Risks and benefits of lethal male fighting in the colonial, polygynous thrips *Hoplothrips karnyi* (Insecta: Thysanoptera)

Bernard J. Crespi

Museum of Zoology and Department of Biology, University of Michigan, Ann Arbor, MI 48109-1079, USA

Summary. Males of *Hoplothrips karnyi* (Hood) (Insecta: Thysanoptera), a colonial fungus-feeding thrips, fight each other in defense of communal egg mass sites, where they mate with females that come to oviposit. Fighting males stab each other with their enlarged, armed forelegs and hit each other with their abdomens. Escalated fights occur between large males of similar size. Fights are often lethal; males that died during observations fought more frequently than other males, were stabbed more often and more severely than other males, and were relatively large, but somewhat smaller than their opponents. Large males tend to win fights and guard egg masses, and they secure about 80% of last matings before ovipositions. Guarding males apparently assess female reproductive condition by putting their forelegs partially around females' abdomens; guarding males, but not non-guarding males, mate preferentially with females that have yet to oviposit. Non-guarding males mate with females away from egg masses, sneak matings at egg masses, and occasionally challenge guarding males. Challenges tend to follow matings by non-guarding males at egg masses. Each of four observed or inferred takeovers was followed by the death of the guarding male that lost. Male fighting strategies are discussed in terms of the consistency of lethal fighting with game theory models. Guarding males appear to pursue a classical "hawk" strategy of "escalate until injured or victorious". This strategy may be advantageous because only large males become guarders, the mating success of guarders greatly exceeds that of non-guarders, and high population viscosity ensures that benefits from killing an opponent accrue directly to guarders. The occurrence of challenges by large non-guarders implies that fighting ability and resource value asymmetries between males change over time; such changes may result from the energetic costs of guarding, injury to guarding males, or depletion of guarding males' supply of sperm.

Introduction

Game theory models of animal conflict were originally developed to explain the rarity of damaging and lethal combat (Maynard Smith and Price 1973; Maynard Smith 1974). These models demonstrated that populations in which animals fight until injured or victorious can be invaded by individuals that assess their fighting ability relative to their opponents, evaluate the resource under contention, and fight only when expected net benefits exceed costs. Although empirical studies have established the ubiquity of assessment of fighting ability (Davies and Halliday 1978; Clutton-Brock et al. 1979; Sigurjonsdottir and Parker 1981; Arak 1983; Austad 1983; Ramer et al. 1983; Suter and Keiley 1984; Thornhill 1984; Otronen 1984; Robinson 1985; Crespi 1986a, b) and resource value (Rand and Rand 1976; Riechert 1978; Ewald 1985), measuring the actual costs and benefits of fighting has proven to be much more difficult (but see Austad 1983; Ewald 1985).

The most obvious costs of fighting are injury and death. However, there have been few game-theoretic studies of animals that routinely kill one another. Lethal fighting has been described in mites (Potter et al. 1976; Timms et al. 1980; Cowan 1984), fig wasps (Hamilton 1979), parasitic wasps (Matthews 1975; Van den Assem et al. 1980; Godfray 1987), gall aphids (Aoki and Makino 1982), queen honeybees (Seeley 1985), spiders (Austad 1983), beetles (Tiemann 1967), anurans (Kluge 1981), and ungulates (McHugh 1958; Wilkinson and Shank 1976; Clutton-Brock et al. 1979;

Clutton-Brock 1982). Two hypotheses may explain the distribution and prevalence of lethal fighting: either lethal fights occur when assessment mechanisms are inadequate or irrelevant (e.g., Parker and Rubenstein 1981; Suter and Keilly 1984), or species with lethal fighting share particular social or ecological conditions that cause the rewards of lethal fighting to offset its costs. If the latter hypothesis is correct, species with lethal fighting might be expected to show especially well-developed mechanisms for assessment of fighting ability, resource value and ownership status (e.g., Clutton-Brock et al. 1979; Austad 1983).

