Influence of male relatedness on lethal combat in fig wasps: a theoretical analysis

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In many fig wasp species, flightless males fatally fight with rivals. In a recent comparative analysis, West and colleagues found no influence of male relatedness on the frequency of fatal fighting. Inspired by this study, I used a simple theoretical model to examine the conditions that should influence the probability of fatal fighting in a closed mating system. I show that, without kin recognition, relatedness can be expected to have no influence on the frequency of fatal fighting. Under such conditions, males should fight if their chance of winning is greater than a threshold determined by the number of competitors. If males recognize kin, a non-linear relationship between relatedness and the frequency of fatal fighting can be expected. However, two other factors should also be important when there is kin recognition: male number and variance in male fighting strength can be shown to have decisive influences on the frequency of fatal fighting. My results thus corroborate and explain one finding of the empirical study—that there is no significant influence of relatedness on fatal fighting—but point to a role for other factors besides foundress number—male number and male variance in fighting strength. These are probably important factors determining the occurrence of lethal combat in fig wasps.

Keywords: fatal fighting; kin selection; intrasexual competition; kin recognition; *Ficus*

1. INTRODUCTION

Since related individuals share genes, owing to a common origin, it can be expected that individuals show more altruism and less aggression towards related than towards unrelated individuals (Hamilton 1964*a,b*). For theoretical reasons, it has been proposed that this cornerstone of Hamilton's kin-selection theory is not applicable when competition between relatives is high (Enquist & Leimar 1990; Taylor 1992; West *et al.* 2002). Under such a scenario, competition between relatives has accordingly been predicted to cancel the advantages of altruism towards kin. In a recent comparative analysis, West *et al.* (2001) found, in line with these arguments, no influence of male relatedness on the frequency of fatal fighting in fig wasps.

Fig wasps are tiny gall-building hymenoptera and their parasitoids develop within the fruits of fig trees. These species include mutualistic pollinating species as well as parasitic non-pollinating species. In many species, flightless non-dispersing males hatch prior to females, search the fruit for virgins and compete with rivals (Hamilton 1979; Murray 1987; Cook *et al.* 1997). In some species of non-pollinating fig wasps these flightless males are highly modified for combat, possessing huge mandibles and armoured bodies (Frank 1987; Murray 1990). Compared with pollinating species, non-pollinating fig wasps often have fewer individuals per fig syconium and less female-biased sex ratios (Hamilton 1979). Based on local mate-competition theory and on the lower sex-ratio bias in non-pollinating fig wasps, Hamilton (1979) suggested that pollinating species show fewer adaptations to fight competitors, because in these species the competing males are often closely related. Since pollinating fig wasps are prob-

ably monophyletic (Herre *et al.* 1996; Rasplus *et al.* 1998), the various species cannot be treated as independent. A reliable analysis of comparative data therefore has to use phylogenetically independent information on relatedness and the frequency of fatal fighting. In their recent analysis, West *et al.* (2001) used the independent contrasts of interspecific differences in male injury levels to examine the relationship between the frequency of fatal fighting and male relatedness. For their analysis they estimated male relatedness contrasts from wasp sex ratios. These relationship estimates are based on the effect relatedness has on the evolutionarily stable sex ratio in line with local mate-competition theory (see Nee *et al.* 2002 for a recent justification of this method). West *et al.* (2001) found no significant correlation between male injury scores and male relatedness contrasts and concluded that male relatedness does not influence the frequency of lethal combat. The extent of injury among males was, however, found to be negatively correlated with female density in the comparative analysis. West *et al.* (2001) related this result to the expected theoretical effect of increased future mating opportunities on the value of the contested resource (Enquist & Leimar 1990).

Fights over contested resources are a central assumption of most previous theoretical studies examining the evolution of fatal fighting (Grafen 1979; Murray 1984; Murray & Gerard 1985; Enquist & Leimar 1990; but see Colegrave 1994). This assumption probably has its roots in the widespread use of contests over resources in game theory. Even though male fig wasps do guard galls containing females, fatal fighting, but not mating, seems to be most intense during the first hour after male emergence from the galls (Murray 1987). Fatal fighting is thus unlikely to result only from contests over specific females but may serve to exclude potential competitors from reproduction. In line with this argument, the paternity of

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the offspring produced by the females in a syconium can be regarded as the contested resource.

