

# Live and let die: why fighter males of the ant *Cardiocondyla* kill each other but tolerate their winged rivals

Carl Anderson, Sylvia Cremer, and Jürgen Heinze

LS Biologie I, Universität Regensburg, Universitätsstrasse 31, D-93040 Regensburg, Germany

Unlike most social insects, many *Cardiocondyla* ant species have two male morphs: wingless (ergatoid) males, who remain in the natal nest, and winged males who disperse but, strangely, before leaving may also mate within the nest. Whereas ergatoid males are highly intolerant of each other and fight among themselves, they tend to tolerate their winged counterparts. This is despite the fact that these winged males, like ergatoid males, represent mating competition. Why should ergatoid males tolerate their winged rivals? We developed a mathematical model to address this question. Our model focuses on a number of factors likely to influence whether ergatoid males are tolerant of winged males: ergatoid male–winged male relatedness, number of virgin queens, number of winged males, and the number of ejaculates a winged male has (winged males are sperm limited, whereas ergatoid males have lifelong spermatogenesis). Surprisingly, we found that increasing the number of virgin queens favors a kill strategy, whereas an increase in the other factors favors a let-live strategy; these predictions appear true for *C. obscurior* and for a number of other *Cardiocondyla* species. Two further aspects, unequal insemination success and multiple mating in queens, were also incorporated into the model and predictions made about their effects on toleration of winged males. The model is applicable more generally in species that have dimorphic males, such as some other ants, bees, and fig wasps. *Key words*: alternative dispersal tactics, ants, *Cardiocondyla*, ergatoid males, fighting, male dimorphism, toleration. [*Behav Ecol* 14:54–62 (2003)]

In insect societies, and particularly in ants, males are by far the neglected sex. One reason for the relatively little attention paid to them is that males often have limited life spans, in many cases simply acting as “flying sperm packets” that die immediately after insemination during nuptial flight (Hölldobler and Bartz, 1985; Hölldobler and Wilson, 1990). This common tactic gives males little chance to mate multiply. However, a few ant species exhibit a radically different life history in which mating occurs inside the nest (“intranidally”) before dispersal. In a number of species, such a trait is correlated with wing reduction in males—either a reduction in size or complete loss (e.g., Loiselle and Francoeur, 1988). In some species, only these wing-reduced males are present, but in others both male morphs coexist.

The ant genus *Cardiocondyla* includes a number of species with such a male dimorphism (*C. emeryi*, *minutior*, and *obscurior*; Kugler, 1983; Heinze et al., 1998; Heinze, 1999). In other *Cardiocondyla* species only wingless “ergatoid” males remain (*C. batesii*, *elegans*, *mauritanica*, and *uljanini*; Marikovski and Yakushkin, 1974; Kugler, 1983; Heinze, 1999). Dimorphic males differ in many aspects of morphology, physiology (spermatogenesis, see below), and behavior. Ergatoid males typically do not leave their maternal nest but engage in intranidal mating with eclosing virgin queens. These females thus become a defendable resource such that fighting occurs among locally competing males. Ergatoid males tend to patrol the colonies, especially the brood piles, and in some species they attempt to kill freshly emerged ergatoid males by biting

through the callow’s soft cuticle (*C. emeryi*, *mauritanica*, and *minutior*; Heinze et al., 1993, 1998; Kinomura and Yamauchi, 1987). In other species, males have evolved extraordinary saber-shaped mandibles that are used to fight other adult males. In addition to these mandibles, they release a propaganda substance, a chemical that elicits worker aggression, leading to the death of the attacked male (*C. obscurior* previously described as *wroughtonii*; Kinomura and Yamauchi, 1987; Stuart et al., 1987; Yamauchi and Kawase, 1992). Consequently, such ergatoid–ergatoid killing means that in many *Cardiocondyla* species, only a single or a few ergatoid males are found per nest (see Table 1).

In striking contrast, winged males behave peacefully and leave the nest a few days or weeks after emergence to mate outside the colony with non–nest-mate queens (Kinomura and Yamauchi, 1987). Hence, winged males behave like typical ant males except that they also perform intranidal matings before emigration, and they have the capacity to mate and inseminate multiply (Kinomura and Yamauchi, 1987; Cremer et al., 2002). Ergatoid males, even though highly aggressive toward other ergatoid males, usually tolerate their winged counterparts (Kinomura and Yamauchi, 1987; Cremer, personal observation). This is despite the fact that winged males represent a competitive threat for intranidal matings (Kinomura and Yamauchi, 1987; Stuart, 1990; Heinze et al., 1998; Cremer, personal observation). The intriguing question arises: why should ergatoid males tolerate their winged rivals?

In this study, we developed a mathematical model to help understand which factors may favor a peaceful “let-live” strategy rather than an aggressive “kill” strategy on the part of ergatoid males toward winged males. Unlike an earlier and related (and in light of recent research, flawed; see Discussion) model (Tsuji et al., 1994), our model includes the number and quality of mating partners (i.e., emerging virgin queens), both in the maternal colony and extranidally, and ergatoid male–winged male relatedness. Hence, this is an inclusive fitness model, developed from the perspective of

Address correspondence to C. Anderson, who is now at the School of Industrial and Systems Engineering, Georgia Institute of Technology, Atlanta, GA 30332-0205, USA. E-mail: carl@isye.gatech.edu. Authorship is in alphabetical order.

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**Table 1**  
**Comparison of seven *Cardiocondyla* ant species in terms of colony life-history traits**

Species	Queen number	Male morphism	No. of ergatoid males	No. of gynes <sup>a</sup>	No. of workers <sup>b</sup>	References
<i>C. elegans</i>	1	EM only	1–17 (mean of 3)	High	High	Eberhardt A, unpubl. data; Mercier JL, unpubl. data
<i>C. ulianini</i>	1	EM only	2–12	High	High	Marikovski and Yakushkin, 1974
<i>C. batesii</i>	1	EM only	1–2	Medium–High	?	Schrempf A, unpubl. data
<i>C. mauritanica</i> <sup>c</sup>	<10	EM only	1–20 (mean of 3)	Medium	Medium	Creighton and Snelling, 1974; Heinze et al. 1993; Yamauchi and Kinomura, 1993
<i>C. obscurior</i> <sup>d</sup>	<10	EM + WM	1 only	Low–Medium	Low	Heinze, 1999; Kinomura and Yamauchi, 1987; Cremer, personal obs.
<i>C. emeryi</i>	<5	EM + WM	Usually 1 <sup>e</sup>	Low	Low	Creighton and Snelling, 1974; Heinze et al., 1998
<i>C. minutior</i>	<5	EM + WM	Usually 1 <sup>e</sup>	Low	Low	Heinze et al., 1998; Heinze, 1999; Phillips, 1934

Nomenclature follows that of B. Seifert's (in preparation) recent revision of the genus (EM = ergatoid males, WM = winged males).

<sup>a</sup> Low: <10; medium: 10–50; high: >50.

<sup>b</sup> Low: <50; medium: 50–150; high: >150.

<sup>c</sup> Previously *C. nuda* (Heinze et al., 1993).

<sup>d</sup> Previously referred to as *C. wroughtonii* (Heinze, 1999; Kinomura and Yamauchi, 1987).

