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Where does male-to-male "aggression" compromise "cooperation"?

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Abstract

We discussed how the diverse nature of aggression and cooperation is understandable, if we focus our attention on where aggression reaches a compromise with peace and/or cooperation in response to the relatedness between interactors. First we addressed whether the Hamilton's rule is applicable for explaining the variation of male-to-male aggressiveness. Next we showed that the variation in aggression and cooperation known in males of social spider mites (Saito 1995) is explainable from the change of relatedness (i.e. inclusive fitness) and effect of cooperative defense (synergistic effect). Then we learned there is a sufficient condition of cooperation which is determined primarily by two factors; the relatedness and synergistic effect of males. Furthermore, we expect that there is a condition where the aggression between males varies depending upon the relatedness close to the sufficient condition of cooperation.

Problems focused on

Animal cooperation and aggression are two fundamental themes that have attracted numerous sociobiologists so far (Wilson 1975; Alcock 1979; Maynard Smith 1982a; Trivers 1985; Krebs and Davis 1987; Dugatkin 1997). However, both have been treated as separate phenomena to be focused on from the view of sociobiology. For example, Wilson (1975) discussed "cooperative breeding" in chapter 5 and "aggression" in the chapter 11 of his seminal book "Sociobiology". Dugatkin (1997) 's review of animal cooperation also discussed these phenomena separately, even though the game theory reasoning about cooperation with kin-ship (Hines and Maynard Smith 1979; Grafen 1979) involves a bud of new ideas to treat these phenomena inclusively.

However, several doubts remain over how the increase of inclusive fitness through cooperation between relatives (kin selection) influences individual fitness through resource competition between them (individual selection), and where (and when) these two extremes compromise in group living animals (Maynard Smith 1982b; Queller 1985; West et al. 2001; Glron et al. 2004)? Such questions may be related to a tendency to start any focus on the evolution of aggression or cooperation "from neutral to highly aggressive behaviors" or "from neutral to highly cooperative ones" in group living animals, and not from aggression to cooperation. Another related problem is that interactions between individuals in the context of social evolution have been considered *a priori* to be phenomena in "group forming" animals, even though most animals are in a continuum from solitary to group living, and there are few animals that live "solitary" throughout their life-times (Krause and Ruxton 2002).

We feel that such fragmentary views have sometimes rendered the rule(s) underlying aggression and cooperation in animals indistinct. Hereafter, whenever possible, we consider aggression and cooperation to be a continuous trait in group living animals, and solitary and group living (≥ 2) to be distinct traits in order to make the discussion clearer. We then attempt to discuss how aggression and cooperation in animals are understandable from relatedness, if we focus our attention on where aggression reaches a compromise with peace and/or cooperation when different selections simultaneously operate upon the same interacting group.

Hamilton's rule and fig wasp males

In order to specify the point discussed hereafter, we first access a famous and inclusive theory of aggression and/or cooperation. Hamilton (1979) explained the variation in aggression of wingless fig wasp males; "***a difference in mean relatedness between rivals*** accounts for the different male behaviours." Although he did not say that it is the sole factor for the difference, the above statement is sometimes believed to correspond to Hamilton's rule of altruism, i.e. $rB-C > 0$1, where r is Wright's coefficient of relatedness to the recipient, B (≥ 0 *per se* the primary definition) is the benefit associated with the trait the gene codes for and C (≥ 0) is the donor's cost which accrues from the decrease of mating opportunity (Dugatkin, 1997), to explain the fig wasp male case (Trivers 1985; Frank 1985; West et al. 2001). However, Saito (2000) stated that it is simply not rational that high relatedness between males must decrease male pugnacity. If there is even a small difference in mating success between males through aggression, sexual selection will favor more aggressive males. Thus aggression might evolve in males of every population regardless of their relatedness when $r < 1$.

Thus we have to re-examine whether " $rB-C$ " tends to increase more than "0" as r increases in male-to-male competition. The cost ($C \geq 0$) in the inequality 1 accrues from the withdrawal of an actor male (donor) from competition for females and the benefit accrues from the increase in mating chances provided to the other males (recipients) by the actor's withdrawal. Under the assumption that females can be inseminated at all, let's imagine that there are x males and N females in an arena and mating is only performed between them simultaneously (herein a non-reciprocal game is assumed). When a male decreases its aggression level and loses mating chances for d ($=C$), then another male will get a surplus benefit $d/(x-1)$ ($=B$). Inequality 1, $rB-C = r(x-1)\{d/(x-1)\} - d > 0$ is satisfied, only when $d(r-1) > 0$. Because $r > 1$ is always required. In other words, it means that the cost d paid by the actor as the decrease of mating opportunity is "intact", and is evenly divided among the other males, so that there is no way to increase the inclusive fitness of the actor under $r < 1$. Therefore from the beginning, it is very unlikely that inequality 1 can ever be applied to the varying competition in mating of fig wasp males, if the competition is non-reciprocal (once a lifetime, Maynard Smith 1982a). In fact, it was recently demonstrated that the level of fighting between fig wasp males shows no correlation with the estimated relatedness of interacting males, but is negatively correlated with mating opportunities (West et al. 2001). If we still intend to apply it to the fig wasp case, we have to search for plausible conditions where any decrease of an actor's mating opportunity can significantly increase its kin's mating chances (i.e. $B > C$).