Here, I use a simple mathematical model to examine whether male relatedness can be expected to have an effect on the occurrence of mortal combat. The assumptions used in the model were inspired by some aspects of fig wasp biology but are meant as a general representation of conflict over mating partners in a closed system (Colegrave 1994). I assumed a closed system, like a fig syconium, with male fighting occurring before the mating period, and I also assumed that males can somehow detect their winning chances before they start fatal fighting. Implicitly I also assumed that attacked males cannot always escape and that consequentially at least some attacks lead to mortal combat. In a first analysis I assumed that males do not recognize kin and I examined whether the level of relatedness among males has an influence on the winning-chance threshold (hereafter called the fighting threshold), which should determine whether males engage in mortal combat. In a second analysis, I compared the obtained results with the case in which males have the ability to distinguish related from unrelated males.

2. THE MODEL

I assume that n (more than 1) male fig wasps develop within a fig fruit and that for a specific male a proportion y (0 to 1 inclusive) of the other $n - 1$ males are sibs and that the remaining males are unrelated. The coefficient of relatedness of the related males is given as r . For mathematical tractability I further assume that male fighting, if it occurs at all, occurs before any females can be detected and that all surviving males share reproductive success randomly or evenly. Without fatal fighting, the inclusive fitness of a specific male under consideration can be represented for these assumptions by the term T_1 :

$$T_1 = \frac{1}{n} + r \frac{y(n-1)}{n}. \quad (2.1)$$

The first part of this equation gives the expected share the male under consideration has in the total reproduction of the syconium, and the second part gives the reproductive success of his male sibs multiplied by their relatedness coefficient, i.e. the male's indirect fitness component. In an encounter between a specific male and an unrelated male, the inclusive fitness of the male under consideration resulting from fatal fighting can be represented by T_2 when the chance of winning the fight is given by x (0 to 1 inclusive):

$$T_2 = \frac{x}{n-1} + rxy + ry(1-x). \quad (2.2)$$

Here, the first part gives the direct fitness component when winning the fight, the second part gives the indirect fitness component when winning the fight and the third part gives the indirect fitness component when losing the fight. In a similar way, the term T_3 represents the fitness of the male under consideration when fatal fighting occurs with a related male:

$$T_3 = \frac{x}{n-1} + r \frac{x[(n-1)y-1]}{(n-1)} + ry(1-x). \quad (2.3)$$

Figure 1. Theoretical effect of the number of males in a fig fruit on the threshold above which fatal fighting is advantageous. If males correctly perceive their winning chance to be greater than the fighting threshold, they benefit from initiating fatal fighting. The solid line shows the threshold if kin recognition is absent or if males do not differ in relatedness. The other two lines indicate the thresholds if kin recognition is present and two (dotted line) or three (dashed line) females contribute full-sib offspring to a syconium.

In my model I assume that males can estimate x , their chance of winning a fight, and that they should initiate fatal fighting only if fighting increases their average fitness. For the case of no kin recognition, we can therefore easily calculate the conditions under which fatal fighting is beneficial. Males should initiate fatal fighting if the chance of fighting an unrelated male times the resulting fitness, plus the chance of fighting a related male times the resulting fitness is larger than the inclusive fitness without fighting. This means that males should initiate fatal fighting when:

$$(1-y)T_2 + yT_3 > T_1. \quad (2.4)$$

Following the insertion of equations (2.1) to (2.3) into equation (2.4) and with a little algebra, equation (2.4) can be simplified to:

$$x > \frac{n-1}{n}. \quad (2.5)$$

This result means that the conditions for the induction of fatal fighting are totally independent of male relatedness if males are unable to differentiate related from unrelated competitors. According to this equation, the occurrence of fatal fighting depends only on male number and the chance of winning a fight. For $n = 2$, fatal fighting can thus be expected to occur whenever one of the males correctly perceives himself to have a slight advantage against the other male. Such an advantage could be asymmetry in fighting strength or any asymmetry resulting from surprise attack or fighting position. For larger numbers of competing males, individuals can benefit from fatal fighting only if their chances of winning are much greater than their chances of losing a fight. Males can benefit from fatal fighting and therefore should initiate fighting only when they are able correctly to perceive their winning chance to be greater than $(n-1)/n$. This means that with an increasing number of males, the necessary winning chance approaches 1 (figure 1). It can therefore be expected that