The purpose of this paper is to describe the social behaviour, mating system and male mating tactics of the colonial thrips *Hoplothrips karnyi*, in order to explain in game-theoretic terms its high frequency of lethal male fighting. Thrips are haplodiploid insects exhibiting sexual dimorphism in foreleg development (Ananthakrishnan 1979, 1984), female-biased sex ratios (Stannard 1957; Lewis 1973; Hamilton 1979; Crespi unpubl.), and frequent overlap of generations. *H. karnyi* is a black, heavily-sclerotized, wing-polymorphic thrips about 3 mm long that lives on shelf fungi and feeds on mycelium (Stannard 1968). Males possess enlarged forelegs armed at the apices with pointed fore-tarsal teeth that are used for fighting in defense of communal female oviposition areas. Male fighting has been described in two other species of thrips, *Hoplothrips pedicularius* (Crespi 1986a) and *Elaphrothrips tuberculatus* (Crespi 1986b), neither of which provides direct evidence for male mortality from combat. However, in *H. karnyi* lethal fighting appears to be common. If game theory reasoning can explain cases of deadly combat as well as its absence, its status as a unifying framework for the study of animal conflict will be enhanced (see also Clutton-Brock et al. 1979; Austad 1983).

Methods

Collection and observation

Hoplothrips karnyi was collected at three sites: (a) Washtenaw Co., Michigan (from a large colony), maintained in the lab at 22° C, 16L:8D for several generations at a large population size (>200 adults) on *Polystictus versicolor* fungus (colonies 1 and 2), (b) Livingston Co., Michigan, observed as field-collected adults (colony 3), and (c) Berrien Co., Michigan, observed as field-collected adults (colony 4). Males in colonies 1 and 2 had moulted to adulthood 3–6 days before observations were begun.

The thrips were observed in the 0.5–2 mm space between pieces of sassafras (*Sassafras albidum*) wood containing *Polystictus versicolor* mycelium and clear hard plastic. In colonies 1 and 2, 8 × 3 cm pieces of wood were put in the bottom of 8 cm diameter round plastic petri dishes, and in colonies 3 and 4, rectangles of hard plastic, 3 × 6 cm and 4 × 7 cm respectively, were sealed at the edges with clay against the wood. Each colony contained six males and 8–10 females, individually marked on the thoraces with Testor's enamel paint. Colonies of approximately this size and composition have been collected in the field (Crespi unpublished data). Observations were conducted between 1000 and 2300 h at 20–22° C under low light intensity with a dissecting microscope. During five to six consecutive days, the colonies were observed for 2–10 h daily, for a total of 40 h of observation on each colony.

The identities of all individuals engaging in copulations, ovipositions, male-male interactions, and several other behaviours (described below) were recorded within 4 mm (the body length of gravid females) of egg masses. In addition, in colony 4 the identities of females at oviposition sites were recorded every 5 min. After observation, male femoral length was measured to the nearest 0.001 mm with a LASICO movable hairline ocular micrometer on a WILD M8 microscope at 50-fold magnification. So that the size distributions of males and females could be compared, the fore-femoral lengths of 170 field-collected individuals from Washtenaw Co., Michigan, were also measured.

Analysis

Because only four winged males were included in this study, the data were analysed with respect to male size but not wing morph. Winged and wingless males differ in size and shape (Crespi in prep.), but their fighting and mating behaviours are not clearly distinguishable (Crespi pers. obs.).

Statistics were computed using the Michigan Interactive Data Analysis System (Fox and Guire 1976), and all tests were two-tailed. Since the assumptions of normality and equal variances were generally not met, non-parametric tests were used. The G-test, a form of the χ^2 test, was used for assessing independence.

Contingency tables depicting first-order transition frequencies between behaviours were used in analyses of whether or not males mated following "reverse-climb" behaviour (in relation to subsequent ovipositions), and of the effect of recent matings by non-guarding males on whether or not they subsequently challenged guarding males (see below). Slater (1973) describes the statistical assumptions underlying such transition matrix analyses; the most important assumption is stationarity, that is, constant unconditional probabilities of the behaviours. In the former analysis, this assumption was met in colonies 2, 3, and 4 (i.e., mating and oviposition rates remained roughly constant throughout the observations). In the latter analysis, potential non-stationarity was mitigated by including only observation periods (2–10 h in duration) during which challenges occurred. For this analysis, sample sizes in colonies 1 and 2 were too small for meaningful statistical analysis. Sets of 2 × 2 contingency tables were combined using the Mantel-Haenszel test (Snedecor and Cochran 1980, p. 212).