Indeed, the above calculation is so simple that most people might consider it a self-evident conclusion. However, as mentioned before, it is undeniable that some people have believed that Hamilton's rule (note that this rule is only a part of his kin selection theory) is applicable to the fig wasp case. Rather, the second paragraph in Hamilton (1979) explaining the variation of male aggression, i.e. "many of the females are his sisters, and he doesn't wish to risk that

some sisters remain unmated" may involve truth, if there are excess females per male in a fig and competition between males increases unfertilized females. This means that there is no time for males to compete, because males are so busy. We think that this explanation corresponds to the result obtained by West et al. (2001).

On the other hand, the case of polyembryonic encyrtids appears contradictory (Gron et al. 2004). In this group, there is variation correlated with r in soldiers' aggressiveness between lineages. We believe that the difference between this case and the wingless fig wasp case is in the quantity of games. Although the game in wingless fig wasp males is only taken place for getting mates, the soldiers of polyembryonic wasps have roles other than competition, such as defending resources against other species of parasitoids, so that they are considered to confront another selection pressure (this case is analogous to the case of spider mite males mentioned hereafter).

In short, variation in male aggression (at least for variation from neutral to high aggression) is not the case of Hamilton's rule. Therefore, we need another kind of reasoning to explain such variation. The increase of life-time mating success in non-fighting males (Enquist and Leimer 1990) and/or the high risk of disability to the winner male (Saito unpublished) should be considered in relation to Hamilton's kin selection theory (Hamilton 1964).

Phenomenon focused on

Next we examine whether there are other conditions under which relatedness can account for the variation in male aggression of animals. For this purpose, we should point out that so far the discussions about the variation in male aggression have only focused on the comparison between "non-aggression" and "aggression", both of which result in a fitness change to a male through its own and its kin's mating success (i.e. individual and kin selections in the sense of Maynard Smith 1982b). If males are confronting with another different selection pressure (e.g. synergistic effect in Maynard Smith 1982b), the scenario will change thoroughly (Queller 1985). Another example of variation in male-to-male aggression are the social spider mites, *Stigmaeopsis* spp. in Saito (1995; 1997) and Saito and Sahara (1999).

<Fig. 1

The spider mites, *Stigmaeopsis longus* (Saito) and *S. miscanthi* (Saito) are sibling species (Sakagami 2002; Saito et al. 2004) in Tetranychidae (small haplo-diploid phytophagous arthropods) and both have highly developed sociality (communal sociality, Mori and Saito 2005b). They live in large woven nests and their social lives are characterized by three "cooperative" behaviors, i.e. nest building, nest maintenance (nest sanitation, Saito et al. 2003), and nest defense against predators (bi-parental defense, Saito 1986a;1990) by a number of adult females and male(s). The defensive success increases with the density of adult females in a nest (Saito 1986a,b, 1990; Yano et al. unpublished). Because there is little potential cost to female aggregation (they rarely show aggressive behavior among themselves, Saito 1986a), the defense behavior of females considered a kind of by-product cooperation (Dugatkin 1997). This kind of female cooperation in the defense and care of young is well documented in arthropod sociality (Ito 1993; Mappes et al. 1995; Avele's 1997). Although the female cooperation in spider mites itself is another interesting theme from a behavioral view point (whether there are castes or not, as known in gall thrips, Crespi and Mound 1997; Mori and Saito 2005b), we consider it to be basically analogous among the species and populations under discussion (see Saito 1986a,b and 1997).

On the other hand, the cooperation in offspring defense observed between adult males in these species is extraordinary and can-not be regarded as only by-product cooperation,

because it is accompanied by an extremely high cost for males. If there are several males in a nest, they may lose mating opportunities even if they defend their offspring effectively. Therefore, males must inevitably adopt two traits for two different selections, namely "cooperation in offspring defense against predators" and "aggression for getting mates". In many spider mite species, like other animals, male-to-male relationships are more or less antagonistic. They perform precopulatory mate guarding and fight conspecific males to ensure mating priority (Potter et al. 1976; Saito unpublished observations). The males of *S. miscanthi* also have extremely high aggressiveness (Saito 1990) perhaps the strongest in the animal kingdom. Winning males often cannibalize losing males, even though they have a phytophagous food habit (Fig. 1). This suggests that for competing males there is little opportunity to improve their fitness other than through confrontation.

