given by equation 3 and assuming no inherent differences among the sites in female survival such that $\sigma_i = \sigma_j = \sigma_0$). (B) Case 2: When males decrease female survival or fecundity, both males and females are predicted to deviate from resource matching (shown for $\gamma = 10$). (C) Case 3: When other females have a positive effect on female survival or reproduction, females and males are predicted to overmatch the relative abundance of resources (shown for $\gamma = 0$ and $\alpha = 2$). In general, interactions within and between the sexes (Cases 2 and 3) can cause deviations from the perfect resource matching prediction of classic mating systems theory.

where again $\gamma$ represents the strength of the effect of males on female survival (and $\gamma \geq 0$). In both cases, larger values of $\gamma$ are consistent with a larger effect of males on female survival. When female survival depends on the ratio of males to females in a site (equation 4), the stable relative distribution of males and females among two sites $i$ and $j$ occurs where $V_i = V_j$ and $W_i = W_j$ (from equations 1 and 2) or where

$$\left(\frac{\sigma_0}{1+\gamma\left(\frac{m_i}{f_i}\right)}\right)\left(\frac{r_i}{f_i}\right)=\left(\frac{\sigma_0}{1+\gamma\left(\frac{m_j}{f_j}\right)}\right)\left(\frac{r_j}{f_j}\right) \text{ and } \left(\frac{\sigma_0}{1+\gamma\left(\frac{m_i}{f_i}\right)}\right)\frac{r_i}{m_i}=\left(\frac{\sigma_0}{1+\gamma\left(\frac{m_j}{f_j}\right)}\right)\frac{r_j}{m_j} \tag{6}$$

Through simplification and substitution, this can be shown to imply that

$$\left(\frac{r_i}{r_j}\right)=\left(\frac{f_i}{f_j}\right)=\left(\frac{m_i}{m_j}\right) \tag{7}$$

Therefore, in the case where the effect of males on females is ratio-dependent and there are no inherent differences among sites in female survival, the predictions do not differ from the classic case where there is no conflict between the sexes (equation 3; Fig. 1A). Females are predicted to match the relative distribution of resources and males are predicted to match the distribution of females.

In contrast, if female survival is affected by the presence of males in a site (equation 5), the stable relative distribution of males and females among sites will occur when

$$\left(\frac{\sigma_0}{1+\gamma m_i}\right)\left(\frac{r_i}{f_i}\right)=\left(\frac{\sigma_0}{1+\gamma m_j}\right)\left(\frac{r_j}{f_j}\right) \text{ and } \left(\frac{\sigma_0}{1+\gamma m_i}\right)\left(\frac{r_i}{m_i}\right)=\left(\frac{\sigma_0}{1+\gamma m_j}\right)\left(\frac{r_j}{m_j}\right) \tag{8}$$

which through simplification and substitution can be shown to imply that

$$\left(\frac{f_i}{f_j}\right)=\left(\frac{m_i}{m_j}\right)=\left(\frac{r_i}{r_j}\right)\left(\frac{1+\gamma m_j}{1+\gamma m_i}\right) \tag{9}$$

which is also equivalent to

$$\left(\frac{r_i}{r_j}\right)=\left(\frac{m_i}{m_j}\right)\left(\frac{1+\gamma m_i}{1+\gamma m_j}\right)=\left(\frac{f_i}{f_j}\right)\left(\frac{1+\gamma m_i}{1+\gamma m_j}\right) \tag{10}$$

Equation (9) implies that males are predicted to match the relative distribution of females but neither sex is predicted to match the distribution of resources among sites. From equations (9) and (10) (see Appendix for further details), we can predict the relationship between the relative abundance of resources ($r_i/r_j$) and the relative abundance of males ($m_i/m_j$) and females ($f_i/f_j$) among sites (Fig. 1B). More males and females are predicted to be found in lower resource sites and fewer males and females in higher resource sites than expected by resources alone (equation 10; Fig. 1B). This is because the greater presence of males in sites with more resources is predicted to decrease female expected survival in these sites, while sites with fewer resources have greater expected female survival to reproduction. Predictions are identical if males affect female fecundity rather than female survival.

These results imply generally that conflict between the sexes can cause deviations from simple resource matching for both males and females. In fact, if the effect of males on females is sufficiently high, there may be no detectable relationship between resources and the distribution of males and females among sites. One might then draw the false conclusion that the resources were not important to reproduction and hence be puzzled by the observation that resources do in fact increase female fecundity. It is also worth noting that the fecundity of females is predicted to differ among sites but this difference is counter-balanced by differences in female survival. Similarly, if we consider male mating success and female fecundity alone, male reproductive success would appear to differ among sites. It is only through the consideration that female survival to reproduction also affects male fitness that the distribution among sites could be understood. Finally, whether males and females are predicted to exhibit resource matching (Fig. 1A) or undermatching (Fig. 1B) depends on whether females are affected by the ratio of males to females or the total presence of males in the site. Thus, it will also be very important to understand the effect of males on female survival or fecundity. Overall, these results indicate that the distribution of males and females among sites that differ in reproductive resources can only be understood through the joint consideration of competition for mates, competition for resources, and conflict between the sexes.