Data are presented as means ± one standard deviation.

Systematics

The systematic position of *Hoplothrips karnyi* is somewhat uncertain; this thrips keys to *Hoplothrips beachae* in Stannard (1968), but actually belongs to the *Hoplothrips karnyi* (Hood) species complex, which comprises "a number of closely related and ill-defined species from North America and Europe" (L. Mound and J. Palmer, pers. comm.). The thrips observed in
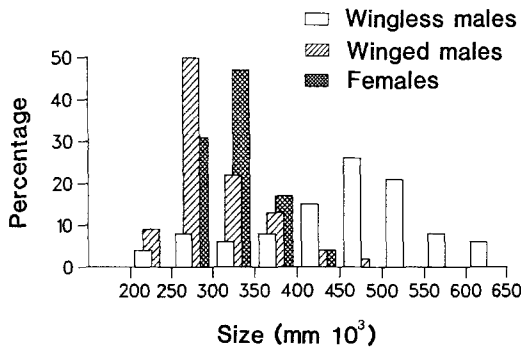
Fig. 1. Size (fore-femoral length) distributions for wingless males, winged males, and females of *Hoplothrips karnyi*. On average, males have larger forelegs than do females

Fig. 2. Male fighting and sneaking behaviour at an egg mass area. Male *1* is stabbing male *2*, and male *3* is approaching a female in an attempt to sneak a copulation

this study were morphologically indistinguishable in taxonomic characters such as antennal colour, and different colonies interbreed freely. Voucher specimens have been deposited in the University of Michigan Museum of Zoology insect collection.

Results

Male and female fore-femoral length distributions

The fore-femoral length distributions of field-collected males and females are shown in Fig. 1. The fore-femora of males are larger (mean = 0.380 ± 0.109, $n = 100$), than those of females (0.321 ± 0.034, $n = 70$; $P < 0.05$, Mann-Whitney U-test), and are also more variable in size (non-parametric Levene test, $P < 0.01$). The variation in male and female fore-femoral length for the observed thrips was similar to that found in these populations.

Male fighting

Males fought with two tactics: stabbing and wagging. Stabbing consists of one male grasping his opponent with his forelegs and squeezing, driving his pointed fore-tarsal teeth against his opponent's exoskeleton. During 135 (98%) of 138 observed stabs the stabbing male grasped his opponent around the abdomen from the rear; in the other three cases stabs occurred head-to-head. The stabbing male's forelegs usually slipped off his opponent's body, apparently from the force of the grasping motion and the movements of the stabbed male. However, during five stabs the stabbed male was held securely around the abdomen, for 10 s to several minutes. Wagging involved jerking the abdomen sharply from side-to-side several times, and it usually occurred in conjunction with stab-
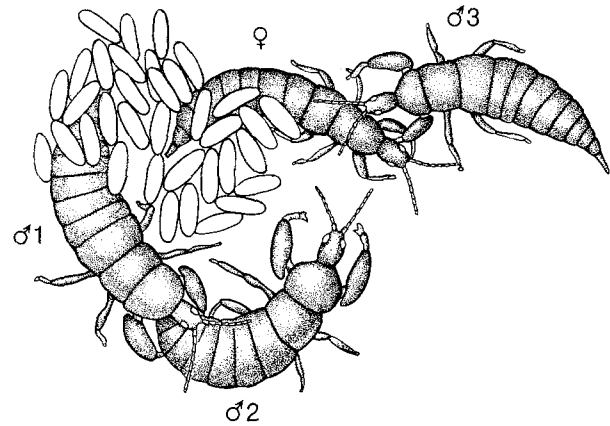
bing by an opponent. During a typical fight males alternately grasped at their opponent's abdomen and wagged when their opponent attempted to grasp them. Sometimes males grasped one another simultaneously, moving around in a circle, or wagged at each other back-to-back. Fights lasted from several seconds to 16 min ($n = 15$ fights in which both males stabbed), and fights ended with the retreat of one male from the egg mass area, often after he had been stabbed. Escalated fights are defined here as fights in which each combatant stabbed his opponent, and non-escalated fights are defined as comprising stabs by one male and wagging (rather than immediate retreat) by the other.