<Fig.2

Saito (1995) revealed that male pugnacity in *S. miscanthi* varies geographically and a negative correlation exists between the intensity of aggression and "expected relatedness" (Fig. 2, and see Appendix 1). Conversely, *S. longus* males enjoy a very amicable relationship with their conspecific male nestmates (Fig. 1, Saito 1990; 1997; 2000). Such haploid-male amicability is very extraordinary among spider mite species as well as among many arthropod species (Hamilton 1972). Furthermore, if there are two males in a nest, the nest defense success against predators increases approximately twofold (Fig. 3, Saito 1986b). Therefore, great variation in male pugnacity exists between sibling species and between populations of these social spider mites.

Next we address whether the *S. miscanthi* case is analogous with the case of fig wasp males or not. Saito et al. (2000) checked the relationships between the aggressiveness of *S. miscanthi* males (LW group in Saito and Sahara 1999) and several population parameters. Because of high male mortality due to combat and to the difficulty in identifying dead males in the field, we evaluated the male mating opportunity by "the number of 3rd stage quiescent females per 3rd stage quiescent male" in each nest from Saito et al. (2000). Note that the 3rd quiescent stage of spider mites is just prior to maturity and the females usually mate just after molting. Furthermore the first male precedence is known to be quite high in *Tetranychus urticae* Koch (Helle et al. 1967). Thus this value equates to the potential number of females per potential male. Male aggressiveness, which was evaluated in the laboratory by the same garden analysis (see Fig. 2 and Saito 1995), never correlated with males' mating opportunities ('male aggressiveness' v.s. 'potential number of females/potential male', $\tau = -0.005$, $P > 0.90$ by Kendall's ranked correlation) in the field. This showed that the variation in the aggressiveness of *S. miscanthi* males is not explainable by the "resource (=mate) competition" hypothesis proven in the fig wasp case by West et al. (2001). Therefore an alternative explanation that the variation in male aggressiveness of *S. miscanthi* is caused by the change of relatedness and by the selection pressure for cooperation (Saito 1995; Saito and Sahara 1999) is more plausible (Saito et al. 2000).

Condition of cooperation

The variation in male aggression of *S. miscanthi* and *S. longus* is thus thought to be closely related to the effect of cooperative defense by males. Next let us see what kinds of offspring-based benefits and costs are expected in x males interacting in a nest.

Offspring-based benefits:

b-1. If a single male mates with and defends partners (females) in a nest, he gets S offspring in his life-time. Thus S is considered as final income (fitness) of a male after his all reproductive

and defensive behavior.

b-2. x -male cooperation equally increases the survival of their offspring at rate a (see Appendix 1).

b-3. If the cooperators are his kin, he increases his inclusive fitness through the cooperators' offspring at rate r (relatedness).

Offspring-based costs:

c-1. If x males live altogether, mating opportunities decrease and thus the number of offspring decreases because of the competition. Because any decrease of mating opportunity for a male is convertible to the number of offspring produced from him, the cost can be regarded as the decrease of male's offspring in order to apply the same term as the benefit of cooperation. The

cost per male when x males cooperate is thus $S - \frac{S}{x}$.

From the above parameters, we can search for the condition under which cooperation will evolve, i.e. "cooperating male's inclusive fitness" > "solitary male's fitness". Thus we obtain the following inequality:

$\frac{aS}{x} + \frac{arS(x-1)}{x} > S$. Because $S > 0$, it can be reduced to

$a(1-r) + x(ar-1) > 0$2.

If two individuals interact ($x=2$), then inequality 2 is simply expressed as

$a(1+r) > 2$3. Note that there is no way to convert these inequities to the inequality 1 (Hamilton's rule) that has been also considered to be a rule of "cooperation" (Dugatkin 1997), if we follow the primary definitions of B and C , namely $B = \text{benefit} \geq 0$ and $C = \text{cost} \geq 0$.

Inequality 3 suggests that if $a > 2$, cooperation will evolve regardless of r value. It means that there is a condition under which cooperation occurs unless interacting individuals are non-kin. The cases reported in paper wasps (Ito 1984; 1993), many species of communal spiders (Fowler and Gobbi 1988; Uetz and Hieber 1997) and termites (Matsura et al. 2002) may partly correspond to this condition. Furthermore inequality 3 clearly indicates that males' relatedness is also important, namely r is the primary determinant of the evolution of cooperation, if $1 < a < 2$. Inequalities 2 and 3, therefore, indicate that the parameters a and r must be essential for understanding the cooperation, and here we again meet Hamilton's kin selection (Hamilton 1964).