### Case 3: Interactions among females improve female survival

Finally, positive interactions may also occur. Imagine, for example, that females cooperate in anti-predator defence. The presence of other females at a site would then increase the probability any individual female would survive. Assume that females continue to compete for resources and female survival is also negatively affected by the presence of males in the site (as in Case 2 and equation 5 above). Then, the proportion of females at the site will increase female survival (while also increasing competition among females for resources) such that

$$\sigma_i = \left(\frac{f_i}{\alpha + f_i}\right)\left(\frac{\sigma_0}{1+\gamma m_i}\right) \tag{11}$$

where α represents the strength of the positive effect of other females on female survival ($\alpha \geq 0$). As before, we search for the conditions in which $V_i = V_j$ and $W_i = W_j$ (given equations 1, 2, and 11). The predicted stable distribution of males and females among sites is then given by

$$\left(\frac{m_i}{m_j}\right) = \left(\frac{f_i}{f_j}\right) \text{ and } \left(\frac{r_i}{r_j}\right) = \left(\frac{\alpha + f_i}{\alpha + f_j}\right)\left(\frac{1+\gamma m_i}{1+\gamma m_j}\right) \tag{12}$$

This implies that males are predicted to match the distribution of females and neither sex is predicted to exhibit resource matching. Given equation (12) (see Appendix for details), we can also examine the predicted relationship between relative abundance of resources ($r_i/r_j$) and the relative abundance of males ($m_i/m_j$) and females ($f_i/f_j$) among sites (Fig. 1C). If the benefits of females to female survival or reproduction outweigh the negative impact of males, then both sexes are predicted to overmatch the resources in high resource sites and undermatch the resources in low resource sites (Fig. 1C). In contrast, if the negative effect of males outweighs the positive effect of other females, then individuals are predicted to undermatch resources. If the effect of females on female fitness is sufficiently positive, then a detectable relationship between resource abundance and the abundance of males or females would not exist. Furthermore, the positive effect of females on other females predicts a skewed distribution of females and males among sites when the benefits of abundant resources and positive interactions among females coincide. Clearly, any negative effects of males on female survival or male fitness will reduce the benefits of overmatching the resources in high resource sites for both sexes. Predictions are identical if we assume instead that males or females affect female fecundity rather than survival.

## DISCUSSION

It is important to realize that no single factor (resources, competition, survival, or sexual conflict) is the most important predictor of male or female behaviour (Fig. 1). Instead, a combined understanding of the links between these key variables is necessary to explain the predicted patterns. In many cases, a constant relationship is not predicted between relative resource abundance and the proportion of either males or females in a reproductive site. The relative abundance of resources is predicted to affect the relative distribution of males and females among sites, but the strength of this relationship is modified by interactions within and between the sexes. In general, when interactions within or between the sexes decrease either survival or reproduction, undermatching of the relative abundance of resources is predicted. Similarly, even when strong competition for resources occurs, positive interactions are predicted to lead to an overmatching of resources. Generally, an understanding of individual fitness and behaviour as well as population level reproduction and distribution patterns will require knowledge of how resources affect males and females, the connections between male and female fitness, and how interactions within and between the sexes affect current and future reproduction.

Many of the predicted patterns are intuitive after the fact (as good theory should be) based on a complete understanding of the combined effect of resources, conflict, and competition. However, these factors have not been considered either theoretically or empirically, and thus the conclusions we draw regarding male and female reproductive behaviour and fitness may often be incomplete or even incorrect. Clearly, most species are not expected to exhibit an ideal free or ideal despotic distribution even in the absence of sexual conflict because many other factors influence male and female reproductive behaviours. This scenario is used as a simple baseline to examine the potential importance of the key variables under consideration. The theory developed here indicates that something as simple as the distribution of individuals among reproductive sites requires an understanding of the links between sexual conflict, competition within a sex, the availability of resources, and life-history trade-offs.

Imagine that females aggregate in sites where there is more male harassment and these females have lower fecundity. It would be difficult to explain why females would be more common in sites where they are harassed more and have more competition for resources unless one also knew that female survival was higher in these sites due to a positive interaction among females. More generally, it is worth noting that positive interactions among females may favour a skewed distribution that increases conflict between the sexes and competition among males. Positive interactions within a sex may influence (and even increase) conflict between the sexes and competition in the opposite sex. Interactions within and between the sexes cannot be considered in isolation from one another.