Behaviour of guarding and non-guarding males

Guarding males remained on or near communal egg masses and attacked males with whom they came into contact (Fig. 2). When females were present at egg masses, guarding males usually walked around the egg mass area, climbing onto the females' backs and mating frequently. Ovipositing females mated with guarding males an average of 1.5 ± 1.8 times prior to ovipositions ($n = 487$ matings in 342 ovipositions). Guarding males sometimes ($n = 61$) rubbed the last few segments of their abdomen against the substrate next to the eggs for a few seconds; this behaviour may be associated with the abdominal glandular area found in male thrips (Bode 1978).

Non-guarding males mated with females away from egg masses, made occasional incursions into egg mass areas to attempt matings there, and avoided the guarding male by running from physical contact with him. In 859 (53%) of 1614 encounters between guarding males and non-guard-

ing males, guarding males did not respond to the contact (aversions), whereas in 755 (47%) of the encounters guarding males chased non-guarding males for 1–20 mm and attempted to stab them (attacks). When non-guarding males were being chased they sometimes lifted the end of their abdomen up at an angle, preventing the guarding males from stabbing them. However, in 59 (8%) of the attacks the guarding male stabbed the non-guarder.

Aversions and attacks interrupted 128 initiated mating attempts by non-guarders, which represented 13% of 961 total initiated matings by non-guarders. Apart from interruption of matings, the effect of aversions and attacks was to keep non-guarders out of egg mass areas. Contact between non-guarding males usually elicited neither attacks nor aversions. However, large non-guarders sometimes chased smaller ones for short distances and non-guarders occasionally avoided one another when near the egg mass. Challenges to the guarding male by non-guarders are described below.

Mating and oviposition

Females usually fed on fungal mycelium away from oviposition sites. When they were ready to oviposit, females walked to an egg mass and began alternately tugging gently at the eggs with their forelegs, walking slowly around the egg mass area, lifting their abdomens up at a 30–40° angle with the apex probing against the eggs or the edge of the egg mass with short side-to-side motions, and remaining still. Females spent an average of 21.6 ± 19.4 min at egg masses until oviposition, with an average duration of 8.2 ± 5.8 min from the start of oviposition behaviour (tugging and probing at the eggs) until egg-laying ($n = 82$, data from colony 4). Eggs were laid singly onto the edges of egg masses, usually at the site of the most recent prior ovipositions. After oviposition, females remained at egg masses for an average of 12.7 ± 20.9 min ($n = 88$, median = 6 min). The number of females at an egg mass varied from 0 to 8, with a mean of 2.5 ± 2.0 females ($n = 71$ scans at 30 min intervals in colony 4). In colonies 2–4, all of the females were visibly gravid throughout the observations.

Mating occurred when a male contacted a female with his antennae, climbed onto her back, and inserted his genitalia. Females were not observed to reject mating attempts. Mating lasted from 8 to 42 s (19.2 ± 4.1 s, $n = 436$). After climbing onto a female, a male frequently turned toward the female's abdomen and put his forelegs partially

Table 1. Transition matrices showing the temporal relationships between male reverse-climb behaviour and subsequent copulation, in relation to whether or not females oviposited within the 20 min following the reverse-climb. Following reverse-climbs, guarding males copulated preferentially with females that had yet to oviposit on their current visit to the egg mass area ($P < 0.001$, Mantel-Haenszel test); however, for non-guarding males, copulations following reverse-climbs in egg mass areas were apparently independent of subsequent ovipositions ($P > 0.50$)

