PREY KILLS PREDATOR: COUNTER-ATTACK SUCCESS OF A SPIDER MITE AGAINST ITS SPECIFIC PHYTOSEIID PREDATOR

YUTAKA SAITŌ

Institute of Applied Zoology, Faculty of Agriculture, Hokkaido University, Kita-ku 060, Sapporo (Japan)

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ABSTRACT

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Success of counter-attack by the spider mite, *Schizotetranychus celarius* (Banks), against its specific phytoseiid predator, *Typhlodromus bambusae* Ehara, was examined under experimental conditions. The success of counter-attack by prey females ("mothers") against a predaceous larva depended upon the former's density per nest. About 30% of the predaceous larvae were killed when they intruded into a nest containing eight females and their offspring. On the other hand, the prey males ("fathers") effectively killed the predators, i.e. one male in the nest killed ca. 40% of the predators while two or three males destroyed up to 80%.

The presence of prey parents in a nest considerably enhanced the success of the counter-attack. One male and two young females could kill 70% of the predator's larvae, while two males and two females killed 90% of such larvae. This suggests a kind of cooperative brood defence amongst *S. celarius* parents.

Although more robust, protonymphs of the predator also suffered damage by the prey's counter-attack. However, prey male and female could not destroy the predator's eggs and adult females, whilst the latter often killed spider mite adults.

From these as well as previous experiments, it is concluded that *S. celarius* has evolved some kind of biparental care for its offspring. It is further proposed that the predator—prey interactions observed in this study provide a unique contribution towards understanding "predator—prey coevolution".

INTRODUCTION

Spider mites (Tetranychidae) and predators of the family Phytoseiidae constitute suitable material for studying predator—prey interactions. It has recently been shown that spider mites possess various defence mechanisms against predators associated with their webbing (cf. Gerson, 1985). However, in most predator—prey systems, defence and/or escape behavioural modes of prey usually function only to lessen the probability of individual death by predation.

Saitō (1985) recently reported that males and females of the spider mite

Schizotetranychus celarius (Banks) (long seta form) exhibit parental defence behaviour. This was mainly manifested as counter-attack behaviour against their natural enemy, *Typhlodromus bambusae* Ehara, in defending nest and offspring. Such counter-attacks sometimes caused the death of the predaceous larva. Although the bionomics and parental behaviour patterns were examined in the previous report (Saitō, 1985), many problems remained. These included whether the mites defend their offspring or themselves, how effective is parental counter-attack behaviour, which stages of the phytoseiid predator suffer most from the prey's counter-attack, and how effective are combinations of prey males and females in defending their offspring and nest. I attempt to answer such questions here.

MATERIALS AND METHODS

Materials

The long seta form of *S. celarius* and its specific phytoseiid predator, *T. bambusae*, that were used were progenies of mites collected on 23 August 1983 from the dwarf bamboo, *Sasa senanensis* (Franch. et Sav.), growing wild in the small deciduous forest in the campus of Hokkaido University, Sapporo. A stock culture of each species was initiated on a piece of sasa leaf (leaf underside positioned upward) spread on a piece of polyurethane mat, placed in an experimental dish (15 cm in diameter) and fully moistened with water. *S. celarius* were consistently supplied as prey in the predator stock cultures. These cultures were kept in a room at 25 ± 1°C and a photoperiod of 15L—9D.

Host plant leaves of *S. senanensis* were occasionally collected from the same forest as where the mites had been obtained.

Methods

The experiments were carried out on the underside of detached sasa leaves, including the midrib (in the same way as the stock cultures were maintained), except for the following procedures. A leaf area of 2 cm × 2 cm was prepared by surrounding it with water-soaked tissue paper. Prey mites were first introduced into the experimental area in the combinations shown in Table 1 and kept at 25 ± 1°C, 40—70% RH and a photoperiod of 15L—9D during five days. After the adults had constructed their nests and deposited some eggs in it, the experiments listed in Table 1 were carried out. Predator eggs, larvae (which do not feed) and unfed protonymphs were at most 1 day old when used in the experiments. The age of female predators was not determined, but only vigorous individuals were employed.

Experiments 1—3, 5 and 6 were initiated by releasing one predator on each experimental leaf surface outside the prey's woven nest. In experiment 4, the prey's woven nest was partly opened with a fine needle and two eggs

of the predator were carefully placed inside. After introducing the predators, each experimental area was periodically observed (after 2, 4, 6, 8, 24 and 48 h in experiments 1—3 and 5, and after 24, 48, 72 and 96 h in experiment 4) to monitor the interactions between prey and predator.