<Fig.3

Next let us see whether these inequalities are surely applicable to the spider mite case. In inequalities 2 and 3, the adult-based benefits and costs, such as male survival and competition for food were ignored, because they are *a priori* included in offspring-based benefits and costs. Anyhow they are expected to be very low in these mite species, because the death rate of 2 males approximately equalled that of a single male (near 100%) when a predator adult intruded into their nest (Saito 1986b) and because the males are small and feed very little during their lives (Saito unpublished data). There is a question of whether the variation in cooperation and aggression seen in *S. miscanthi* is affected by the variation of predation pressure (e.g. Aoki S in 22nd IEC, Kyoto; Saito 1995). As seen in inequality 2, the fitness of the solitary male (represented by S) completely disappeared, such that the intensity of predation itself is not related to the variation. However, if there is a difference in predator fauna between populations, such a differences may affect a . There are actually co-occurring predator species in the habitats of *S. longus* and *S. miscanthi* (Saito 1990; Chittenden and

Saito 2001; Mori and Saito 2004), and although these predator species are hypothesized to be one of the driving forces behind speciation in *Stigmaeopsis* (Mori and Saito 2004), we have no strong evidence that there is a big difference in predator fauna between cooperative populations (distributing in cooler areas) and aggressive ones (in warmer areas) of *S. miscanthi* LW group.

On the other hand, the relatedness (r) between males may vary strongly in these mite species. Males have low dispersal trends (natal philopatry, Saito unpublished data), such that there is a high probability of interaction between close relatives. As is the nature of male-haploid organisms, there is low relatedness between males if they are under outbreeding conditions (Hamilton 1972). Contrarily, if they are under inbreeding conditions, relatedness drastically increases as calculated by Saito (1990). Therefore, the structure of the mating population must greatly influence the relatedness between males. Mating population structure is thought to be greatly affected by the number of foundresses per nest (Saito 1987), the fertilization status of overwintering females and the male overwintering probability, especially in spring, because mating takes place within the nest. While the former is not considered to change with climate between populations (Saito unpublished data), the remaining two latter strongly depend upon the winter temperature (Saito 1995). Thus Saito (1995) and Saito and Sahara (1999) could represent male relatedness by the winter harshness (Appendix 1).

The parameter $a \geq 2$ evaluated experimentally in the case of *S. longus* (Fig. 3; Saito 1986b) is now meaningful in accordance with inequality 3. If $a > 2$, there is no option for the male mites other than cooperation regardless of r , though Saito (1990; 1997; 2000) stressed the importance of higher r . Therefore, both higher a and r are now explain why we observed only cooperative males in this species.

<Fig. 4.

Further problems

We could show that aggression would be replaced by cooperation in relation to the relatedness of interacting individuals. However, only from the inequality 3, we can not learn how aggression trait compromises cooperation trait and whether there are conditions under which "aggression (or cooperation)" gradually changes with the change of relatedness (r) or the effect of cooperation (a) as seen in Figs .2 and 4. The inequality only shows the threshold over which cooperation evolves. In other words, it is still an open problem whether the phenomena observed by Saito (1995) and Saito and Sahara (1999) is logically supportable or not. One of the authors has been revealed that there is an area where these two reach compromise (i.e. mixed strategy) by a game theory approach (Saito unpublished) by introducing cost of aggression (Maynard Smith 1982a). Even if there is no such area, variation in environmental factors which affect a and r may realize some observable variation in male pugnacity among populations.

Finally, in relation to the recent theory of "cooperation and competition between relatives" (Taylor 1992; Queller 1994; West et al 2002), we have to address the difference between their theories and the present discussion. Taylor (1992) and Queller (1994) discussed how the benefits of increased relatedness that arise as a result of limited dispersal are exactly cancelled out by the cost of increased competition (if they are equally local) between relatives. In fact, West et al. (2001) showed that the Hamilton's (1979) rule is not applicable to wingless fig wasp taxa: the level of fighting between males shows no "negative" correlation with the estimated relatedness of interacting males, but is negatively correlated with the number of females (mating opportunities) in a fig. As they said, this finding is very consistent with the

theoretical prediction by Taylor (1992). Then West et al. (2002) proposed that if we intend to apply Hamilton's rule to some "altruistic" behaviors between relatives, "effective relatedness" adjusted by the decrease of kin effect which accrues from kin competition should be introduced. For example, if kin individuals cooperate to some extent and they compete for something (e.g. mates), the effect of kinship (relatedness) should be discounted. How the kin effect must be discounted by such competition depends upon the pattern of dispersal (viscosity) and the scales at which competition and cooperation occur, thus the effective relatedness between individuals should be determined from two kinds of relatedness, i.e. when cooperating and when competing. They concluded that the reason there is no relationship between the relatedness and male aggressiveness in fig wasp males is that the effect of the relatedness when cooperating is just the same as the cost when competing (thus the former is completely offset by the latter).

However, we have suggested in this review that there is a condition where aggression compromises cooperation at the same spatial scale through the classic relatedness, if we focused on several different selection pressures, namely individual, kin and synergistic selections (Maynard Smith 1982b). The case of polyembryonic encyrtids reported by Glron et al. (2004) may be another example of this scenario. In these cases, there is no difference in spatial scale between competition and cooperation, but the levels of aggression and cooperation would vary with the classic relatedness between individuals.

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Figure legend:.

