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Antipredator benefits of group living in colonial web-building spiders: the 'early warning' effect

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The Mexican colonial web-building spider *Metepeira incrassata* is frequently attacked by predatory wasps from a number of families. Previous studies have shown that wasps often attack more than one spider during a 'run' on a colony, but capture success declines as colony size increases, and that spiders in the central core of the colony have lower risk (Rayor & Uetz 1990, *Behavioral Ecology and Sociobiology*, **27**, 77–85; Uetz & Hieber 1994, *Behavioral Ecology*, **5**, 326–333). We used data from direct observation of attacks and field experiments to test the hypothesis that colonial web-building spiders benefit from 'early warning' of predator approach through vibrations in the colony web. Analysis of 135 naturally occurring wasp attack 'runs' (attacks on 454 spiders) showed that the per-attack run and per-spider capture success of wasps decreased significantly with increased spider colony size. Spider defensive and evasive behaviours observed in a subset of these attacks varied with the attack sequence. Evasive responses by spiders were more frequent later in the attack, suggesting advance warning of predator approach. Experiments using a predator-simulating vibration source demonstrated that mean reaction distance of spiders increased with increasing colony size. Adult female spiders in core positions reacted at greater distances than those on the periphery, but immature spiders, whose capture risk is lower, showed no difference. Behaviour of spiders during simulated attacks was similar to observed encounters with wasps: evasive responses were more frequent and response latency was shorter in spiders attacked later in the sequence, and in many cases, spiders took evasive action prior to any contact with the stimulus. Additional experiments testing isolated cues (web contact, airborne vibration, web-borne vibration) suggest spiders respond to web-borne vibrations generated by predators and evasive behaviours of other spiders. Together, these results support the 'early warning' hypothesis of antipredator benefits for colonial web-building spiders.

Increased rate of attack by predators is a major cost of sociality for many animals (see reviews by Vulinec 1990; Mooring & Hart 1992; Hart et al. 1997). However, these costs may be offset by a number of antipredator mechanisms inherent in group living. Some of the best-known mechanisms include the 'encounter effect' and the 'dilution effect', which are effective at different stages of the predator's attack, but create a combined 'attack-abatement' strategy (Hamilton 1971; Turner & Pitcher 1986; Inman & Krebs 1987; Wrona & Dixon 1991). These mechanisms derive from population dispersion and numerical dilution, respectively, and may be either passive or active, depending on the behaviour of the group members. In addition, the cover-seeking behaviour of group members creates a geometric 'selfish herd' effect (Hamilton 1971), whereby animals in the centre of a group decrease their risk of predation by surrounding themselves with others.

While demonstrations of antipredator benefits deriving from one or more of these proposed antipredator defences are increasing in the literature (Hart et al. 1997), somewhat less attention has been paid to the proximate mechanisms involved in their operation. The mechanistic basis of antipredator benefits of group living are assumed to involve either: enhanced sensory detection (e.g. the 'many eyes' vigilance system seen in flocks of birds; see Bertram 1978; Kenward 1978; Lima 1995a)

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or communication and information sharing (e.g. the 'Trafalgar' effect shown by ocean skaters (Insecta: Gerridae) and shoals of fish; see Treherne & Foster 1981; Godin et al. 1988). However, these hypotheses have only rarely been tested directly (Elgar 1989; Lima & Dill 1990; Lima 1995b). Mobility and flight responses of prey often make assessment of group size and observation of individual behaviours during predator attacks difficult, creating a major impediment to understanding the behavioural dynamics of many animal groups.

Colonial orb web-building spiders provide an excellent model system for investigating the antipredator mechanisms inherent in group living. Because of their sedentary nature and relatively fixed individual locations, it is possible to observe and quantify predator attacks and spider responses at all stages of the predator–prey encounter (Uetz & Hieber 1994, 1997; Uetz 2001). Orb-weaving spiders are able to detect and discriminate both airborne and web-borne vibrations (Klarner & Barth 1982; Barth 1986; Landolfa & Barth 1996; Barth & Holler 1999). Other studies have suggested that spiders recognize predators by wingbeat frequency, and that the network of interconnected silk webbing provides 'early warning' of a predator's approach (Lubin 1974; Buskirk 1975; Uetz 1986; Hodge & Uetz 1992; Uetz & Hieber 1994, 1997). In this study, we test the 'early warning' hypothesis, and investigate the proximate mechanism(s) involved, using both observation of naturally occurring predator attacks and experiments with simulated predator stimuli.