In order to determine whether prey adults defend their offspring or themselves, two sets of behavioural observations (experiment 6 in Table 1) were performed. After the introduction of predatory females, behaviour was filmed by a video tape recorder (VTR) under room conditions (at 20—25°C). Mode of encounter and behaviour were recorded for 10 min following the first encounter between prey and predator. If an outcome of "escape of prey" occurred during this time, only the interactions from the initial encounter to the "escape" were analyzed. In the case when no clear outcome could be observed after 10 min, interactions filmed during this 10-min period were analysed.

RESULTS

Figure 1 represents sketches of typical counterattack behaviour of *S. celarius* males. As soon as a male finds a larva of the predator in his woven nest, the former chases the latter (called "direct pursuit" behaviour in Saitō, 1985) and/or occasionally captures the latter's body with its anterior pair of legs ("capturing" behaviour). The male then pushes its mouth parts against the predator's body for some time, after which the predator often dies. Although the term "counter-attack" may sometimes inadequately describe these modes of behaviour, because the phytoseiid larva which mostly sustains damage by the prey's "counter-attack" is not an attacking stage, I prefer to use it because the other stages of the predator, such as protonymph and adult, which are also "counter-attacked" by prey often attack the prey adults and sometimes feed on them.

Experiment 1

This experiment was carried out in order to gauge the effectiveness of the defence (counter-attack) behaviour of females in relation to their density. Mated spider mite females aged 10 to 20 days (after maturity) were used in this experiment. Figure 2 shows the survivorship curves of predator larvae introduced individually near nests containing various densities of the spider mite females. In the nest with one female, killing of larvae occurred only rarely. As spider mite density increased, the survival rate of the predators decreased. The success of defence appears to depend on the density of mothers, though the difference in the survival rate of predators is significant ($P = 0.04$) only between densities 0 and 8 after 48 h, by Fisher's exact probability test (FEP-test; one-sided test). Even if there were eight females in a nest, about 70% of the predator larvae could still survive and become protonymphs, the first stage which actively feeds.

TABLE 1

Experimental designs of interactions between prey females (mothers) and/or prey males (fathers), and predators

Exp.	No. of tests	Initial prey conditions		Conditions for test			
				No. of prey in a nest			Predator
		Male	Female	Eggs	Male	Female	
1. Female vs. predator larva							
a	17	0	8	20—40	0	1	1 larva
b	24	0	8	20—40	0	2	1 larva
c	13	0	8	20—40	0	4	1 larva
d	14	0	8	20—40	0	8	1 larva
2. Male vs. predator larva							
a	20	1	3 (TC)	10—20	1	0	1 larva
b	21	1	3 (TC)	10—20	2	0	1 larva
c	15	3	3 (TC)	10—20	3	0	1 larva
3. Young female and male (parents) vs. predator larva							
a	19	1	3 (TC)	10—20	0	2	1 larva
b	33	1	3 (TC)	10—20	1	2	1 larva
c	23	2	3 (TC)	10—20	2	2	1 larva
4. Young female or male vs. predator egg							
a	17	1	3 (TC)	10—20	0	2	2 eggs
b	17	2	3 (TC)	10—20	2	0	2 eggs
5. Young female or male vs. predator protonymph or adult							
a	13	2	3 (TC)	10—20	2	0	1 proto-nymph
b	18	1	3 (TC)	10—20	0	2	1 female
c	16	2	3 (TC)	10—20	2	0	1 female
6. Behavioural observations							
a	11	1	3 (TC)	10—20	0	1	1 female
b	12	1	3 (TC)	10—20	1	0	1 female
Control 1 (for experiments 1—3)	19	0	8	10—20	0	0	1 larva
Control 2 (for experiment 4)	18	1	3 (TC)	10—20	0	0	2 eggs
Control 3 (for experiment 5a)	15	1	3 (TC)	10—20	0	0	1 proto-nymph
Control 4 (for experiment 5b, c)	14	1	3 (TC)	10—20	0	0	1 female

TC, teleiochrysalis female.