Fig. 1. There is a big difference in male pugnacity between *S. miscanthi* and *S. longus* when 2 males were introduced in a nest. The photograph and drawing inserted in the figure is, "A male is cannibalizing the other one in *S. miscanthi*" and "precopulatory mate guarding by multiple males of *S. longus*". (after Saito & Sahara 1999)

Fig. 2. In *S. miscanthi* (LW form in Saito et al. 2002), there is clinal variation in male aggression, which is probably related to the relatedness between interacting males. Male

aggression of each population (circle) was evaluated as a mortality rate of one of the paired males introduced into a nest with several eggs for 5 days under constant conditions. The numbers of replicates for each population were 30 ± 3 . The detail explanation of the abscissa is appeared in Appendix 1 and Fig. A. (after Saito 1990)

Fig. 3. Cooperation between *S. longus* males greatly increases defense success against predators. (after Saito 1986b)

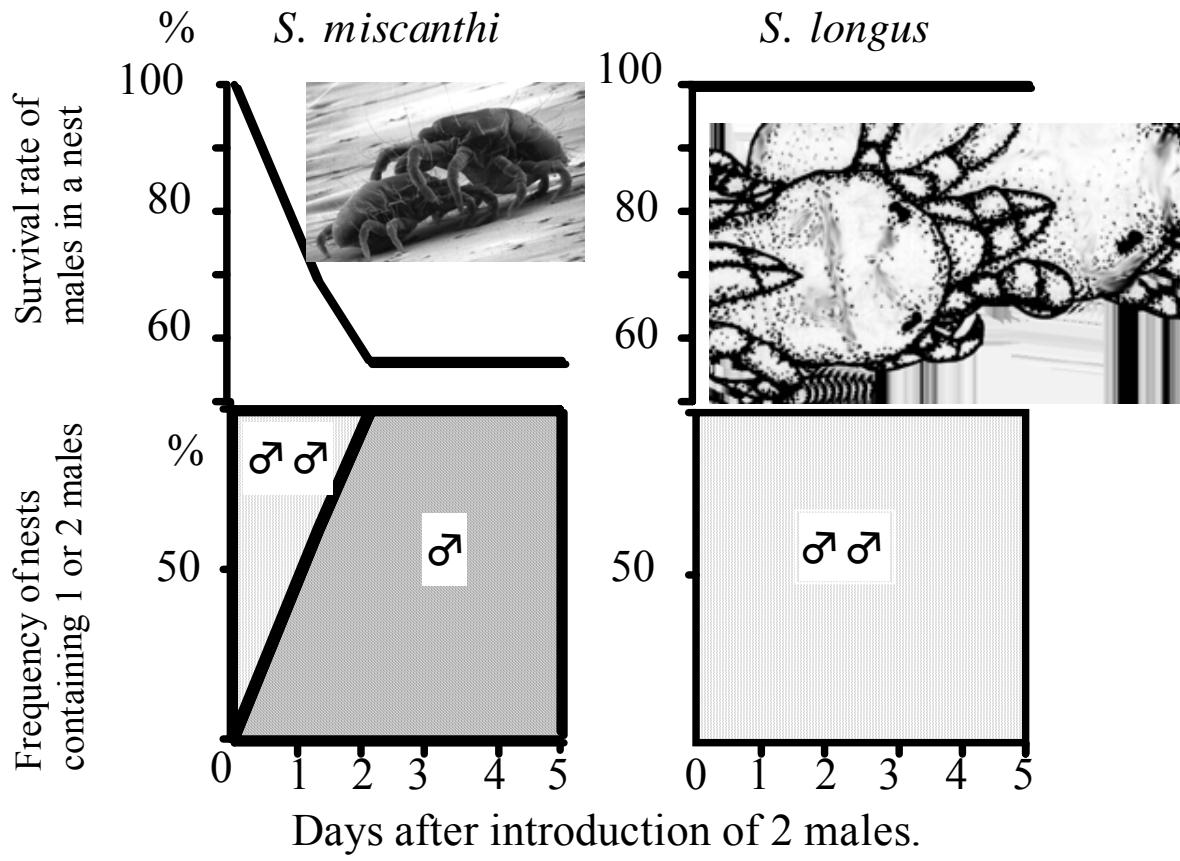
Fig.4. Schematic relationship between male aggressiveness and relatedness in mite males. Where they reach a compromise may be determined by the relatedness between males if there is sufficient net effect of cooperation (see text). In *S. longus*, the defence effect is sufficiently high, such that it is still obscure whether the effect of the relatedness is important or not (see text).