<sup>e</sup> Mean of 1, but up to 3 in large colonies.

an ergatoid male, which incorporates three components: its own direct fitness from mating intranidally and indirect fitness benefits from the winged males' matings both inside and outside the nest. Our main motivation for developing the model was the question of why ergatoid males tolerate winged rivals. However, we also anticipated that the model would shed some light on factors leading to high aggression among ergatoid males. Similarly, we considered life-history parameters (e.g., number of reproducing queens, number of male and female sexuals produced, and colony size) that might have led to the complete loss of the winged male morph in some species, which is supposedly the ancestral state (Roff, 1986, for insects in general). Our model is mainly based on ideas developed for *C. obscurior* but can be generalized for other *Cardiocondyla* species, or indeed adapted to other species with dimorphic males (e.g., in *Hypoponera* ants, halictine and andrenid bees, and fig wasps; Hamilton, 1979; Kukuk and Schwarz, 1988; Yamauchi et al., 1996; Danforth, 1991; Fellowes et al., 1999; see also Appendix C).

## The models

### General assumptions and terminology

Notation is summarized in Appendix A. Developing the model primarily for *C. obscurior*, we assume that a colony contains a single ergatoid male (hereafter EM) and one or more,  $W$ , winged males (hereafter WMs; see Table 1). When there is a single WM (i.e.,  $W = 1$ ),  $r$  represents the relatedness between the EM and WM. We consider four situations: that the two males are brothers ( $r = 0.5$ ), cousins ( $r = 0.375$ ), unrelated ( $r = 0$ ), or clones ( $r = 1$ ). With multiple WMs ( $W > 1$ ), the average relatedness between each WM and the EM is denoted  $\langle r \rangle$ . The EM is not sperm limited while each WM has  $S$  ejaculates (justified in Discussion). Both male morphs use one ejaculate per mating.

A colony contains  $Q$  virgin queens that eclose sequentially. As each virgin queen ecloses, all WMs with at least one remaining ejaculate compete with the EM for the mating. Initially, we assume that both male morphs are equally competitive at mating with a queen—that is, the probability that the EM will obtain the mating when competing with a single WM is 50%—but we later relax this assumption. Also, we assume that the queen's mating frequency ( $M$ ) is 1, that is,

queens are only single mated, but this assumption too is later relaxed.

We assume that the EM adopts one of two strategies: to kill all of its WM rivals or to “let live,” that is, to tolerate the presence of all WMs in the nest. We assume that there are no costs to killing (in terms of time, risk of injury, and so on; however, this assumption is relaxed in Appendix C) and that the EM is always successful. All models are developed in terms of fitness benefits to the EM under these two strategies.  $F$  is some fitness benefit from an intranidal mating. If the EM gains the mating, he receives a fitness benefit of  $F$ , but only  $rF$  or  $\langle r \rangle F$  if it is the WM who mates with the virgin queen.  $B$  represents the overall fitness benefit from an extranidal mating, and as only WMs can leave the nest, such a mating contributes  $rB$  or  $\langle r \rangle B$  to the EM's fitness.  $B$  can be considered to contain several components: the probability that WMs can find extranidal females and mate successfully, the proportion of their remaining ejaculates they actually use before dying, WM mortality rate, as well as the quality of the mating (including the benefit of outbreeding) and the female per se. Last, we assume that WMs can unerringly detect whether potential intranidal matings are available and that EMs do not show any behavior to drive WMs from the nest (e.g., Tsuji et al., 1994).

We should stress that although our model considers two strategies, kill and let live, it is not in fact a game theoretic model in which we demonstrate that a particular strategy is evolutionarily stable. Instead, we view the variables (e.g.,  $Q$ ) as reflecting different species and not the evolution of a trait within a species. For instance, when we consider high  $Q$  versus low  $Q$ , we are in effect considering whether in a species with many virgin queens a tolerant strategy is more or less favored than in a species with few virgin queens. Our model is a strict inclusive fitness model which incorporates relatedness multiplied by the benefits, some combination of  $F$ ,  $B$ ,  $Q$ , and  $S$  (with no assumed costs) of one strategy versus the other. As such, it is Hamiltonian (1963, 1964a,b) in flavor. Moreover, all of the models below are formulated as  $F/B > f(r \text{ or } \langle r \rangle, M, Q, S, W)$ , as this most easily enables us to compare results across models, but they can easily be rearranged to a more Hamiltonian form in which the net benefit of kill appears on the left of the inequality and the net benefit of let live, weighted by relatedness, appears on the right. These forms appear in Appendix C.

### Single winged male and single virgin queen

( $Q = 1; M = 1; W = 1; S \geq 1$ )

We start with the simplest scenario: one virgin queen ( $Q = 1$ ) who will singly mate ( $M = 1$ ) and a single WM ( $W = 1$ ) with multiple ejaculates ( $S \geq 1$ ). This scenario illustrates the general process and logic by which these models are formulated and evaluated.

*Let live.* Under a let-live strategy, both males compete equally for the mating. If the EM mates with the queen, its fitness is  $F + rBS$ . The first term describes the direct fitness benefit of its own mating, and the second term describes the indirect fitness it obtains from the WM who must mate extranidally. If the WM mates with the queen, however, the EM's fitness is  $rF + rB(S - 1)$ . Here both terms represent indirect fitness to the EM, the first from the WM's intranidal mating ( $rF$ ) and the second from  $S - 1$  extranidal matings. Taking into account the relative probabilities of each outcome (in this case, 50%), EM's expected inclusive fitness is  $\frac{1}{2}[F + rBS] + \frac{1}{2}[rF + rB(S - 1)]$ .

*Kill.* Under a kill strategy, the EM's fitness is simply  $F$ , as it gains the single intranidal mating but no indirect fitness.

*Conditions favoring kill.* Kill is a better strategy than let live if and only if  $F > \frac{1}{2}[F + rBS] + \frac{1}{2}[rF + rB(S - 1)]$ , which can be rearranged to give

$$\frac{F}{B} > \frac{r}{1-r}(2S-1). \quad (1)$$

$F/B$  represents the relative fitness benefit of an intranidal ( $F$ ) versus an extranidal mating ( $B$ ). Thus, for instance, when  $B$  is low,  $F/B$  is high, and the inequality above is more likely to hold true: killing is favored.

Figure 1 shows the relationships between critical  $F/B$  values (the value above which killing is favored) and  $S$  for four values of  $r$ . When males are unrelated ( $r = 0$ ) killing is always favored (i.e., Equation 1 requires  $F/B > 0$ , which is always true). With clones ( $r = 1$ ), however, let live is always favored (Equation 1 gives  $F/B > \infty$ , which is never true). For intermediate relatedness, brothers and cousins, the critical  $F/B$  value depends linearly on  $S$  (Figure 1).

*Why is there only a single ergatoid male?* The situation above helps illustrate why killing among EMs is observed so that only a single EM remains. Imagine that the WM above is in fact another EM. There are two simple ways to view this: (1) an EM can only gain its own direct fitness ( $1 \times F$ ) or an intranidal indirect fitness ( $r \times F$ ), and, except for clones ( $r = 1$ ), the latter is always lower, thus favoring kill; (2) as the male is wingless he cannot leave the nest, and thus  $B = 0$ . Substituting this value into the models, specifically the  $F/B$  component, makes the left-hand sides of the inequalities infinite and thus always true, except, again, with clones.