It should be noted, however, that only predator death due to direct killing by spider mites is depicted in Fig. 2. By including individuals trapped by the water barrier in "death", the predator larvae dying at the density of four females in a nest increased by 40% (numerals in parentheses in Fig. 2). As shown by Saitō (1985), the main result of the female's counter-
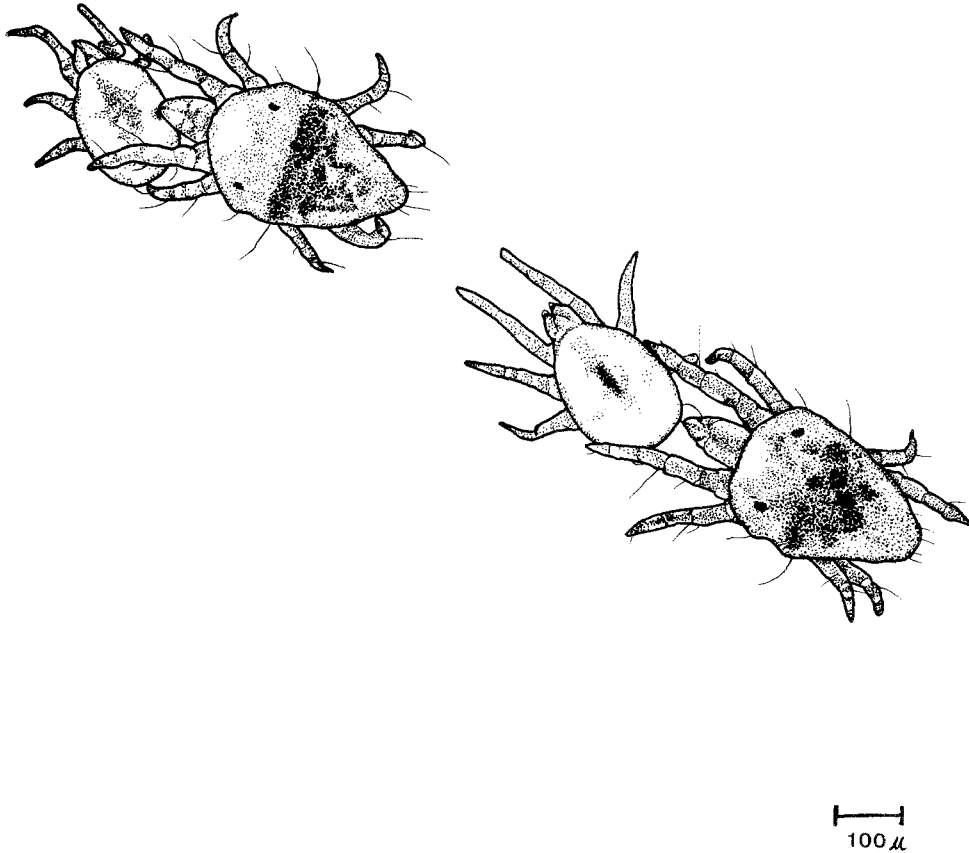
Fig. 1. Sketches of counter-attack behaviour by males of the long seta form of *Schizo-tetranychus celarius* (Banks) against larvae of the predator, *Typhlodromus bambusae* Ehara. Right, "direct pursuit"; left, "capturing".

attack is the expulsion of predators from the nests ("direct pursuit"). Furthermore, very few water-trapped individuals were observed in the other experiments. Thus the percent of water-trapped predator larvae would seem to reflect the success of the female's counter-attack behaviour. Under natural conditions, very few predator larvae, driven from the nests, die by such traps and some of them possibly return to the same nests, whilst others disperse to find different nests.

Experiment 2

Figure 3 shows the survivorship curves of the predator larvae which had invaded male-guarded nests. In these cases the male ("father") killed the predator and effectively defended its offspring as well as its nest. Forty-five percent of the predators were killed when a single father was present
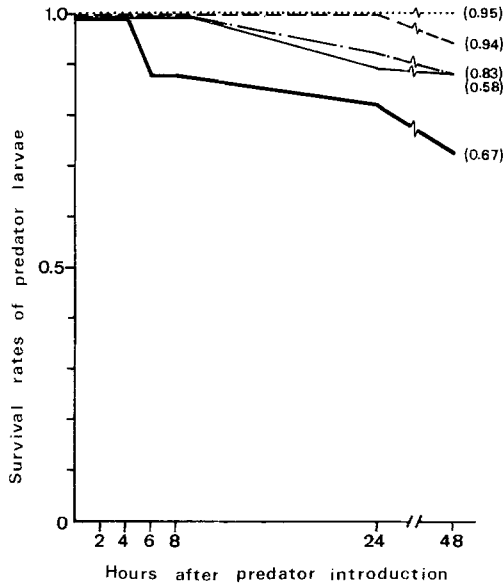
Fig. 2. Effect of various densities of *Schizotetranychus celarius* females (mothers) on success of counter-attack against predator larvae. (........) Control 1 (eggs with no prey adult); (— — —) 1 female (experiment 1a); (— · — · —) 2 females (experiment 1b); (———) 4 females (experiment 1c); (━━━) 8 females (experiment 1d). Numbers in parentheses show survival rate, including death by the counter-attack plus trapping by the water barrier.
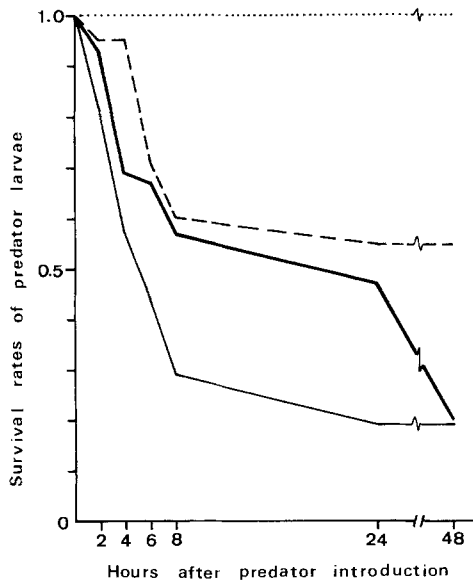