METHODS

Study Species

In contrast to most (solitary) web-building spiders, colonial orb weavers join individual webs together within a communal web framework. Within the colony, individuals build and occupy their own webs (Burgess 1978; Buskirk 1981; Burgess & Uetz 1982; D'Andrea 1987; Uetz & Hieber 1997). Among the best known of these species is *Metepeira incrassata* F.P. Pickard-Cambridge, from tropical rainforest/agricultural habitats in Veracruz, Mexico. Colonies range in size from tens to tens of thousands of individuals, and the benefits and costs of group living across this wide range of group size have been extensively documented (see review in Uetz & Hieber 1997).

Several attack–abatement mechanisms and selfish herd effects have been observed operating against predatory wasps that attack *M. incrassata* (Rayor & Uetz 1990, 1993; Uetz & Hieber 1994). The encounter rate between wasp predators and spider colonies increases as colony size increases, but is far less than would be expected for the smallest and largest colonies (the 'encounter avoidance effect'; Inman & Krebs 1987). Solitary individuals and very small colonies (<10) have never been observed by our research group under attack by wasp predators, despite dozens of person-hours observation over several field seasons. While it may simply be that such attacks are exceedingly rare, we have suggested elsewhere that small colonies are so few and far between that they are below a landscape-level threshold of encounter or detection (see Hieber & Uetz 1994). The disparity in frequency of attacks between smaller and larger colonies supports earlier arguments that colonial web building in spiders is not a response to predation (Spiller & Schoener 1989; Uetz & Hieber 1994, 1997). Alternatively, it may be that wasp predators of colonial *M. incrassata* may not attack small colonies because larger colonies are more profitable foraging locations. Even so, rates of encounter do not increase beyond the level seen for mid-sized groups ($\approx$500), suggesting a 'visual apparency effect' (i.e. the true size of a three-dimensional colony is masked from view; Vine 1971, 1973; Treisman 1975). Because individual spacing within a colony becomes more compact in larger colonies (Uetz et al. 1982; Uetz & Hodge 1990), spiders in large groups may benefit from increased protection because they are no more likely to be located than when in smaller groups. Previous studies on *M. incrassata* have also found that predator attack and capture rates vary with the spatial position of spiders within the three-dimensional volume of the colony; risk of attack by several species of wasps was higher for spiders on the periphery (Rayor & Uetz 1990, 1993).

Within a colony, an individual's risk of attack and capture during each predator attack run are predicted to be an inverse function of colony size by a numerical 'dilution effect', an essentially passive mechanism (Hamilton 1971; Foster & Treherne 1981; Inman & Krebs 1987; Wrona & Dixon 1991). Data from field observations of *M. incrassata* support this prediction (Uetz & Hieber 1994), but also reveal that the relationship is more complex than simple mathematical dilution (see Bednekoff & Lima 1998). This is apparently caused by two different factors operating simultaneously. First, wasps may attack more than one spider once a colony is located, which could offset any gain in fitness from a dilution effect (Inman & Krebs 1987; Uetz & Hieber 1994). Second, despite multiple attacks, the capture success of wasp predators decreases with increasing group size (Uetz & Hieber 1994), creating an overall decreased risk for individual spiders living in groups. Our previous observations of wasp attacks have suggested that spiders are forewarned of a wasp predator's approach, as spiders attacked later in a 'trapline run' are more likely to escape by an evasive manoeuvre we call 'bailing out', in which they retreat from their web into the vegetation below (see Rayor 1997). These observations suggest that an 'early warning' system may be the mechanism underlying the antipredator benefits of group living for colonial web-building spiders.