### Single virgin queen and multiple winged males

( $Q = 1; M = 1; W \geq 1; S \geq 1$ )

Suppose that there is a single virgin queen ( $Q = 1; M = 1$ ) and one or more WMs ( $W \geq 1$ ) each with one or more ejaculates ( $S \geq 1$ ). Table 2 gives the possible outcomes and associated probabilities. Kill is favored if and only if:

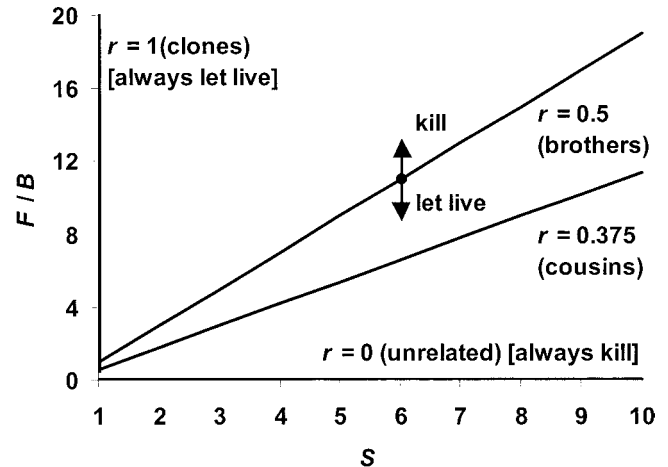
$$\frac{F}{B} > \frac{\langle r \rangle}{1 - \langle r \rangle}(S + WS - 1) \quad (2)$$

where  $W \geq 1, S \geq 1$ . Thus, let-live strategy is favored with increasing  $S, W$ , and  $\langle r \rangle$ .

### General model: multiple males and multiple virgin queens

( $Q \geq 1; M = 1; W \geq 1; S \geq 1$ )

Suppose that there are one or more virgin queens ( $Q \geq 1$ ) with mating frequency 1 ( $M = 1$ ) and one or more WMs ( $W \geq 1$ ) each with one or more ejaculates ( $S \geq 1$ ). Assume too that



**Figure 1**

The relationship between  $F/B$  and the number of ejaculates ( $S$ ) for four values of relatedness ( $r = 0, 0.375, 0.5, 1$ ) between the ergatoid male and the single winged male ( $Q = 1; M = 1; W = 1$ ). For a particular value of  $S$ , the curves represent the critical  $F/B$  value above which a kill strategy is favored; the critical value of  $F/B = 11$  (black dot) is illustrated for  $S = 6$ . This figure is a graphical interpretation of Equation 1.

each WM could potentially inseminate each of the queens, i.e.,  $S \geq Q$ . (With  $S < Q$ , the mathematics is more complicated because there is the potential for a WM to run out of sperm (essentially equivalent to its death), so that the number of EM's competitors may decrease over time depending on the history of earlier matings.)

*Let live.* Let  $P(Q, x, n)$  represent a binomial probability. That is,

$$P(Q, x, n) = \frac{Q!}{n!(Q-n)!} x^n (1-x)^{Q-n}, \quad (3)$$

where  $n \in \{0, 1, \dots, Q\}$  and  $x$  represents the probability that the EM mates with a queen when competing with all the WMs. In this case,  $x = 1/(W + 1)$ . EM's fitness, given he had  $n$  matings, is

$$nF + \langle r \rangle F(Q - n) + \langle r \rangle B(WS - Q + n)$$

(= direct + indirect intranidal + indirect extranidal, respectively).

$$= n[F(1 - \langle r \rangle) + \langle r \rangle B] + \langle r \rangle [FQ + B(WS - Q)]. \quad (4)$$

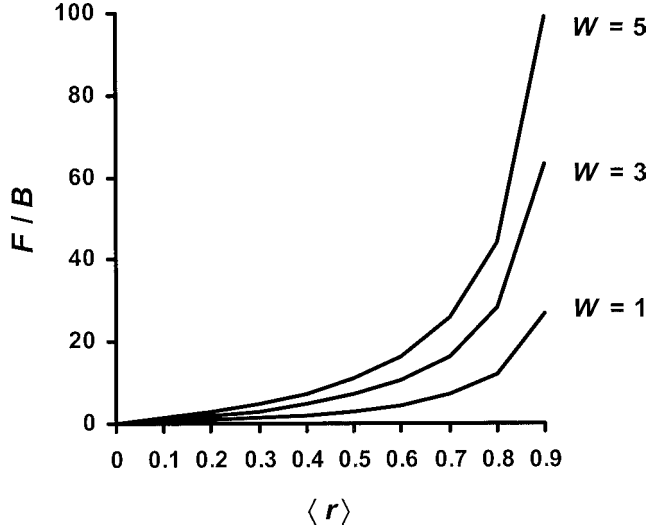
Therefore, EM's expected fitness is Equation 3  $\times$  Equation 4, summed over  $Q$ :

**Table 2**

**Possible outcomes and associated probabilities when a single virgin queen ecloses among multiple winged males ( $Q = 1; M = 1; W \geq 1; S \geq 1$ )**

Strategy	Outcome	Probability	EM's fitness
Let live	EM mates intranidally	$1/(W + 1)$	$F + \langle r \rangle BWS$
	One WM mates intranidally	$W/(W + 1)$	$\langle r \rangle F + \langle r \rangle B(WS - 1)$
Kill	EM mates intranidally	1	F

EM, ergatoid males; WM, winged male.



**Figure 2**  
The effect of ergatoid male–winged male average relatedness,  $\langle r \rangle$ , and number of winged males ( $W$ ) upon critical  $F/B$  values. Higher relatedness and higher number of winged males both favor a let-live strategy. (From the general model, Equation 6, with  $S = 10$  and  $Q = 5$ .)

$$\sum_{n=0}^Q [P(Q, x, n)(n[F(1 - \langle r \rangle) + \langle r \rangle B] + \langle r \rangle[FQ + B(WS - Q)]), \quad (5)$$

which, because Equation 4 is linear with respect to  $n$  and we are summing over a complete probability distribution function, can be simplified to

$$Qx[F(1 - \langle r \rangle) + \langle r \rangle B] + \langle r \rangle[FQ + (WS - Q)]. \quad (6)$$

*Kill.* Under a kill strategy, EM's fitness equals  $QF$ .