Fig. 3. Effect of various densities of *Schizotetranychus celarius* males (fathers) on success of counter-attack against predator larvae. (........) Control 1 (eggs with no prey adult); (— — —) 1 male (experiment 2a); (———) 2 males (experiment 2b); (━━━) 3 males (experiment 2c).

in a nest, and only 20% of the predators survived in a nest guarded by two or three males (FEP-test, $P < 0.001$ between 0 and 1, $P = 0.02$ between 1 and 2, and $P = 0.04$ between 1 and 3 males, but $P > 0.50$ between 2 and 3 males after 48 h). It should be noted that there is no difference between the defence successes of two males and three males after 48 h, but there are some differences before that (e.g. $P = 0.07$ by FEP-test between 2 and 3 males after 24 h).

Experiment 3

It became evident from the above two series of experiments that counter-attack by fathers of the prey was stronger and more effective than that of mothers. The effectiveness of counter-attack in the presence of various combinations of parents in a nest was explored next. In experiment 3 (and also when setting up experiments 2, 4 and 5), young females of *S. celarius* were used as shown in Table 1, to assure conjugal relations between males and females in a nest. The presence of two young females alone in a nest did not result in the predator's death (Fig. 4), although two older females had some effect (Fig. 2). However, when two young females and a male (two mothers and one father) were present in a nest, they killed about 70% of the predator's larvae. One male in a nest killed 40% of the predators whilst two young females did not kill any ($P = 0.04$ by FEP-test between
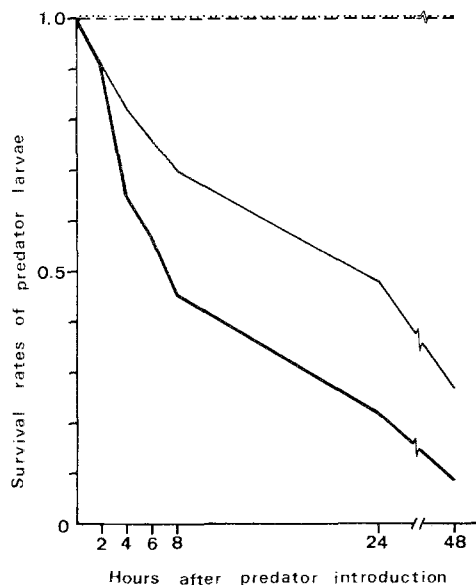

Fig. 4. Effect of various combinations of *Schizotetranychus celarius* parents on success of counter-attack against predator larvae. (........) Control 1 (eggs with no prey adult); (— — —) 2 females (young) (experiment 3a); (———) 1 male + 2 females (experiment 3b); (━━━) 2 males + 2 females (experiment 3c).

TABLE 2

Hatchability of predator's eggs in a nest guarded by *Schizotetranychus celarius* males or females (experiment 4)

No. of prey	No. of tests	No. of pred-ator eggs	Hatch-ability (%)[a]
0 (control 2)	18	36	88.9
2 females	17	34	91.2
2 males	17	34	85.3

[a]There is no significant difference between any combinations of prey density (by Fisher's exact probability test, $P > 0.25$).