If an early warning mechanism exists in colonies of *M. incrassata*, several predictions can be made about its impact at the colony and individual level. At the colony level, the degree of web interconnection increases with colony size (Uetz & Hodge 1990), and is greater in the core where spiders are surrounded by webbing in all directions. Therefore, the per-attack run and per-spider-attack capture efficiency of wasp predators should decrease as colony size increases, and be lower in the core of colonies. For the same reasons, the distance at which spiders respond should increase as colony size increases, and be greater for spiders in the core of colonies. At the individual level, if spiders are forewarned of approaching predators, their response behaviours should vary depending on their relative position in the sequence of attack (i.e. more effective escape behaviours should become more frequent as the attack proceeds). Additionally, response latency should be lower for spiders approached later in the attack sequence. In this study, we test these predictions with direct observation of naturally occurring wasp attacks and spider responses, as well as experimental simulated predator attacks.

Study Site

The Mexican colonial orb weaver *M. incrassata* occurs in the east–central mountains above the Gulf of Mexico, in Fortin de las Flores, Veracruz. Here the habitat is primarily moist tropical (second growth) forest vegetation with banana and coffee plantations, high rainfall (170–220 cm/year), high humidity (68–99%), and a moderate daily temperature range (20–32 °C). These spiders live in dense groups ranging in size from less than 10 individuals to several thousand individuals, spanning large spaces between trees along the forest edge in coffee and banana plantations, and in power lines along roadsides (for more details on the study site, see Benton & Uetz 1986; Uetz & Hodge 1990; Uetz & Hieber 1997).

Observations of Naturally Occurring Predator Attacks

We collected data on naturally occurring wasp attacks as part of a larger field study of *M. incrassata* group size and predation risk conducted from 1990 to 1993. We used these data to test predictions of the 'early warning hypothesis': (1) wasp capture efficiency decreases as colony size increases, and is lower in core versus periphery positions of the colony), and (2) response behaviours of spiders under attack vary as a function of their position (rank) within the order of the wasp's attack sequence. While some of the data from these studies are already published (Uetz & Hieber 1994, 1997), detailed data on wasp capture attempts and the response behaviours of individual spiders that are pertinent to testing the early warning effect were not analysed at that time. We extracted data on the antipredator behaviour of spiders during naturally occurring wasp attacks from field notes and tape recordings of ad libitum observations made during July and August of 1990–1993. As observations of predator attacks and spider responses are relatively rare and unpredictable events at any given colony or time, we pooled a subset of data, from 13 extensively documented attack runs by wasps involving 45 spiders, among years.

Simulated Predator Experiments

We conducted experiments using a simulated predator stimulus during field seasons in 1990 and 1991. We used a high-sensitivity microphone and a Marantz field-portable tape recorder to record the wingbeat frequencies of caged wasp predators of *M. incrassata*. We digitized the recorded sound on a laptop PC, analysed the recordings with the Canary® Bioacoustic software package (Cornell University Laboratory of Ornithology, Ithaca, New York, U.S.A.) and found that the two most common wasp predators (*Poecilopompilus mixtus* (Pompilidae), *Trypoxolon* sp. (Sphecidae)) had wingbeat frequencies ranging from 92 to 115 Hz. Based on this information, we used a battery-operated vibration source with a constant frequency of 95 Hz as a simulated predator stimulus. Spiders responded to this stimulus in the same manner as they did to a live wasp, displaying typical antipredator behaviours (Rayor 1997).

In the field season of 1990, we censused spider colonies on two roadside transects (15 × 4 km) along the edges of coffee and banana plantations (typical habitat for this species). We located 61 colonies with more than 10 individuals (the threshold colony size for wasp attacks; Uetz & Hieber 1994). From the censused population, we chose five colonies for experimental studies in each of the following colony size classes: 10–49, 50–149, 150–499, 500–999, 1000–1999 and greater than 2000 spiders/colony (which reflect the range of naturally occurring colonies used in previous studies). Choice of colonies within each size category was arbitrary, based on observer access (within 1–2 m of ground level). To ensure that experimental observations were independent of one another (i.e. did not follow immediately at the same colony) and that observations were made with equal frequency throughout the entire daily activity period, we assigned experimental trials at random in advance to colony size classes and time periods. In addition, we assigned experimental trials at random to different positions within colonies of the six size categories (above): (1) core: central positions where spiders were completely surrounded by webs; (2) periphery: on the edge of a colony or within one to two web layers of the edge. We selected individuals from one of three age/sex classes (females with egg sacs, females without egg sacs, and immature spiders) at random from each of the previously designated categories.