*Conditions favoring kill.* For general  $x$ , kill is favored if and only if:

$$\frac{F}{B} > \frac{\langle r \rangle}{1 - \langle r \rangle} \left[ \frac{WS}{Q(1 - x)} - 1 \right], \quad (7)$$

which in a more Hamiltonian form (Appendix C) is  $FQ(1 - x) > \langle r \rangle[FQ(1 - x) + B[WS - Q(1 - x)]]$ , and for this particular value of  $x$  becomes:

$$\frac{F}{B} > \frac{\langle r \rangle}{1 - \langle r \rangle} \left[ \frac{S(W + 1)}{Q} - 1 \right]. \quad (8)$$

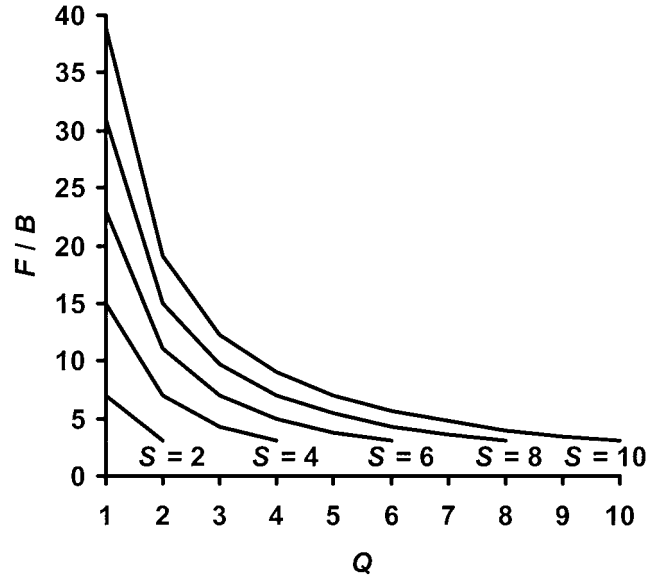
By appropriate substitution for  $W$  and  $Q$ , it can easily be shown that Equation 7 encompasses both Equations 1 and 2.

#### Results from the general model

*Effect of relatedness,  $\langle r \rangle$ , and number of winged males,  $W$ .* Figure 2 shows the relationship between the critical  $F/B$  values for increasing EM–WM average relatedness,  $\langle r \rangle$ , and three values of  $W$ . Higher relatedness increases  $F/B$  nonlinearly, thus favoring let live. An increasing number of WMs also increases critical  $F/B$  values, thus also favoring let live.

*Effect of the number of WM ejaculates,  $S$ .* Figure 3 plots the critical  $F/B$  values against increasing virgin queen number ( $Q$ ) for several values of  $S$  (but only where  $S \geq Q$ ). It is clear that increasing  $Q$  decreases the critical  $F/B$  values, thus favoring a kill strategy. Conversely, increasing number of WM ejaculates,  $S$ , increases the critical  $F/B$  values, thus favoring let live.

*Effect of virgin queen number,  $Q$ .* Equation 8 and Figure 3 show



**Figure 3**  
The effect of the number of virgin queens,  $Q$ , and number of winged male ejaculates,  $S$ , on the critical  $F/B$  values. Higher queen number favors a killing strategy, whereas higher  $S$  favors let live. (From the general model, Equation 6, with  $\langle r \rangle = 0.5$  and  $W = 3$ . Curves for a particular value of  $S$  are only valid, and plotted, where  $S \geq Q$ .)

that the more virgin queens there are, the more a kill strategy is favored. At first sight this might seem counterintuitive, as higher  $Q$  would imply reduced competition for the EM (it is sure to obtain a mating), but, in fact, the reverse is true. This can easily be shown by considering the case of a single WM with a single ejaculate ( $W = 1$ ;  $S = 1$ ) and one or more queens ( $Q \geq 1$ ;  $M = 1$ ). The probability that the WM mates intranidally is  $1 - \frac{1}{2}Q$ , therefore, higher  $Q$  means a greater likelihood that the EM will miss out on an intranidal mating. The outcomes under the two strategies are shown in Table 3.

Thus, higher  $Q$  weights EM's fitness toward  $(Q - 1)F + rF$ , which is lower than  $QF + rB$  as  $r < 1$ ,  $F > B$ , and the number of matings is lower ( $Q$  intranidal matings only vs.  $Q$  intranidal matings + 1 extranidal). For these conditions, kill is favored if and only if:

$$\frac{F}{B} > \frac{r}{(1 - r)(2Q - 1)}, \quad (9)$$

where  $Q \geq 1$ , and it is clear that higher  $Q$  decreases the value of the right-hand side of the inequality.

#### Other biological factors

At least two others factors (but for which relatively little is known about *Cardiocondyla* biology) likely affect whether kill or let live is favored: unequal mating competitiveness between the two male morphs and multiple mating by young queens.

#### Unequal mating competitiveness

Let  $p$  represent the probability that the EM will gain the mating and inseminate the female when competing with a single WM. Thus,  $p : 1 - p$  represents the relative mating competitiveness between the two male morphs. (In the previous models we have implicitly assumed that  $p = \frac{1}{2}$ .)

With  $W$  winged males, each with relative mating ability  $(1 - p)$ , and a single EM with relative mating ability,  $p$ , all competing for a particular queen, the probability that the

Table 3

Possible outcomes and associated probabilities when one or more queens ( $Q \geq 1$ ;  $M = 1$ ) eclose among a single ergatoid male and single winged male who has a single ejaculate ( $W = 1$ ;  $S = 1$ )

Strategy	Outcome	Probability	EM's fitness
Let live	EM mates with all virgin queens	$\frac{1}{2}Q$	$QF + rB$
Kill	WM mates intranidally	$1 - \frac{1}{2}Q$	$(Q - 1)F + rF$
	EM mates intranidally	1	$QF$

EM, ergatoid male; WM, winged male.

EM obtains the mating is the weighted average  $p/[W(1-p) + p]$ . EM's fitness for  $n$  matings is as for Equation 4 and so substituting  $x = p/[W(1-p) + p]$  into Equation 7 gives:

$$\frac{F}{B} > \frac{\langle r \rangle}{1 - \langle r \rangle} \left[ \frac{S}{Q} \left( W + \frac{p}{1-p} \right) - 1 \right], \quad (10)$$

where  $0 < p < 1$ .

These modified probabilities are such that the effect of  $p$  and  $W$  are antagonistic in terms of whether EM's fitness comes from direct fitness (EM garners the matings) or indirect fitness (whether intra- or extranidal). Higher  $p$  clearly favors the EM, as he both increases his proportion of direct fitness and also forces WMs to mate externally, thus increasing the total number of matings and hence absolute fitness. While increasing  $W$  decreases the proportion of EM's fitness that is direct, the absolute value of fitness is proportional to  $W$ . Thus, both higher  $p$  and higher  $W$  should favor a let-live strategy, relationships that are borne out in Equation 10 and Figure 4.

#### Multiple mating of young queens

We now consider the case of multiple mating ( $M > 1$ ) in females (gynes). As in the general model above, the simplest case concerns the situation in which a single WM could potentially inseminate each queen, here  $S \geq MQ$ . When  $S \geq MQ$ , then this matches the general model (Equation 8) in which  $Q$  can be replaced by  $MQ$ . That is, kill is favored if and only if:

$$\frac{F}{B} > \frac{\langle r \rangle}{1 - \langle r \rangle} \left[ \frac{S(W+1)}{MQ} - 1 \right], \quad (11)$$

where  $S \geq MQ$ ,  $W \geq 1$ . Thus, for  $S \geq MQ$ , at least, the effect of multiple mating is qualitatively the same as increasing virgin queen number (see Figure 3): higher  $M$  means killing is more favored. Note that Equation 11 does not specify how the  $n$  matings are divided among the  $MQ$  possible matings but simply gives the probability distribution function of  $n$ .