"one male + two young females" and "one male"; and $P < 0.001$ between the former and "two young females" after 48 h); therefore, it may be argued that these parents effectively cooperated to defend their offspring as well as their nest. This was also indicated in the experiment with two females and two males (Fig. 4). Only 9% of the predator's larvae survived after 48 h following introduction ($P = 0.08$ by FEP-test between "one male + two young females" and "two males + two young females" after 48 h). In other words, biparental defence by two pairs of prey mites was very effective in defending their nest and offspring from phytoseiid larvae.

Experiments 4 and 5

The counter-attacking ability of *S. celarius* against the predator larvae had now been established. Whether spider mites could also defend their offspring from the other stages of phytoseiid mites was explored next.

The results of experiment 4 show that hatchability of the predators' eggs in the prey's nest was consistently high, regardless the presence of adult prey ($P > 0.30$ by FEP-test in all combinations of hatchabilities in Table 2). In other words, spider mite females and males do not kill the predator's eggs.

Figure 5 summarizes the results of experiment 5 as well as those of experiment 2b. It clearly shows that the success of prey counter-attack depends on the predator stages. Eggs (Table 2) and adult stages of the predator were not killed by prey females and males, whereas larvae and protonymphs sustained damage by the prey males. Though predator deuto-nymphs have not yet been examined, the probability of their death by counter-attack seems to be low. There is a significant difference by FEP-test between predator larvae and protonymphs ($P = 0.009$), between larvae and females ($P = 0.001$), and between protonymphs and females ($P = 0.002$) after 48 h (Fig. 5).

On the other hand, in interactions between female predators and females or males of the spider mites (experiments 5b and 5c), the phytoseiid female
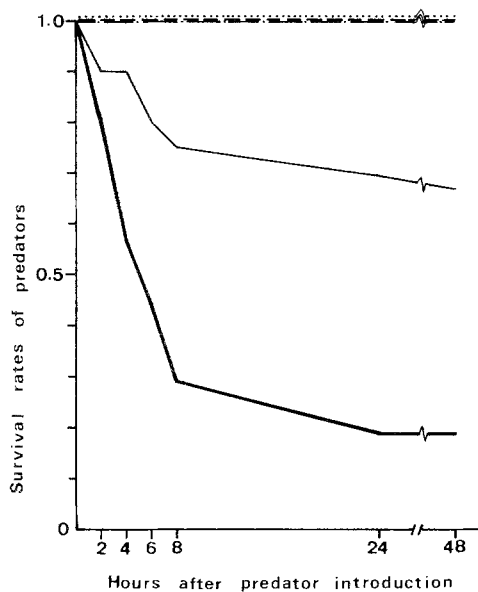
Fig. 5. Success of counter-attack by two males of *Schizotetranychus celarius* against various stages of the predator. (........) Control 3; (— — —) control 4; (━━━) larval predator (experiment 2b); (———) protonymphal predator (experiment 5a); (—·——) adult female of predator (experiment 5c).
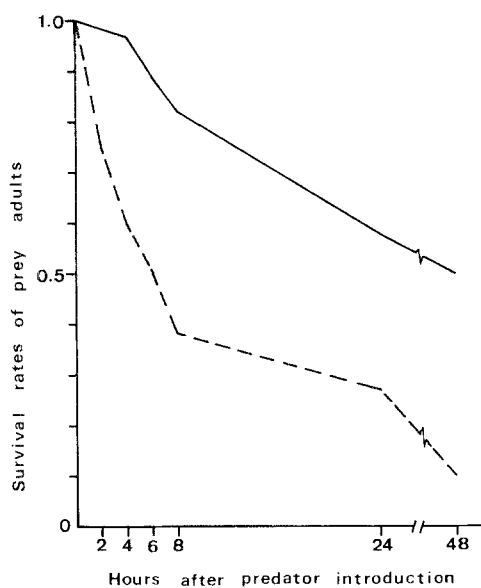

Fig. 6. Results of interactions between *S. celarius* females or males and the predator adult female: (———) 2 prey females (experiment 5b); (— — —) 2 prey males (experiment 5c).

was never killed. One of two mothers in a nest were fed upon by the predator and the other escaped and deserted its offspring (Fig. 6). Most of the fathers were eventually killed by the predator (although no prey adults were ever killed by the predator in experiments 1—4, and 5a). There is a big difference between survival rates of prey males and females ($P < 0.001$ by FEP-test after 48 h).

Experiment 6

The results of experiments 5b and 5c posed the question as to whether these parent mites were killed as a result of counter-attacking at the risk of their lives. This is related to the question whether the mites defend their offspring or themselves. In order to answer them, behavioural observations were conducted on VTR.