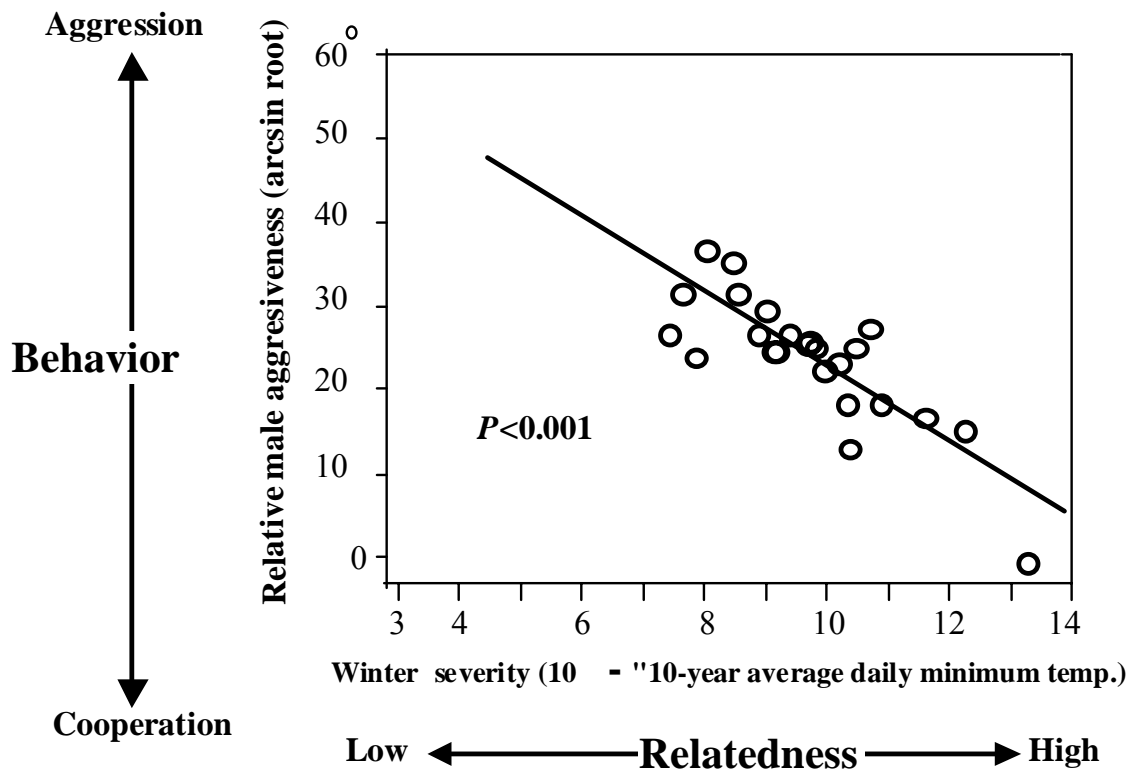
Fig. A-1. How to evaluate the expected relatedness between males of *S. miscanthi* and *S. longus*.

Appendix 1.

Expected relatedness from field data

Saito (1987) observed that 8.7-21.1% of *S. longus* females overwintered in an unfertilized state in a northern region (Sapporo, Hokkaido, Japan). Furthermore, max. 36% of *S. miscanthi* females also overwintered in an unfertilized state in southern areas of Japan (Kyushu, Saito unpublished data). Male spider mites generally have no diapause ability (Veerman 1985), such that male overwintering probability depends primarily upon winter harshness (Saito 1995). Because most overwintering females found their spring nests solitarily (Saito 1987; unpublished data), many unfertilized females reproduce haploid males and thereafter perform mother-son inbreeding in cooler regions where few males exist in spring (Saito et al. 2000; Fig. A-1). The probability of mother-son mating is expected to be a function of the overwintering probability of males. Thus male overwintering probability must greatly influence the relatedness of males in a nest. Winter minimum temperature is thus the prime factor in changing the relatedness of males and can be regarded as "the expected relatedness" in these two spider mite species, if all other things are equal (Fig. A-1).





Cooperation between haploid males is extraordinary!