## DISCUSSION

We have developed a model to predict conditions under which *Cardiocondyla obscurior* ergatoid males should kill or tolerate their winged counterparts who are competitors for matings inside the nest. In this respect, this species differs from other male dimorphisms in andrenid (Danforth, 1991) and halictine bees (Kukuk and Schwarz, 1988), *Technomyrmex* ants (Yamauchi et al., 1996), and most fig wasps (Cook et al., 1997; Fellowes et al., 1999; Hamilton, 1979; but see West and Herre, 1998) in which we find a clear separation of intranidal mating performed exclusively by wingless males and extranidal matings performed exclusively by WMs. Whereas in these species aggression between the two male morphs is neither expected nor found, the situation is not so clear in *C. obscurior*. Hence, we studied

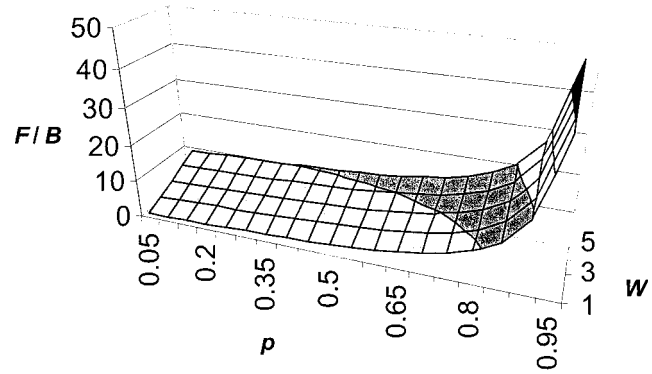


Figure 4

The relationship between critical  $F/B$  values, the number of winged males,  $W$ , and the mating competitiveness of the ergatoid male,  $p$ . Both increasing  $p$  and  $W$  produce larger critical values and thus favor let live. (From Equation 11 with  $r = 0.5$  and  $Q = 5$ .)

several factors that might be important to predict the level of aggression of EMs toward WMs in *C. obscurior*.

### General model predictions

Our model (Equation 6) predicts that the higher EM-WM relatedness ( $r$  or  $\langle r \rangle$ ), the more a let-live strategy is favored. This is a result of increased indirect fitness, which could arise from intranidal matings where relatedness is high, but principally from extranidal matings which the EMs typically cannot perform (but see below). Consequently, any factors that increase the number and likelihood of successful WM extranidal matings also favor the EM. These factors include, first, greater WM mating success and extranidal queen and mating fitness (both included within  $B$ ; Figures 1–4), which together decrease  $F/B$ ; second, higher WM sperm availability ( $S$ ; Figures 1 and 3); and, third, greater number of WMs ( $W$ ; Figure 2). Some initially counterintuitive predictions are made: that a greater number WMs should favor let live; one might have thought that this would represent increased intranidal competition, but this result makes sense when inclusive fitness is considered. In contrast to other contest models (e.g., Enquist and Leimar, 1990; Murray, 1987, 1989), we predict that a larger number of intranidal virgin queens ( $Q$ ; thus perhaps representing less competition for the EM) favors killing (Figure 3; but see “Aggression among ergatoid males”). This latter situation makes sense when one considers the probability of the EM gaining matings (detailed earlier).

### Life-history traits of *Cardiocondyla* males

Based on laboratory data, we incorporated realistic parameter values for *C. obscurior* into the model ( $S, Q \in \{1, 2, \dots, 10\}$ ;  $W \in \{1, 2, \dots, 5\}$ ;  $r \in \{0, 0.375, 0.5\}$ , Cremer, unpublished data; Figures 1–3) revealing a large number of situations in which killing is favored. However, observations (Yamauchi and Kinomura, 1993; Cremer, personal observation) show that WMs are unlikely to be killed in reality, at least under laboratory conditions. How can this be explained? The models initially assumed equal mating competitiveness among the two male morphs ( $p = \frac{1}{2}$ ), but this probably does not hold true as EMs exhibit behavioral and physiological adaptations that may act in their favor ( $p > \frac{1}{2}$ ). First, *Cardiocondyla* EMs are the only Hymenopteran males known so far that have life-long spermatogenesis. This is in contrast to the WMs, and even EMs of other ant genera, in which spermatogenesis is

completed early in life and who are sperm limited (Heinze, 2000; Heinze and Hölldobler, 1993; Heinze et al., 1993, 1998). Therefore, given that EMs are not sperm limited, it is logical that they copulate for longer (Kinomura and Yamauchi, 1987) and transfer more sperm per ejaculate (Heinze et al., 1998) than WMs. As EMs additionally have a longer life span than WMs (Heinze, 1997; Heinze et al., 1998), we are confident that EMs do indeed have a higher mating competitiveness than the WMs. Incorporating this elevated mating competitiveness into the model ( $p > \frac{1}{2}$  in Equation 10) predicts more tolerant (let live) behavior (Figure 4).

Two factors that favor let live are a small number of virgin gynes in the nest and single rather than multiple mating by those females (Equation 11). Data show that *C. obscurior* queens may copulate multiply (Kinomura and Yamauchi, 1987; Cremer, personal observation), but this is not the same as demonstrating that paternity is multiple: genetic analyses reveal that the two are not necessarily correlated and that copulation frequency often overestimates effective paternity (Boomsma and Ratnieks, 1996). Unfortunately, genetic markers are not currently available for *Cardiocondyla*, and so further work is needed to resolve this issue. If we now consider multiple matings by females outside the nest, the probability (compared to single mating) that WMs will gain some paternity is increased. Let live will be favored because  $B$  will effectively be increased, thus lowering the actual  $F/B$  values obtained (left-hand sides of inequalities), making them more likely to be lower than the critical values (right-hand sides). A confounding factor, though, is that multiple mating may increase the chance that a WM depletes his sperm store before leaving the nest. Thus, the overall effect is far from clear. Two further factors that may favor let live are any ecological conditions, such as habitat structure, that enhance the survival and mating success of WMs, and also any deleterious inbreeding effects within the EM's colony, in short, that increase  $B$ . Finally, implicit in our model is the assumption of perfect recognition on the part of the EM—that is, that he would not kill a virgin queen by mistake.

In fact, recognition does not seem perfect, as EMs have been observed to mount WMs. Recent data suggest (Cremer et al., 2002) that WMs may chemically mimic virgin queens. This would render them undetectable to the EMs and might explain the disparity between observed behavior and the model's predictions. Female mimicry by the less aggressive male morph has been suggested for a mite and for another ant species (mites: *Rhizoglyphus robini*, Radwan et al., 2000; ants: *Hypoponera bondroitii*, Yamauchi et al., 1996). Let live is less costly than killing a virgin queen.

### Loss of winged males

The discussion above covered a suite of factors that may explain why WMs are tolerated in *C. obscurior*. We now expand the focus to explain why in some species of this genus the presumably ancestral WM morph has been lost (but which is found in all other ant genera). To do this, one assumes that a situation favoring a kill strategy would, over generations, lead to the loss of the WM morph. Table 1 lists typical values for a number of relevant colony traits (number of reproducing queens [as an estimate for male–male relatedness], gynes [i.e., virgin queens,  $Q$  in our model], EMs, and workers) and the types of male observed for seven *Cardiocondyla* species. Brood size has been found to be an important predictor of the male morph type in fig wasp colonies (Hamilton, 1979); large broods are more likely to contain offspring of both sexes, whereas smaller broods, for simple statistical reasons, are likely to be single sex. (As colony size positively correlates with brood size in social insects [e.g., Cole, 1984; Schmid-Hempel et al., 1993], we frame

the rest of the discussion in terms of colony size.) Thus, in contrast to large colonies, small colonies are likely to contain no males and thus represent a lucrative patch for an arriving disperser male. Species with small colonies/small brood size have WMs and large colonies have EMs only (Cook et al., 1997; Hamilton, 1979). Whereas Danforth (1991) obtained only weak agreement in *Perdita* bees, Heinze (1999) found a trend in the expected direction in *Cardiocondyla* ants. Our model comes to the same conclusion, but for a different reason: a high number of intranidal matings, high  $Q$ , favors killing; hence we can confirm the results of the studies mentioned above.