Frequency of each encounter mode between prey and predator, and the behavioural mode of the former as observed in experiment 6 are shown in Fig. 7. Modes of encounter were the same as those in the previous report (Saitō, 1985), prey behavioural modes being classified into seven categories: behaviour B = "direct pursuit by prey"; C = "repeated jabbing"; D = "beating by legs or drawing back"; Ea = "avoiding"; Es = "escaping" and F = "disregarding or tapping". Behaviour Pr is a new mode which had not previously been defined, and was defined as "biting action of predator". Behaviour A ("capturing by prey") and G ("mounting") mentioned by Saitō (1985), were not observed.

The first encounter in experiment 6a frequently occurred when a female predator moved while a prey female was inactive (encounter mode 3 in Fig. 7a). However, if we include all encounters, those observed when both prey and predator moved increase (mode 2). This indicates that the predator found the prey female first and that both then began to move actively.

In experiment 6b, the encounter mode was roughly similar to that observed in experiment 6a, although encounter 3 was relatively infrequent (Fig. 7a, b). A comparison of the results of experiment 6b with those of 6a shows no significant difference in the modes of encounter, if all encounters are included (df = 2, χ^2 = 3.36 and $P > 0.10$).

From the encounter patterns between predator female and prey female or male, it appears that both nest owner (prey female or male) and intruder (predator) interfered with each other, with much activity in the nest.

Upon meeting, the prey (whether female or male) performed certain behavioural acts against an intruder. Figure 7 (c, d) shows the frequency of each behavioural mode. Escaping behaviours (Ea and Es) as well as aggressive ones (B, C and D) were often observed in both experiments 6a and 6b. Behaviour F, regarded as a "friendly" action was, on the other hand, quite rare. Although the predator's biting behaviour (Pr) was observed only once in both experiments, this behaviour is thought to be important because it usually caused the prey's death. There was a small but

significant difference between the behavioural modes of prey female and male, if all encounters were included (excluded modes F and Pr, df = 4, χ^2 = 7.95, 0.05 < P < 0.10). Behaviours B—D were lumped together as a category of "aggressive behaviour" along with Ea and Es as "fearing behaviour", and the frequencies of these two categories were then compared between prey male and female. This analysis showed that there was no significant difference (df = 1, χ^2 < 0.01, P > 0.90). It might be concluded that both male and female prey responded to a predator female in two ways, namely fighting and escaping.

Only a single kind of consequence arose in these experiments during 10 minutes. All prey females escaped from their nest after dingdong inter-
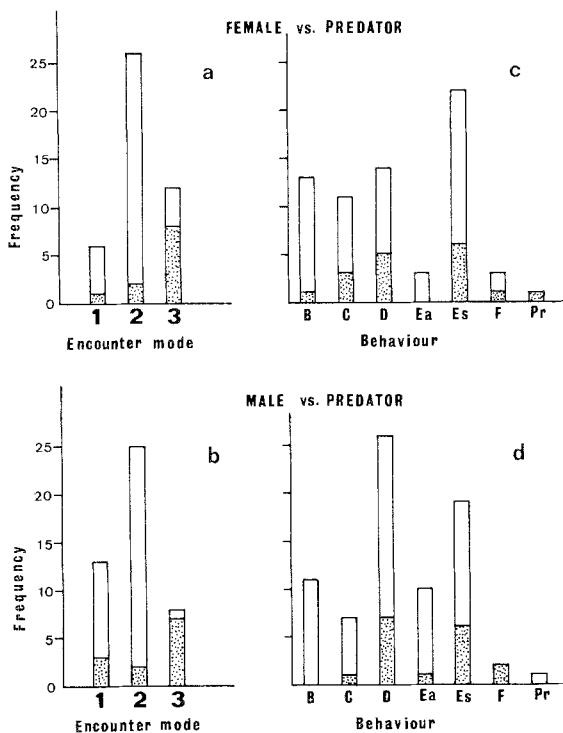

Fig. 7. Frequency of behavioural patterns of *Schizotetranychus celarius* adults (prey) against the predator adult female. (a) Encounter modes between prey female and predator female; (b) encounter modes between prey male and predator female; (c) prey's (and partly predator's) behavioural modes after an encounter between prey female and predator female; (d) as (c), after an encounter between prey male and predator female. Encounter modes: (1) the prey moved against the resting predator; (2) prey moved against the moving predator; (3) the moving predator met the resting prey. Behavioural modes: (B) direct pursuit; (C) repeated jabbing; (D) beating by legs or drawing back; (Ea) avoiding; (Es) escaping; (F) disregarding and tapping; (Pr) biting action of predator. B, C, D, Ea, Es and F refer to behaviour of prey, Pr to that of the predator. Dotted bars show the first encounter, dotted plus undotted bars show all encounters.

actions, and the prey males, in 10 out of 12 replicates, likewise escaped. There was no conclusion in the remaininig two cases after 10 minutes. Thus it is believed that a prey male, as well as a female, can not succeed in defending their nests and offspring against predator females, and "immediate escape from the nest" is the best self-defence in this situation.