Colony	Copulation	Guarding			Non-guarding		
		Ovp.	No ovp.	G	Ovp.	No ovp.	G
2	Copulation after reverse-climb	41	44	7.76*	9	27	0.58
	No copulation after reverse-climb	10	33		4	8	
3	Copulation after reverse-climb	64	49	4.97*	9	40	0.00
	No copulation after reverse-climb	18	30		3	14	
4	Copulation after reverse-climb	33	25	2.32	2	24	1.10
	No copulation after reverse-climb	7	12		3	13	

* $P < 0.05$

around it, a behaviour that was called a "reverse-climb". The temporal relationship between ovipositions and reverse-climbs by guarding and non-guarding males was investigated by creating transition matrices for the transitions between mating or not mating after a reverse-climb, and whether or not females would oviposit in the next 20 min (the average time from female arrival to oviposition) (Table 1). Whether or not mating followed reverse-climbs depended upon the guarding status of males and if females had yet to oviposit during their current visit to the egg mass area. Guarding males mated preferentially with females that had not yet oviposited, whereas, for non-guarding males, mating decisions at oviposition sites were apparently independent of ovipositions. However, the proportion of females mated following reverse-climbs did not differ between guarders and non-guarders; guarders mated following 256 (70%) of 366 reverse-climbs, and non-guarders mated following 111 (71%) of 156 reverse-climbs.

Male size, guarding status, and mating success

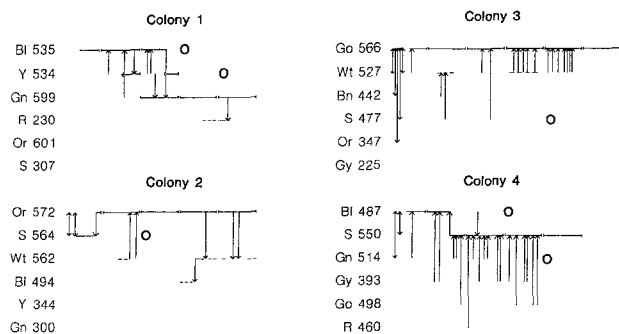Figure 3 shows the guarding status of males in the four colonies and the occurrences of fights.

Fig. 3. Summary of male fighting and guarding behaviour in four colonies of *Hoplothrips karnyi*. Male identity and fore-femoral length (in mm 10^3) are shown *at left*. *Solid horizontal lines* represent times during which that male guarded an egg mass area, and *dashed lines* represent "sporadically-guarding" males. *Double-headed arrows* represent fights that occurred before one male became the guarding male at an egg mass area, *single-headed arrows* represent challenges, and *open circles* represent male deaths. See text for details

Colonies 1, 2, and 3 each contained two egg masses, although nearly all of the ovipositions occurred at only one of these at any given time. Guarding males are defined here as males that remained at an egg mass for at least four hours continuously, during which time they always attacked other males and were always avoided by them (except during challenges); by this definition eight males were guarders. In addition, four males remained at secondary egg masses for periods ranging from several minutes to several hours intermittantly. These "sporadically guarding" males did not consistently attack other males, nor were they consistently avoided by them.

Guarding males were significantly larger (femoral length $= 0.551 \pm 0.033$ mm, $n = 8$) than non-guarding males 0.420 ± 0.116 mm, $n = 16$; $P < 0.01$, Mann-Whitney U-test), and all of the guarding males were wingless. The copulation rate of males while guarding egg masses $(7.25 \pm 2.8$ copulations/ h, $n = 8)$ greatly exceeded that of non-guarding males $(0.56 \pm 0.81$ copulations/h, $n = 16$; $P < 0.001$, Mann-Whitney U-test). Guarding males secured 1397 (65%) of 2148 copulations at egg mass areas, and a higher proportion, 298 (78%) of 380 last matings prior to ovipositions $(G = 27.8, P < 0.001)$.