For all species in Table 1, there is a positive relationship between the numbers of workers and gynes produced. Moreover, as predicted by our model, all species with a moderately high gyne number (which is associated with monogyny) have EMs only (*C. batesii*: up to 50 per nest; Schrempf A, unpublished data; *C. elegans*: mean of 54 [up to 367],  $n = 45$ , Eberhardt A, Mercier JL, unpublished data; *C. uljanini*: mean of 170,  $n = 5$ , Marikovski and Yakushkin, 1974). *C. mauritanica*'s position in this pattern is not as clear because only EMs are present, and this species has a medium number of gynes and workers. Even though gyne number is not high in this species, the large number of reproducing queens (polygyny) leads to a reduced male–male relatedness, which we found to favor kill, and thus may explain the loss of the WMs. Even though monogyny goes hand-in-hand with high male–male relatedness (favoring let live), the high gyne number, associated with the mode of colony founding (Hölldobler and Wilson, 1977, 1990; Keller, 1993), seems to be the best single predictor of whether EMs only are found in a species. The last three species, *C. obscurior*, *C. emeryi*, and *C. minutior*, are polygynous and have a relatively low colony size, and related to this, a low gyne production (*C. obscurior*: mean of 2–11, from different studies, Table 1; *C. emeryi*: range of 5–10,  $n = 13$ ; *C. minutior*: range of 1–8,  $n \geq 9$  colonies). As predicted, both male morphs co-occur in these species. In summary, monogynous species tend to have a high gyne number and EMs only, whereas polygynous species tend to have a low gyne number and both male morphs. Even though relatedness is lower in polygynous species, the typical low gyne number leads to WM tolerance. Hence, relatedness seems to be much less important than mate availability.

Using evolutionary game theory, Tsuji et al. (1994) proposed a similar model to explain *Cardiocondyla* male dimorphism. However, we disagree with their assumption that EMs have a lower insemination ability than WMs. As we discuss above, we find the opposite is true. Also, Tsuji did not incorporate the very important factors of relatedness among males (our  $r$  and  $\langle r \rangle$ ) and inclusive fitness benefits from WM extranidal matings (our  $B$ ).

### Aggression among ergatoid males

Whereas our model was mainly designed to explain aggression levels of EMs to WMs, it can easily be extended to investigate fighting among multiple EMs by removing the effects of external matings (i.e., by setting  $B = 0$ ), which predicts that killing among EMs is always favored. This is only true because there is no cost of fighting for the attacking male because killing mainly occurs when the victims are young (see earlier). These costs, however, may occur in other species, such as fig wasps (Hamilton, 1979; Murray, 1987, 1989; Greeff and Ferguson, 1999; West et al., 2001), mites (Radwan, 1993; Radwan et al., 2000), *Perdita* bees (Danforth, 1991), and *Hypoponera* ants (Hamilton, 1979; Yamauchi et al., 1996). Therefore, to make our model more applicable generally, we have included such costs in Appendix D.

Hamilton (1979) suggested that relatedness between males

could be used to predict levels of male–male aggression. As EMs cannot leave the nest, the competition among them (or alternatively the “spatial scale of competition”; Frank, 1998; Griffin and West, 2002; West et al., 2001, 2002) is completely local. Recent work, both theoretical and empirical, have shown that under such local competition, relatedness is unimportant, and aggression should occur (Frank, 1998; Griffin and West, 2002; West et al., 2001, 2002), except for the extreme case, clones—as predicted by our model, too (although see Appendix D). Parameters other than relatedness, however, such as the encounter rates between males (Murray, 1987, 1989), opportunities of future matings (Enquist and Leimar, 1990; West et al., 2001), as well as the availability of mating partners in space and time (Greeff and Ferguson, 1999) may alter predictions and favor tolerance among EMs.

Whereas our model predicts that only a single EM should be present in a nest at given time, several EMs may co-occur in species with large colonies (Table 1). There are several nonmutually exclusive explanations. First, single EMs may not be able to inseminate the very large number of gynes (up to 473 in *C. uljanini*; Marikovski and Yakushkin, 1974; up to 367 in *C. elegans*; Eberhardt A, unpublished data). Second, in species in which EMs can only kill their rivals soon after their victims eclose and so still have a soft cuticle, they simply may not be located in time in large colonies. However, when males can kill adult rivals, as in *C. obscurior*, no deviations are found from the predicted single ergatoid male. Third, if EMs leave the nest, as has been observed in *C. elegans* (Mercier JL, personal communication), and mate extranidally, then multiple EMs may be favored.

### Perspectives

Our model, for which data for only seven *Cardiocondyla* species were available to test it, shows that what is primarily needed is basic descriptive information (see Tschinkel, 1991) such as number of WMs ( $W$ ) and gynes ( $Q$ ), which are good predictors of tolerant behavior, rather than more difficult-to-obtain data such as relatedness. Moreover, other more detailed data such as sperm production and ejaculate size ( $S$ ), mating activity (related to  $p$ ), mating success, and behavior of WMs once they have left the nest (related to  $B$ ), and so on, would be valuable. *Cardiocondyla*, with around 70 species (Seifert B, in preparation) presumably contains a larger diversity of life histories than discussed above. This genus is therefore likely a significant and informative parallel to the extensively studied male dimorphism in fig wasps. In both ants and fig wasps, male morphology and the place of mating are not completely linked: as observed in *Cardiocondyla* spp., fig wasp winged males sometimes mate inside the nest (Cook et al., 1997; Fellowes et al., 1999; West and Herre, 1998) and apterous males can leave the colony (Bean and Cook, 2001; Cook et al., 1997; Greeff and Ferguson, 1999). Also, the number of wingless males, and hence fighting, is reduced due to adaptive changes in the offspring sex ratio following the degree of local mate competition in fig wasps (Frank, 1985; Hamilton, 1967, 1979; Herre, 1987; West and Herre, 1998) and *Cardiocondyla* ants (Cremer and Heinze, 2002). Overall, our model does shed some important new light on conditions under which male dimorphisms will be maintained and winged males are tolerated (“live and let die”). However, for those males that are killed, if only the title of one of Ian Fleming’s (1964) other James Bond novels were true: “you only live twice.”