DISCUSSION

Defence success of prey

In the present study, the success of defence was only measured as a "perfect" success, i.e. "killing predators". Although offence is the best defence, there is another way of defence in this spider mite species (Saitō, 1985), and thus another success should also be considered. As mentioned in the results of experiment 1, females of *S. celarius* drove the predator larva away from their nest and thus succeeded in defending it. Furthermore, the behavioural observations in Saitō (1985) showed that this type of defence success also occurred when a male defended its nest. Therefore, we believe that the successes noted in the present study do not encompass the entire effect of *S. celarius*'s counter-attack (defence) under natural conditions. In order to estimate the effect of counter-attack behaviour in the field, we should bear in mind the following points. First, the probability of the predator's re-intrusion into the same nest and that of its intrusion into other nests may be important in relation to the distribution pattern of the prey's nests. Second, the risks for the predators outside the nest, which are perhaps related to the abundance of their natural enemies and to availability of prey other than *S. celarius*. It is known that several spider mites (Saitō, 1983) and predaceous mites are candidates for being *T. bambusae*'s prey and natural enemies respectively (Takahashi and Saitō, 1980). Finally, the dispersal and searching ability of *T. bambusae* may also become of importance in this context (M.W. Sabelis, personal communication, 1984). Thus studies on population dynamics of every mite species on the sasa bamboo is probably necessary upon considering a study of multi-species population dynamics.

Prey males more frequently killed predator larvae than drove them away in the present study. Furthermore, the success of counter-attack (killing) increased to some extent with male density. As mentioned previously, males of many spider mites fight against each other, usually in order to defend their partner(s). In the present situation, two or three males usually co-existed in the same nest for a long period and they defended their eggs rather than fought for their partners. Thus it might be said that males of *S. celarius* cooperate to defend their offspring against predators. This is supported by the restricted space within the nest, where males can hardly coexist without interference.

Another interesting point is that the success of counter-attack by two

males was approximately two times (probability = 0.81) as large as that by a single male (probability = 0.45). Although a similar trend was observed with regard to the females, the success values and sample sizes were too low for discussion. This suggests that a mechanism which leads to a two-fold success in the defence by two males is related to the efficiency of the male's searching behaviour. Another possible explanation, that the ability to kill (the predator) is advanced through close cooperation between males, is less acceptable because it does not provide for the two-fold success.

How, then, to explain why the success of three males is similar to that of two males after 48 h? The larval predator seldom intruded into the prey's nest where three males were guarding during the period from 2 h to 24 h (percentage of nest invasion by larval predator at most 5% in this case, and 50—60% in the case of two males), so that there are some differences in the survivorship curve between these two cases (Fig. 3). Twenty-four hours after predator introduction most of the predator larvae became protonymphs outside the nest, and it became neccessary to feed on the spider mites. If we remember that it was somewhat difficult for two prey males to kill this stage of the predator (as mentioned in experiment 5a), overall success of three males is not always the same as that of two, and the former is greater than the latter.

The presence of male(s) and females brought about greater success of counter-attack than when members of either sex occurred alone. As mentioned, two young females could not kill a predator larva. If success had only been obtained as an addition of the success values of both sexes, it should have reached the same values as that of the male(s). The apparently higher successes observed in nests guarded by one or two males and two females thus suggest some sort of cooperative defence mechanism. I once observed on 16 mm film that a female first found a predatory intruder and became excited. Then, as soon as the female contacted a male which had not recognized the intruder, the latter also became excited and began searching within the nest. In a few minutes the male found and killed the predator. Although more observations are necessary, there may be a division of labor in defence and some kind of cooperation between males (fathers) and females (mothers) to defend their offspring as well as nest.

Biparental care?