Guarding may involve substantial energetic and injury costs. Guarding males could not feed without leaving the oviposition site (this is the usual situation in nature), and when females were present these males were usually much more active than non-guarding males; this suggests that guarding is energetically expensive. Males guarding egg masses engaged in fights significantly more fre-

quently $(0.319 \pm 0.166$ fights/h, $n = 8)$ than did non-guarding males $(0.059 \pm 0.104$ fights/h, $n = 16$; $P < 0.001$, Mann-Whitney U-test). Guarding males were stabbed at more than twice the frequency $(0.308 \pm 0.265$ stabs/h, $n = 8)$ of non-guarding males $(0.116 \pm 0.156$ stabs/h, $n = 16)$, but this difference was marginally non-significant $(0.05 < P < 0.10$, Mann-Whitney U-test). However, guarding status was associated with eventual death; four (50%) of eight guarding males died during the observations, versus only two (12.5%) of 16 non-guarding males $(G = 3.85, P < 0.05)$.

Fights, challenges, and death

Fights occurred in three circumstances: when guarding status was being established $(n = 8)$, when two "guarding" males met $(n = 6)$ (see below), and when non-guarding males challenged guarding males $(n = 43)$. Fights between two non-guarding males took place during the initial few hours after males were put in the colonies, and involved relatively large males. Guarding males fought in two situations: when a guarding male went from his egg mass to that of another guarding or sporadically guarding male $(n = 5)$, and when a guarding male left his egg mass to feed, during which time a non-guarding male took up residence there and fought with the original guarder upon his return $(n = 1)$.

Challenges occurred throughout the observations, and were engaged in by relatively large males that had recently mated in egg mass areas. Non-guarding males that challenged guarding males at least once were larger (mean fore-femoral length = 0.517 ± 0.058, $n = 11$) than non-guarding males that did not challenge $(0.366 \pm 0.125$, $n = 9$; $P < 0.01$, Mann-Whitney U-test; test excludes post-guarding males and a male that only guarded). Non-guarding males were more than twice as likely to challenge guarding males if they had mated at the egg mass area within the last three min (Table 2); overall, 22 (51%) of 41 challenges were closely preceded by such matings.

Two of the observed challenges (male Or challenging male S in colony 2 and male S challenging male Bl in colony 4) led immediately to takeovers, one takeover resulted from a guarding male challenging another guarding male and losing (male Bl fighting male Gn in colony 1), and one takeover was inferred (Male Y losing to male Gn in colony 1). The guarding males that lost died within 36 h of each takeover.

Fight intensity varied with male relative and absolute size. Pairs of males that engaged in at

Table 2. Transition matrices showing the relationships between copulations by non-guarding males in relation to subsequent challenges to guarding males. If non-guarding males had copulated in the egg mass area within the 3 min prior to contacting the guarding males, they were more likely to challenge ($P<0.01$, Mantel-Haenszel test). To reduce bias against the null hypothesis, consecutive aversions and attacks within 1 min were pooled

Colony	Copulation	Challenges	Aversions + attacks	Percentage challenges	G
3	Copulation	9	42	0.18	3.3
	No copulation	6	76	0.07	
4	Copulation	8	66	0.11	2.7
	No copulation	11	205	0.05	

Fig. 4. The relationship between male size (fore-femoral length, in mm 10^3), guarding status, and death. Males that died were large, but smaller than the largest males, and had usually guarded egg mass areas previously

least one escalated fight were closer in size (femoral length difference $= 0.039 \pm 0.027$ mm, $n=7$) than pairs of males that engaged in non-escalated fights (0.123 ± 0.106 mm, $n=10$), or pairs of males (one guarding and the other non-guarding) that did not fight (0.175 ± 0.121 mm, $n=17$; $P<0.05$, Kruskal-Wallis ANOVA). Males that engaged in escalated fights were also absolutely larger (mean fore-femoral length $= 0.545 \pm 0.032$ mm, $n=10$) than males that engaged only in non-escalated fights (0.426 ± 0.102 mm, $n=8$), or males that did not fight (0.379 ± 0.141 mm, $n=6$; $P<0.01$, Kruskal-Wallis ANOVA).