## APPENDIX A

### Notation

Parameter/ variable	Description
$Q$	Number of virgin queens in the nest
$M$	Mating frequency of young queens
$W$	Number of winged males per colony
$E$	Number of ergatoid males (this is normally one, but see Appendix D)
$S$	Number of ejaculates per winged male
$F$	Fitness benefit of an intranidal mating
$B$	Fitness benefit of an extranidal mating
$r$	Relatedness between the ergatoid male and a winged male
$\langle r \rangle$	Average relatedness between the ergatoid male and each winged male (when $W > 1$ )
$p$	The probability that the ergatoid male will mate and inseminate the queen when competing with a single winged male. Thus, $p : 1 - p$ defines the relative mating abilities of the two male morphs.
$x$	The probability that the ergatoid male mates with a particular queen when competing with all the winged males. It is thus a function of $p$ and $W$ .
$c_W$	The cost to the ergatoid male of fighting each winged male (Appendixes C and D)
$c_E$	The cost to an ergatoid male of fighting each ergatoid male (Appendixes C and D)

## APPENDIX B

### Most general model

With the most general model, one or more queens ( $Q \geq 1$ ) each singly or multiply mated ( $M \geq 1$ ), multiple winged males ( $W > 1$ ) with multiple sperm packets ( $S > 1$ ;  $S \geq MQ$ ), and unequal mating abilities ( $0 < p < 1$ ), kill is favored if and only if:

$$\frac{F}{B} > \frac{\langle r \rangle}{1 - \langle r \rangle} \left[ \frac{S}{MQ} \left( W + \frac{p}{1 - p} \right) - 1 \right]. \quad (\text{A1})$$

## APPENDIX C

### Hamiltonian forms

The equations in the main text (Equations 1–11) and Equation A1 can all be arranged to a more Hamiltonian form, meaning that the net benefit of the kill strategy appears on the left-hand side of the inequality, while the net benefit of the let-live strategy, multiplied by relatedness, appears on the right (i.e.,  $b_{\text{kill}} > r \cdot b_{\text{let live}}$ , where  $b$  represents net benefit). By net benefit we mean, for the left-hand side, the EM’s direct fitness gain from a kill strategy minus his expected direct fitness benefit which occurs, by chance, under a let-live strategy. For the right-hand side this net benefit is the EM’s expected indirect fitness payoff from all the WMs expected intranidal and extranidal matings. The equations below are rearrangements of Equations 7–10 and A1 (e.g., Equation A2 is simply a rearrangement of Equation 7).

To make these equations as generally applicable as possible (e.g., for fig wasps), we also include the cost to the EM (i.e., the attacker) of fighting each WM, which we denote  $c_W$ . With the Hamiltonian forms, this is trivial to include as it appears as a single term,  $c_W W$ , on the left-hand side of each inequality.

*General model*

For general  $x$ , Equation 7 can be rearranged to give:

$$FQ(1-x) - c_W W > \langle r \rangle \{ FQ(1-x) + B[WS - Q(1-x)] \}, \quad (\text{A2})$$

(that is, EM's net direct fitness payoff – his fighting costs  $> \langle r \rangle \times$  [intranidal matings obtained by WMs + WM's extranidal matings with his/their remaining ejaculates]), and for  $p = 1/2$  and therefore  $x = 1 / (W + 1)$  it is

$$FQ \frac{W}{W+1} - c_W W > \langle r \rangle \left[ FQ \frac{W}{W+1} + B \left( WS - Q \frac{W}{W+1} \right) \right]. \quad (\text{A3})$$

$Q = 1$  and/or  $W = 1$  can easily be substituted into equation A2 to give the Hamiltonian forms of Equations 1 and 2.

*Equation 9*

$$F \left( 1 - \frac{1}{2Q} \right) - c_W > r \left[ F \left( 1 - \frac{1}{2Q} \right) + \frac{B}{2Q} \right]. \quad (\text{A4})$$

*Unequal mating competitiveness*

$$F(1-p) - c_W > r \{ F(1-p) + B[S - (1-p)] \}. \quad (\text{A5})$$

*Appendix B*

By setting  $x = p/[W(1-p) + p]$  and substituting  $MQ$  for  $Q$  in Equation A2, we obtain

$$Fy - c_W W > \langle r \rangle [Fy + B(WS - y)],$$

where

$$y = MQ \frac{W(1-p)}{W(1-p) + p}. \quad (\text{A6})$$

**APPENDIX D****Fighting among EMs**

How does relatedness affect likelihood of fighting among EMs? As before, let us view inclusive fitness from the point of one of the EMs under kill and let live. Let  $E$  represent the total number of EMs. In the absence of fighting costs to the attacker, we obtain:

$$F > \frac{F}{E} + r \frac{F(E-1)}{E}. \quad (\text{A7})$$

(That is, direct fitness  $>$  direct fitness [by chance] + indirect fitness [by chance], respectively.)

When  $r < 1$ , the inequality always holds true and kill is favored. However, when  $r = 1$  we obtain equal payoff for both strategies, and the slightest chance of some risk of fighting cost will favor let live. Let us now explicitly include the cost of fighting (to the attacking EM) when battling another EM, denoted  $c_E$ . We obtain

$$F - c_E(E-1) > \frac{F}{E} + r \frac{F(E-1)}{E}, \quad (\text{A8})$$

which can be rearranged to give:

$$\frac{F}{E} > \frac{c_E}{1-r}. \quad (\text{A9})$$

There are two implications: first, the greater relatedness, the larger the right-hand side of the inequality, and the more likely let live is tolerated. Second, the larger the number of

EMs to kill and/or the greater the fighting cost, the more let live is favored.