Figure 2. Relationship between the number of foundresses that contribute offspring to a syconium and the threshold that determines whether males benefit from initiating fatal fighting. Here, females were assumed to produce four (open diamonds) or six (filled squares) full-sib male offspring and males were assumed to recognize kin.

the frequency of fatal fighting should decrease with male number.

When males are able to differentiate related from unrelated males, T_2 (inclusive fitness when fighting an unrelated male) needs to be greater than T_1 (inclusive fitness without fighting) to render an attack advantageous. This relationship can be solved for x to give the conditions under which males should fight with unrelated males. If males correctly perceive x to be greater than the following threshold, fatal fighting is beneficial when

$$x > (1 - ry) \frac{n-1}{n}. \quad (2.6)$$

In this case, the threshold value of x for advantageous fatal fighting approaches 0.75 with an increasing number of males present, if full brothers and unrelated males occur at about equal frequency. Such a case can be expected if two singly mated females contribute approximately equal numbers of male offspring to a fig fruit. If few unrelated males co-occur with many brothers, the fighting threshold approaches 0.5 for the males with the larger number of brothers. In contrast to the case of no kin recognition, the values of r and y thus clearly matter when there is kin recognition. In figure 1, I compare the winning thresholds that determine whether fatal fighting is adaptive when there is no kin recognition (or when kin recognition is not advantageous because males do not differ in relatedness) with the thresholds when offspring of two or three monogamous foundresses compete and males can differentiate related from unrelated competitors. If many foundresses contributed offspring to a fig syconium, meaning a low y -value, x approaches 1 with increasing foundress number. This result suggests that, with kin recognition, a greater frequency of fatal fighting can be expected between males in syconia that contain male offspring of two females than in syconia that contain only related or mainly unrelated males (figure 2). A non-linear relationship between the frequency of fatal fighting and male relatedness can thus be expected under kin recognition.

3. DISCUSSION

With a simple theoretical model I examined the conditions that should influence the probability of fatal fighting between males in a closed system. In my analysis I show that, without kin recognition, relatedness can be expected to have no influence at all on the incidence of fatal fighting. In this respect, the present results agree well with predictions from more general models: competition between relatives has the potential to cancel kin-selection effects (West *et al.* 2002; Griffin & West 2002). According to my model, the frequency of fatal fighting should depend only negatively on male number and positively on male variation in the chance of winning a lethal combat when there is no kin recognition. This result rests on the assumption that males can detect their chances of winning a fight by evaluating the situation or the competitor. Such an ability of competing males has been shown in various animal species from insects to mammals (Davies & Halliday 1978; Clutton-Brock & Albon 1979; Panhuis & Wilkinson 1999; Schuck-Paim 2000; Hofmann & Schildberger 2001). I therefore suppose that it is likely that at least a behavioural programme such as 'attack if you surprise your rival' or 'attack if bigger' evolves that leads to attacks only when a certain fighting threshold is exceeded.

In my model I assume that males fight their competitors prior to female emergence. There is some evidence that in the fig wasp *Philotrypes pilosa* male fighting is most intense during the first hour after male emergence and that mating frequency is highest later on (Murray 1987). Fighting clearly does, however, also occur after the first copulations. In principle, this deviation from the assumptions should not alter the validity of the conclusions inferred from the model. The equations used also determine the optimal male fighting strategy to maximize the residual reproductive success of males. However, fighting after the first copulations for access to specific females can explain why female number can be important (Enquist & Leimar 1990). As long as the males have no information on the number of still-available females or on the copulation success of their competitors, the model presented here should adequately describe the conditions under which males benefit from initiating fatal fighting. Only when males estimate the value of the future (Enquist & Leimar 1990) to be low, can they be expected to fight fatally for access to the last available females.