Six (25%) of the 24 males died during observations, whereas two (6%) of 34 females died ($G=4.33$, $P<0.05$). There were several differences between males that died and survivors. Males that died: (1) had fought more frequently (0.16 ± 0.05 fights/h) than survivors (0.08 ± 0.12 fights/h; $P<0.05$, Mann-Whitney U-test), (2) were large, but somewhat smaller than their opponents (Fig. 4), (3) had been stabbed more often (8.5 ± 2.6 stabs) than survivors (4.8 ± 6.4 stabs; $P<0.05$, Mann-Whitney U-test), and (4) may have been stabbed more severely than survivors; four of the six males that died had been held by their opponent, whereas only one of the 14 survivors that was stabbed had been held ($G=7.65$, $P<0.01$).

Two of the males that died showed clear signs of injury while still alive. Male S in colony 3 had an indentation in the lateral edge of his abdomen 48 h before death, and male Bl in colony 4 had an injured right foreleg, and walked with a limp, 24 h before he died. Three other males that died (males Bl and Y in colony 1, and male S in colony 2) wandered around the observation areas in an apparently disoriented manner before dying.
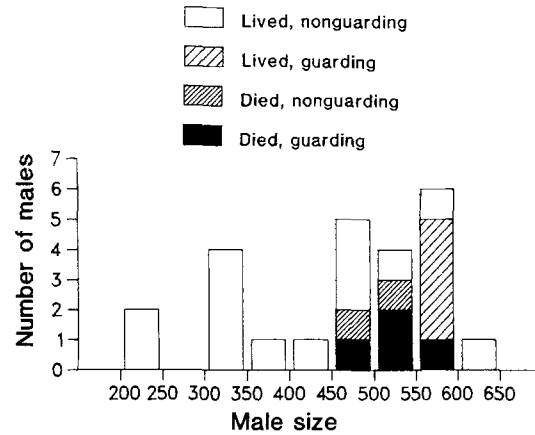
Discussion

Hoplothrips karnyi males fight in territorial defense of oviposition sites. Non-territorial males adopt an alternative mating tactic of sneaking matings at oviposition sites and mating away from oviposition sites. Mating systems comprising a combination of territorial defense and sneak mating tactics have been described for a variety of insects (see Thornhill and Alcock 1983) and vertebrates (see Rubenstein 1980; Arak 1983; Dominey 1984). In *H. karnyi*, as in most other species, expression of the alternative tactics is conditional on body size; large size confers success in fights and acquiring a territory. Body size of *H. karnyi* males is determined primarily by food intake during the second (final) larval instar (Crespi in prep.).

The major benefit of territorial defense in *Hoplothrips karnyi* males in probably increased mating success relative to non-territorial males. Assessing differences between tactics in lifetime reproductive success, however, requires data on sperm competition patterns, sex ratio of the eggs laid (male eggs are unfertilised), and differential, strategy-dependent mortality in field colonies. Deviations from the common pattern of last-male sperm priority (Gwynne 1984), if they occurred here, would tend to equalise reproductive success between guarding and non-guarding males. Similarly, the increased mortality of guarding males relative to non-guarding males shown in this study represents a substantial cost to guarding that offsets its benefits.

The data linking fight frequency, occurrence and severity of stabs, relative male size, and injury

with the death of six males suggest that these males died from wounds incurred in combat. The frequency of lethal fighting in field colonies is unknown. However, the observed deaths were probably not artifacts of laboratory conditions because: (1) wingless males clearly possess lethal weapons (their massive, armed forelegs), (2) males did not attempt to leave the colonies, although in colonies 1 and 2 they could have left, and (3) the observation conditions resemble the crevices under bark where colonies naturally occur. Moreover, the size class of males that died (large, but smaller than the largest males) is what one might expect if lethal fighting were normal. If the apparent size intermediacy of killed males is true in this case and common in other animals with severe fighting (and body size has non-zero heritability), such disruptive selection may help explain the evolution of male dimorphism (see Gadgil 1972; Hamilton 1979; Eberhard 1982).