An enormous diversity of reproductive patterns is observed in the wild. Further theory is needed that considers more complex mating systems and further variables that influence male and female distribution patterns. There is also a general need to examine the links between resources, interactions within and between the sexes, and life-history patterns empirically. These factors have all been studied in isolation for many species. However, I am not aware of any species for which we understand how resources and sexual conflict concurrently affect male and female behaviour and fitness. Yet it is entirely feasible to examine these interactions in any species where these factors are understood in isolation. Experimental tests of these specific models will be possible in species where the resources important to reproduction are known and can be manipulated.

The model presented clearly indicates that conflict between the sexes can clearly cause deviations from perfect resource matching even when male fitness is affected by the negative impact of males on female survival or reproduction. However, another important prediction is that patterns emerge that could easily be misinterpreted if we did not consider all of the key variables and their interactions. For example, one might falsely conclude that the resources under consideration were not very important to reproduction given that resource matching may be weak in the presence of conflict between the sexes. Similarly, differences among females in fecundity are predicted among sites in the presence of conflict between the sexes that could be misinterpreted as differences in fitness unless one also considered the effect of males on female survival. Finally, sites may have very difference levels of male harassment or other measures of conflict between the sexes, and understanding why females are found in sites where they are harassed and experience lower survival requires knowledge of the reproductive resources. It is certainly more difficult to study all of these factors concurrently. However, focusing on one of these key factors only can lead to a misinterpretation of the mechanism driving the patterns we observe and may even misrepresent selection on males and females.

A general purpose of theory is to highlight what information is currently lacking. Clearly, further theoretical and empirical work will be necessary. Although resource dispersion, sexual conflict, and life-history theory have great explanatory power in isolation, they are interconnected to generate the diversity of mating systems, reproductive patterns, and behavioural interactions observed in the wild. Although I focus here on the distribution of reproductive males and female among sites, the results of these models imply that a complete understanding of observed patterns will require a consideration of sexual conflict and resources. Furthermore, an understanding of conflict between the sexes requires knowledge of the relationship between male and female fitness through their offspring. Similarly, positive interactions within a sex or the positive effect of resources on fitness can mask or even accentuate conflict between the sexes. A general understanding of mating systems and reproductive behaviour requires an examination of the combined effects of interactions within and between the sexes, reproductive resources, trade-offs between current and future reproduction, and the extent to which the fitness of males and females are linked through their offspring, because all of these factors can drive deviations from classic predictions of mating systems theory and influence our ability to detect and understand the importance of any single factor.

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## APPENDIX

While equations (9), (10), and (12) give the predicted relationships between all of the key variables, predicting the relative distribution of males ($m_i/m_j$) and females ($f_i/f_j$) among two sites $i$ and $j$ based on the relative abundance of resources ($r_i/r_j$) requires some additional calculations. We know (from equations 3, 9, and 12) that $m_i/m_j = f_i/f_j$ and, by definition, given only two sites $i$ and $j$, that $f_i + f_j = 1$ and $m_i + m_j = 1$. In combination, this implies that $m_i/(1 - m_i) = f_i/(1 - f_i)$, thus showing that $m_i = f_i$ and $m_j = f_j$ must also be true. In addition, let $R = r_i/r_j$, $M = m_i/m_j$, and $F = f_i/f_j$. Given that $m_i + m_j = 1$ and $f_i + f_i = 1$, then it can be shown that $m_i = M/(1 + M)$ and $m_j = 1/(1 + M)$ and similarly that $f_i = F/(1 + F)$ and $f_j = 1/(1 + F)$. Substitution into equation (10) then gives

$$R = M\left(\frac{1 + \gamma M/(1 + M)}{1 + \gamma/(1 + M)}\right) = F\left(\frac{1 + \gamma F/(1 + F)}{1 + \gamma/(1 + F)}\right) \tag{A1}$$

where equation (A1) allows Fig. 1B to be drawn for any value of $\gamma$. For heuristic reasons, the graph of this equation is reversed such that $R$ ($= r_i/r_j$) is shown on the horizontal axis and $F$ ($= f_i/f_j$) and $M$ ($= m_i/m_j$) are shown on the vertical axis. Using similar arguments, we can rearrange equation (12) such that

$$M = F \text{ and } R = \left(\frac{\alpha + M/(1 + M)}{\alpha + 1/(1 + M)}\right)\left(\frac{1 + \gamma M/(1 + M)}{1 + \gamma/(1 + M)}\right) = \left(\frac{\alpha + F/(1 + F)}{\alpha + 1/(1 + F)}\right)\left(\frac{1 + \gamma F/(1 + F)}{1 + \gamma/(1 + F)}\right) \tag{A2}$$

where as before equation (A2) allows Fig. 1C to be drawn for any values of $\gamma$ and $\alpha$.