If males do recognize kin, some change in the frequency of fatal fighting can be expected within figs containing both related and unrelated males in comparison with the case of no kin recognition. Given an equal variance in male winning chance, kin recognition should lead to an increase in the frequency of fatal fighting, since the lower threshold for fights with unrelated males should be exceeded more often. From the absence of an influence of relatedness on the frequency of mortal combat, as found by West *et al.* (2001), it might be concluded that fig wasp males are unable to recognize kin and to treat related competitors less aggressively. However, there is an alternative explanation of the results obtained by West *et al.* (2001) and it is thus still possible that fig wasp males can recognize related and unrelated competitors. West *et al.* (2001) might not have found a correlation between relatedness and fatal fighting in their comparative study

Figure 3. Relationship between number of male fig wasps in a syconium and mean injury score (a score to distinguish between grades of injury where 0 is uninjured and 8 is dead or unable to mate). Shown are average values for 28 species; data are taken from Murray (1989), Zammit & Schwarz (2000) and Bean & Cook (2001).

because the maximum fatal-fighting frequency can be expected to occur with an intermediate relatedness between males (see figure 2). There is some circumstantial evidence of such an effect of relatedness on fighting frequency in the fig wasp *Philotrypes pilosa* (Murray 1987). In this species, injury level was found to peak at an intermediate male density. If foundress number is correlated with male number, it is likely that males in the fig fruits with the highest frequencies of fatal fighting were produced by two or three females. Such a non-linear relationship between relatedness and fighting is difficult to explain with the previously published theory of fatal fighting, but can be expected when males behave differently towards related and unrelated competitors. According to my model, the results presented by West *et al.* (2001) are compatible with either no effect or a non-linear effect of relatedness on the frequency of fatal fighting. The presently available data therefore do not allow the determination of whether or not relatedness has an effect on the frequency of fatal fighting in fig wasps. Thus, future investigators examining this question should not blindly use average values to represent a given species. Only detailed intraspecific studies using direct observations in combination with a genetic method to determine relatedness, as well as experiments in which foundress numbers are varied, will allow us to decide whether kin recognition is involved in fatal fighting (see Cook *et al.* 1999).

Besides variations in relatedness and female number, two other factors are probably important in determining the frequency of fatal fighting: male number and variance in male fighting strength could have decisive influences on the theoretically expected frequency of fatal fighting. In accordance with these expectations, male number and injury levels are negatively correlated with each other (Murray 1989). Comparison of injury levels and average number of males present in a syconium for all fig wasp species where this information is known shows that fatal fighting is common only in species with relatively few competing males (figure 3; data from Murray 1989; Zam-

mit & Schwarz 2000; Bean & Cook 2001). The present results thus corroborate and explain one finding of the comparative study by West *et al.* (2001)—that there is no significant linear influence of relatedness on fatal fighting—but point to the influence of two other factors besides female density—male number and male variance in fighting strength. Although the effect of male size was not significant in the comparative analysis across species (West *et al.* 2001), a trend ($p < 0.1$) could be observed (S. West, personal communication), and it cannot be excluded that this factor is important in determining the occurrence of lethal combat in fig wasps.

In conclusion, the present model shows that no effect of relatedness on fatal-fighting frequency can be expected if males are unable to recognize kin. One possible explanation that can be inferred from the present model and from the observed absence of a negative relationship between relatedness and fatal fighting, is that male fig wasps are unable to distinguish between related and unrelated competitors. However, the alternative possibility of kin recognition and a maximum frequency of fatal fighting between fig wasp males of intermediate relatedness cannot be excluded. In addition, the present model provides a new explanation for the observed negative correlation between the extent of fatal fighting and female number. Since the potential gain from fatal fighting decreases with increasing numbers of competitors, I suggest that the observed correlation is in part caused by variation in male number and that the observed correlation between female number and the frequency of fatal fighting is partly caused by co-correlation between male and female numbers.

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