Game theory models of animal conflict predict that individuals should assess the asymmetries in fighting ability, ownership status, and resource value that affect the outcome of conflicts (Maynard Smith 1982). Are *Hoplothrips karnyi* male mating tactics influenced by assessment of these asymmetries? Variation in fight occurrence and intensity with relative male size suggests that males assess their size relative to that of their opponents. However, the mechanism for such assessment is unclear; males evidently do not engage in assessment displays (Parker 1974; Crespi 1986b) whereby contents can be settled without combat. Moreover, large absolute size is also associated with aggressiveness. This absolute size effect suggests either "assessment" by males of their own size (perhaps hormonally), or a link between size and other factors that promote fighting, such as mating frequency. Evidence for assessment of ownership status includes the well-developed sneaking behaviour of non-guarding males, and the tendency for escalation to occur when a guarding male goes from his oviposition site to that of another male (so-called owner-owner fights) (see Davies 1978; Krebs 1982). The data do not address directly the question of whether or not males assess resource value, defined as the difference in subsequent reproductive success between winning and losing a fight (Parker 1974). However, the temporal link between guarding males' reverse-climb behaviour, copulation, and subsequent oviposition suggests that guarding males may have information about the value of females and oviposition sites that non-guarding males lack. Thus, reverse-climbs may be viewed as a form of male "choice" (see Dewsbury

1982; Nakatsuru and Kramer 1982; Dewsbury and Sawrey 1984). Such behaviour, involving assessment of whether or not a female has yet to oviposit, or, perhaps, of the sex of the egg to be laid, might be expected where guarding males are limited not by access to females but by their rates of sperm production. This hypothesis could be tested by controlled matings followed by sperm counts.

Given that males assess fighting ability and ownership status, what fighting and mating strategies do guarding and non-guarding males pursue? Guarding males always attacked non-guarders, and in each of four takeovers the guarding male that lost died soon afterward. These observations suggest that guarding males pursue a classical hawk strategy of "escalate until injured or victorious" (Maynard Smith and Parker 1976; Maynard Smith 1982). This strategy may be selectively advantageous because only large males become guarders, the mating success of guarders greatly exceeds that of non-guarders, egg mass areas are always few in number relative to the number of males in a colony, and in colonies with a small number of (wingless) males, the benefits of killing an opponent accrue directly to the guarding male (see Matthews 1975; Murray and Gerrard 1984). Alternatively, such a hawk tactic may be non-optimal (i.e., exhausted males should forbear territorial defence) but be maintained partially because of its simplicity; for example, aggressiveness may be inextricably tied to mating frequency, regardless of other contingencies.

Faced with an opponent that always escalates, non-guarding males can either immediately fight to the death, permanently adopt non-guarding status, or adopt non-guarding status, but occasionally challenge the guarding male. Immediate fights to the death are expected when there are no alternatives to fighting; *Hoplothrips karnyi* males have the option of sneaking. The data show that non-guarding males pursue either of the other two alternatives: small non-guarding males consistently sneak, whereas larger non-guarding males sneak, but periodically challenge the guarding male. Game theory reasoning predicts that challenges to guarding males, by males that lost in previous interactions, will not occur unless the asymmetries between contestants have actually or potentially changed since the last interaction. Eventual success of challengers may be affected by the costs of guarding; guarding males are more active than non-guarding males, frequently engage in fights, are frequently stabbed, and cannot feed without leaving their territory. These costs may, over time, create a fighting ability asymmetry favouring non-

guarders. Moreover, if guarding males are limited in their ability to fertilise females, as suggested by their reverse-climb behaviour, then a resource value asymmetry favouring non-guarders also develops over time; non-guarding males (with a larger supply of sperm than guarding males) may have more to gain by winning a fight. Challenges may tend to follow matings by non-guarding males at oviposition sites because securing such matings indicates that fighting ability or resource value asymmetries have changed in their favour.

Thorough understanding of male mating strategies in *Hoplothrips karnyi* requires sperm competition studies, experimental manipulation of asymmetries in fighting ability, resource value, and ownership status, and data on mortality from fighting in natural populations. However, these observations indicate that lethal fighting in this species does not result from inadequacy or irrelevance of assessment mechanisms. In *H. karnyi* and other animals, lethal fighting is consistently associated with extreme localisation of resources and repeated interactions among the same individuals, both of which increase resource value and make severe fighting worthwhile (Hamilton 1979; Crespi 1986a). Thus the rarity of lethal fighting in nature probably reflects the exceptional conditions under which it evolves.

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