As mentioned above as well as in the previous report (Saitō, 1985), some indirect evidence leads to the tentative conclusion that the counter-attack behaviour of the long seta form of *S. celarius* is a form of biparental care. The indirect evidence which has so far been obtained is as follows: (1) both male and female *S. celarius* successfully counterattack against the larval and protonymphal predators; (2) they also counterattack against the predator females, but cannot succeed in such defence, either suffering death by the predator or escaping; (3) Saitō (1985) reported that females

and males of this species respond to different intruders such as a predator larva or a conspecific mite in different ways, i.e. against the predator with highly aggressive behaviour but against the conspecific mite in a relatively mild manner; (4) adult generations of this species overlap with its progeny so as to maintain brood care; (5) as stated in Saitō (1985), females and males show active patrolling behaviour, as if they were guards; (6) males (fathers) cooperate with females (mothers) in defending against the predator.

If we assume that adults of *S. celarius* defend only themselves, they would be expected to counter-attack mostly or only against dangerous stages of the predator. Actually they counter-attack mainly against the larvae of *T. bambusae*, which do not feed (and are relatively unaggressive). Attack against this stage thus becomes unreasonable, unless we speculate that the prey can recognize non-aggressive, potentially dangerous intruders. On the other hand, escape seems to be the best way for self-preservation, if an enemy appears that is overwhelmingly strong, like a predatory female. Spider mite parents often escaped from such an enemy, but they also attempted to counter-attack against it, which I found they repeatedly did.

It is usually difficult to perceive the causes underlying certain modes of behaviour. Regarding the question whether the adults of *S. celarius* defend their offspring or themselves, it seems that the evidence argues more in favour of biparental care than of self-preservation. In either case, it is certain that survival of the offspring is improved by the parents' counter-attack behaviour.

Predator—prey interaction

There is little evidence, for either invertebrates or vertebrates, of a prey animal counter-attacking against its specific predator and of that attack causing the predator to suffer fatal wounds. Vermeij (1982) reviewed some relevant examples. These include ants biting ant lions (Lucas and Brockmann, 1981), sea urchins sitinging cassid snails or biting sea stars (Moitoza and Phillips, 1979; Hughes and Hughes, 1981), crabs autotomizing claws which pinch predacious mammals or damage the shells of gastropods and cephalopods (Robinson et al., 1970; Ward and Wicksten, 1980). On the other hand, Aoki et al. (1984) reported that individuals of an aphid could sometimes kill their predator's eggs. However, these examples are rather fragmentary and the "victims" were not always specific predators. The phenomenon reported in the present study is a clear example of a prey's counter-attack success in predator—prey interaction systems. *T. bambusae* is thought to be a specific predator of *S. celarius*, because it has almost always been collected from the latter's nest (K. Takahashi, unpublished data) and is considered to be an important agent in regulating the population of *S. celarius* (Y. Saitō and K. Takahashi, unpublished data).

The origin of the specific predator—prey system between *T. bambusae* and the long seta form of *S. celarius* is an unsolved problem, but some speculations concerning this point may be offered. First, there is a close resemblance in size between prey and predator mites. Although this relationship is generally observed in spider mite prey and phytoseiid predators, females and males of the prey are always larger than immature predator stages such as larva and protonymph. This size relationship may provide a clue for understanding the evolution of prey counter-attack. It has long been known that immature phytoseiid predators seldom feed on adult spider mites (e.g. Takafuji and Chant, 1976). It is also known that males of many spider mite species are aggressive and sometimes kill conspecific males as well as female deutonymphs of other spider mite species with their stylets (Potter et al., 1976; Lee, 1969). This aggressive behaviour probably evolved through precopulatory fighting between males (Potter et al., 1976) and it may, a priori, have provided a potential ability to kill the predator.

Viewpoint of predator

The present study revealed that immature stages of the phytoseiid predator are sometimes killed by the spider mite. If all stages of the predator are killed by the prey, it cannot be regarded as a predator. However, adults of the predator were not harmed, and could kill and feed on spider mite females and males. This phytoseiid can thus still be considered as a predator of *S. celarius*, but it faces some difficulties in living as a predator. Only from a viewpoint of the predator, we naturally wonder why it did not evolve more strongly than its prey. As mentioned above, this predator is thought to be specific to *S. celarius*, and so this problem becomes important, besides the question as to why the spider mite could develop such effective counter-attack behaviour. We cannot provide answers to these questions, but the fact that the predator's eggs are not killed may be relevant here. If the spider mites were to maximize their counter-attack efficiency against the predator, the best way would be to kill the predator's eggs, because they are immobile and never dangerous to the prey (and are always deposited within the prey's nest). This may suggest that there is a kind of "arms race" (Dawkins and Krebs, 1979) between the prey and the predator, e.g. the more effective the former's counter-attack evolves, the harder the latter's egg shell becomes. Thus a coevolutionary approach between the prey and the predator is necessary to solve the question further.

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