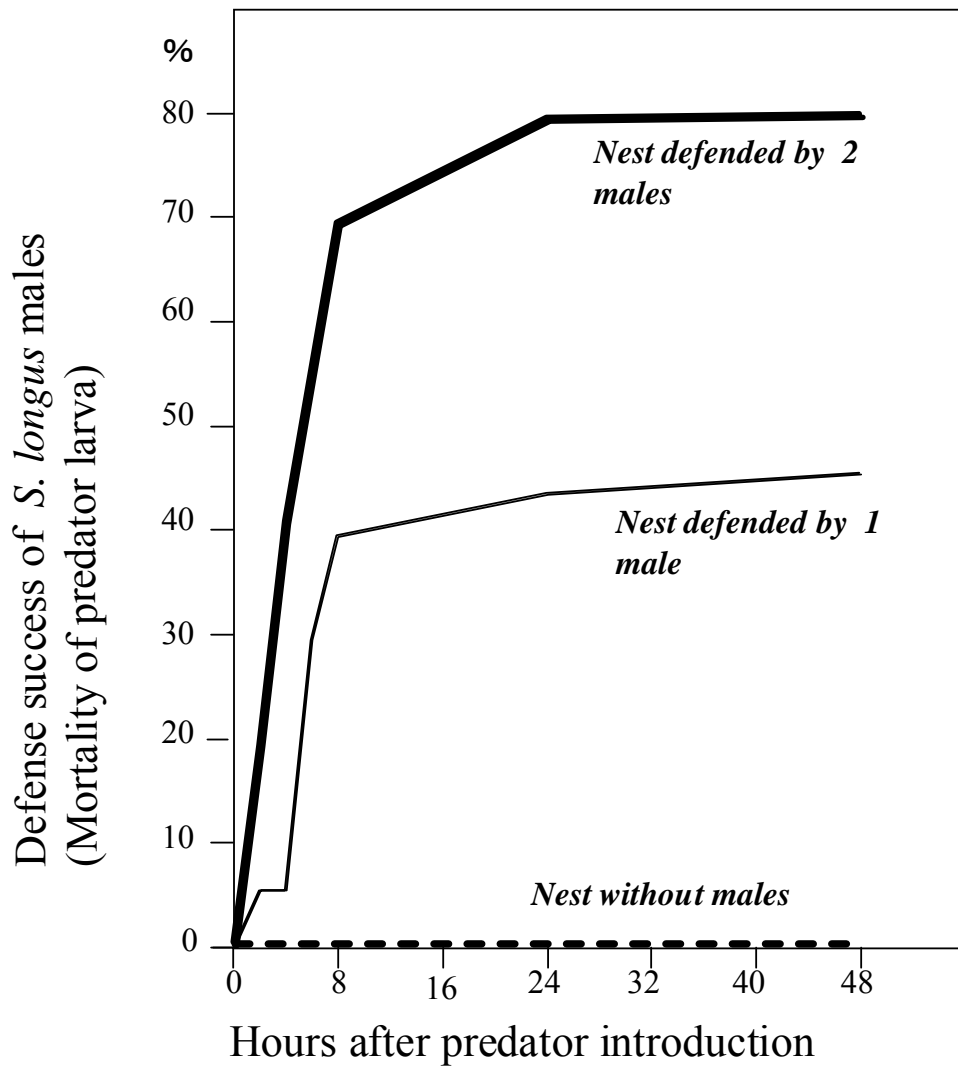


Fig. 3.