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**REFERENCES**

- Bean D, Cook JM, 2001. Male mating tactics and lethal combat in the nonpollinating fig wasp *Sycoscapter australis*. *Anim Behav* 62: 535–542.
- Boomsma JJ, Ratnieks FLW, 1996. Paternity in eusocial Hymenoptera. *Phil Trans R Soc Lond B* 351:947–975.
- Cole BJ, 1984. Colony efficiency and the reproductive effect in *Leptothorax allardycei* (Mann). *Insect Soc* 31:403–407.
- Cook JM, Compton SG, Herre EA, West SA, 1997. Alternative mating tactics and extreme male dimorphism in fig wasps. *Proc R Soc Lond B* 264:747–754.
- Creighton WS, Snelling RR, 1974. Notes of the behavior of three species of *Cardiocondyla* in the United States (Hymenoptera: Formicidae). *J NY Entomol Soc* 82:82–92.
- Cremer S, Heinze J, 2002. Adaptive production of fighter males: queens of the ant *Cardiocondyla* adjust the sex ratio under local mate competition. *Proc R Soc Lond B* 269:417–422.
- Cremer S, Sledge MF, Heinze J, 2002. Male ants disguised by the queen's bouquet. *Nature* 419:897.
- Danforth BN, 1991. The morphology and behavior of dimorphic males in *Perdita portalis* (Hymenoptera: Andrenidae). *Behav Ecol Sociobiol* 29:235–247.
- Enquist M, Leimar O, 1990. The evolution of fatal fighting. *Anim Behav* 39:1–9.
- Fellowes MDE, Compton SG, Cook JM, 1999. Sex allocation and local mate competition in Old World non-pollinating fig wasps. *Behav Ecol Sociobiol* 46:95–102.
- Fleming I, 1964. *You only live twice*. London: Johnathan Cape.
- Frank SA, 1985. Hierarchical selection theory and sex ratios. II. On applying the theory, and a test with fig wasps. *Evolution* 39:949–961.
- Frank SA, 1998. *Foundations of social evolution*. Princeton, New Jersey: Princeton University Press.
- Greeff JM, Ferguson WH, 1999. Mating ecology of the nonpollinating fig wasp of *Ficus ingens*. *Anim Behav* 57:215–222.
- Griffin AS, West SA, 2002. Kin selection: fact and fiction. *Trends Ecol Evol* 17:15–21.
- Hamilton WD, 1963. The evolution of altruistic behavior. *Am Nat* 97:353–356.
- Hamilton WD, 1964a. The genetical evolution of social behaviour, I. *J Theor Biol* 7:1–16.
- Hamilton WD, 1964b. The genetical evolution of social behaviour, II. *J Theor Biol* 7:17–52.
- Hamilton WD, 1967. Extraordinary sex ratios. *Science* 156:477–488.
- Hamilton WD, 1979. Wingless and fighting males in fig wasps and other insects. In: *Sexual selection and reproductive competition in insects* (Blum MS, Blum NA, eds). New York: Academic Press; 167–200.
- Heinze J, 1997. Male reproductive strategies in ants. In: *Proceedings of the international colloquia on social insects* (Kipyatkov VE, ed), Russian Language Section of the IUSSI Socium, St. Petersburg 1997, vols. 3–4. St. Petersburg: Socium; 179–187.
- Heinze J, 1999. Male polymorphism in the ant species *Cardiocondyla minutior* (Hymenoptera: Formicidae). *Entomol Gen* 23:251–258.
- Heinze J, 2000. Testes degeneration and limited sperm supply in ant males with intranidal mating. *Mitt Dtsch Ges Angew Entomol* 12:207–210.
- Heinze J, Hölldobler B, 1993. Fighting for a harem of queens: physiology of reproduction in *Cardiocondyla* male ants. *Proc Natl Acad Sci USA* 90:8412–8414.
- Heinze J, Hölldobler B, Yamauchi K, 1998. Male competition in *Cardiocondyla* ants. *Behav Ecol Sociobiol* 42:239–246.
- Heinze J, Kühnholz S, Schilder K, Hölldobler B, 1993. Behavior of ergatoid males in the ant, *Cardiocondyla nuda*. *Insect Soc* 40:273–282.

- Herre EA, 1987. Optimality, plasticity and selective regime in fig wasp sex ratios. *Nature* 329:627–629.
- Hölldobler B, Bartz SH, 1985. Sociobiology of reproduction in ants. In: *Experimental behavioral ecology and sociobiology* (Hölldobler B, Lindauer M, eds). New York: Academic Press; 167–220.
- Hölldobler B, Wilson EO, 1977. The number of queens: an important trait in ant evolution. *Naturwissenschaften* 64:8–15.
- Hölldobler B, Wilson EO, 1990. *The ants*. Cambridge: Harvard University Press.
- Keller L, 1993. The assessment of reproductive queens in ants and other social insects. *Oikos* 67:177–180.
- Kinomura K, Yamauchi K, 1987. Fighting and mating behaviors of dimorphic males in the ant *Cardiocondyla wroughtonii*. *J Ethol* 5:75–81.
- Kugler J, 1983. The males of *Cardiocondyla emery* (Hymenoptera: Formicidae) with the description of the winged male of *Cardiocondyla wroughtoni* (Forel). *Isr J Entomol* 17:1–21.
- Kukuk PF, Schwarz M, 1988. Macrocephalic male bees as functional reproductives and probable guards. *Pan-Pac Entomol* 64:131–137.
- Loiselle R, Francoeur A, 1988. Régression du dimorphisme sexual dans le genre *Formicoxenus* et polymorphisme comparé des sexes dans la famille des Formicidae (Hymenoptera). *Nat Can (Rev Ecol Syst)* 115:367–378.
- Marikovski PI, Yakushkin VT, 1974. Muravej *Cardiocondyla uljanini* Em., 1889 i sistematičeskoe položenie “paraziticheskogo murav’ya Xenometra.” *Izv Kaz Ssr Ser Biol* 3:57–62.
- Murray MG, 1987. The closed environment of the fig receptacle and its influence on male conflict in the Old World fig wasp, *Philotrypesis pilosa*. *Anim Behav* 35:488–506.
- Murray MG, 1989. Environmental constraints on fighting in flightless male fig wasps. *Anim Behav* 38:186–193.
- Phillips JS, 1934. The biology and distribution of ants in Hawaiian pineapple fields. *Bull Exp Sta Pineapple Prod Ass Univ Hawaii* 15:1–57.
- Radwan J, 1993. The adaptive significance of male polymorphism in the acarid mite *Caloglyphus berlesii*. *Behav Ecol Sociobiol* 33:201–208.
- Radwan J, Czyn M, Konior M, Kolodziejczyk M, 2000. Aggressiveness in two male morphs of the bulb mite *Rhizoglyphus robini*. *Ethology* 106:53–62.
- Roff DA, 1986. The evolution of wing dimorphism in insects. *Evolution* 40:1009–1020.
- Schmid-Hempel P, Winston ML, Ydenberg RC, 1993. Invitation paper (The C. P. Alexander Fund). The foraging behavior of individual workers in relation to colony state in the social Hymenoptera. *Can Entomol* 126:129–160.
- Stuart RJ, 1990. Experiments on colony foundation on the polygynous ant *Cardiocondyla wroughtoni*. In: *Social insects and the environment* (Veeresh GK, Mallik B, Viraktamath CA, eds). New Delhi: Oxford; 242–242.
- Stuart RJ, Francoeur A, Loiselle R, 1987. Lethal fighting among dimorphic males of the ant, *Cardiocondyla wroughtonii*. *Naturwissenschaften* 74:548–549.
- Tschinkel WR, 1991. Insect sociometry, a field in search of data. *Insect Soc* 38:77–82.
- Tsuji N, Yamauchi K, Yamamura N, 1994. A mathematical model for wing dimorphism. *J Ethol* 12:19–24.
- West SA, Herre EA, 1998. Partial local mate competition and the sex ratio: a study on non-pollinating fig wasps. *J Evol Biol* 11:531–548.
- West SA, Murray MG, Machado CA, Griffin AS, Herre EA, 2001. Testing Hamilton’s rule with competition between relatives. *Nature* 409:510–513.
- West SA, Pen I, Griffin AS, 2002. Cooperation and competition between relatives. *Science* 296:72–75.
- Yamauchi K, Furukawa T, Kinomura K, Takamine H, Tsuji K, 1991. Secondary polygyny by inbred wingless sexuals in the dolichoderine ant *Technomyrmex albipes*. *Behav Ecol Sociobiol* 29:313–319.
- Yamauchi K, Kawase N, 1992. Pheromonal manipulation of workers by a fighting male to kill his rival males in the ant *Cardiocondyla wroughtonii*. *Naturwissenschaften* 79:274–276.
- Yamauchi K, Kimura Y, Corbara B, Kinomura K, Tsuji K, 1996. Dimorphic ergatoid males and their reproductive behavior in the ponerine ant *Hypoponera bondroitii*. *Insect Soc* 43:119–130.
- Yamauchi K, Kinomura K, 1993. Lethal fighting and reproductive strategies of dimorphic males in *Cardiocondyla* ants (Hymenoptera: Formicidae). In: *Evolution of insect societies* (Inoue T, Yamane SK, eds). Tokyo: Hakahinsha; 373–402.