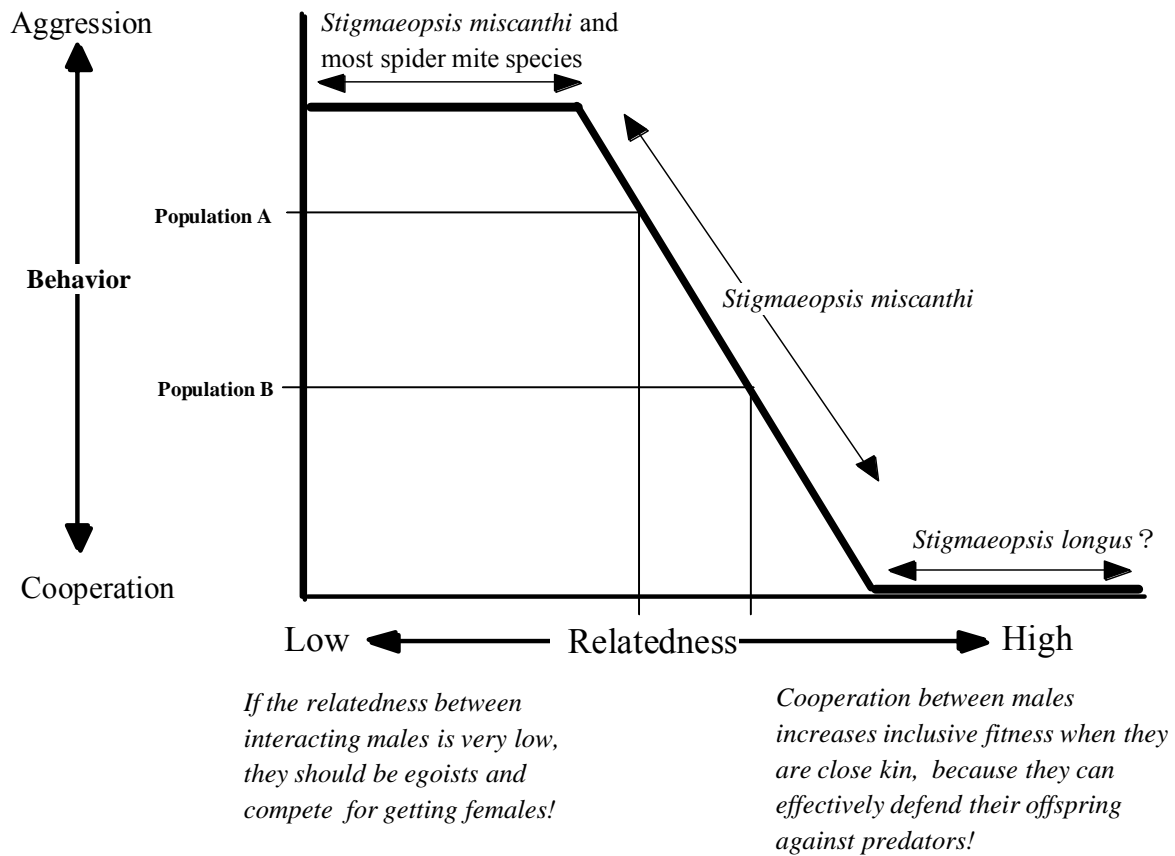
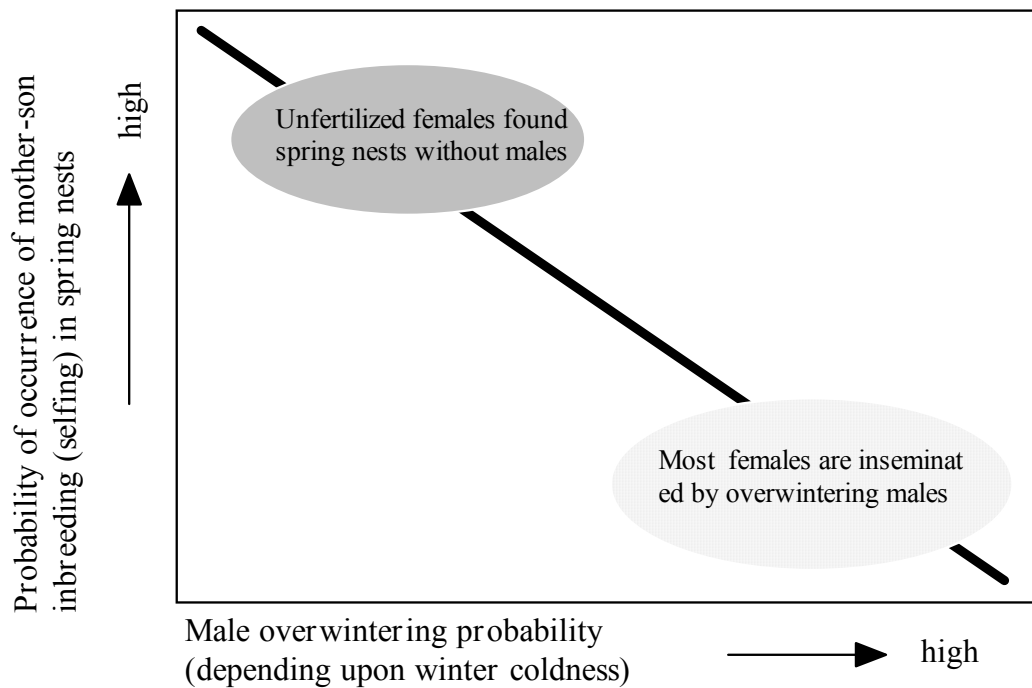


Fig.4.



Male overwintering probability may greatly affect the relatedness among nest members of these subsocial species.

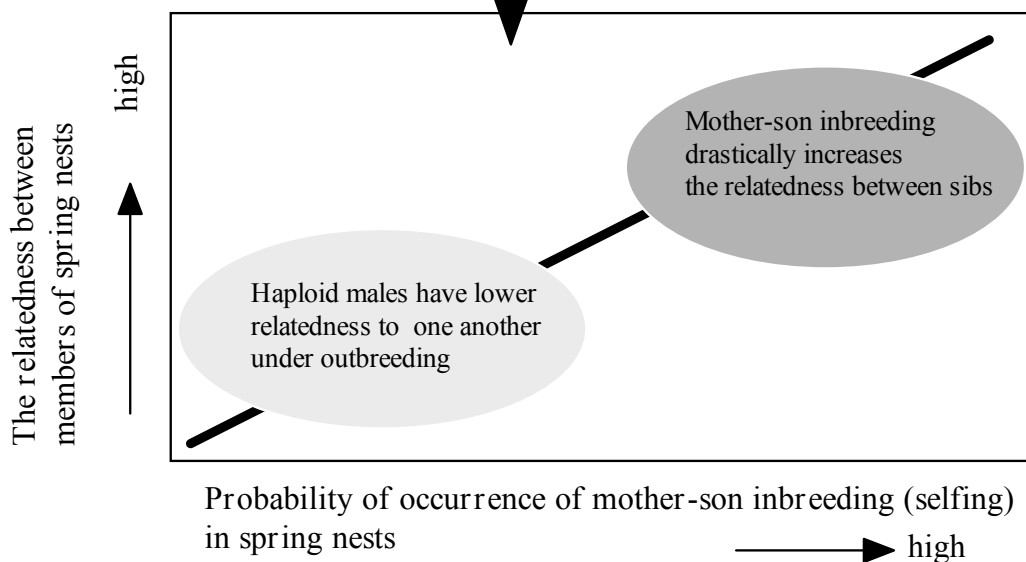


Fig. A-1.