In one set of experiments, we tested predictions of the early warning hypothesis concerning response distance (i.e. the distance at which spiders respond to a predator will increase as colony size increases, and be greater in the colony core versus periphery positions). During each experimental trial, we simulated predator attacks in the following manner: we approached individual spiders directly along a measured path, using the 95-Hz vibration source to vibrate ('buzz') the silk lines of the colony web at 5-cm intervals nearer and nearer to the target spider. We recorded the distance at which spiders responded with defensive or evasive behaviour to the nearest centimetre. As spiders appear to remain alert for a variable amount of time after wasp attacks, we took care to sample only one individual per colony in each colony size class and position within each time period each day ($N=5$ spiders in each category, position and colony size class). Based on previous studies of encounter rates (Rayor & Uetz 1990, 1993; Uetz & Hieber 1994), this sampling protocol allows simulated 'attacks' to be treated as independent replicates in statistical analyses (data were log- or square-root transformed where appropriate).

In a second set of experiments (in 1991), we tested predictions of the early warning hypothesis concerning spider antipredator response behaviours (i.e. spider evasive behaviours will increase in frequency later in the sequence of attack, and response latency of individual spiders will decrease over the attack sequence). We selected 30 colonies for experimental study. As colonies greater than 1000 were too few in this year to be included, there were only four categories. For each colony, we simulated attacks of ‘traplining’ wasps by sequentially buzzing five adult female spiders (which were within 50 cm of each other) in successive 30-s intervals. We recorded the spider response behaviours and response latency (s) throughout the attack sequence on micro-cassette tape, and later transcribed and quantified them.

In an additional study that same field season, we tested the role(s) of multiple sources of vibration that might serve as proximate cues for early warning of predator approach. We approached spiders sequentially in the same manner as above, but varied the nature of the vibration in three ways: (1) web/spider contact only: we touched the web adjacent to each spider a single time to elicit a reaction from the spider; (b) airborne vibration only: we held the (95-Hz) vibration source near the spider (1–2 cm) but never touched the web or spider; (c) web-borne vibration: we buzzed the spider as in previous experiments by applying the (95-Hz) vibration source directly to the web.

RESULTS

Naturally Occurring Predator Attacks

A re-examination of field notes recovered data from 136 (colony level) attack runs by wasps, involving 454 (individual level) attacks on spiders (wasps attacked from 1–20 spiders/run) and 36 captures over the four field seasons (1990–1993). These data were analysed at several levels. An analysis of the frequency of attacks by colony size category (as in Uetz & Hieber 1994) confirmed that capture success of wasps is not independent of colony size or position within the colony (Table 1). As wasp capture efficiency can be measured at the level of the attack run and individual attack, both of which may be influenced by the size of a colony, we also analysed these data using logistic regression with colony size as a continuous variable (Fig. 1a). A two-factor multiple logistic regression model (*df*=133), including (ln-transformed) colony size and number of attacks/run as independent variables, and capture success or failure as the dependent variable was significant (whole model: χ^2=7.37, *P*=0.022). Separate analyses of the independent variables revealed significance for an effect of colony size (χ^2=7.11, *P*=0.0077) but not the number of attacks/run (χ^2=0.07, *P*=0.791). A subsequent analysis of wasp capture success at the individual spider attack level (Fig. 1b) with multiple linear regression of the (arcsine square-root transformed) proportion of captures/attack on (ln-transformed) colony size and number of attacks/run had similar results (whole model: $F_{2,133}$=8.82, *P*=0.0003; R^2=0.117). Separate analyses of the independent variables revealed significance for an effect of colony size (*t*= − 3.29, *P*=0.0013) but not the number of attacks/run (*t*= − 1.26, *P*=0.208). Taken together, these results support the first set of predictions of the early warning hypothesis (i.e. that wasp capture efficiency is lower in larger colonies and in core positions within the colony, where spiders are surrounded by webbing; Fig. 1, Table 1).

Table 1. Number of spiders attacked and captured by wasps across a range of colony sizes (from Uetz & Hieber 1994) and positions within the colony (includes data from Rayor & Uetz 1993)

	Attacks observed	Captures	Capture success (%)
Colony size class			
50–149	25	7	28.0
150–499	44	9	20.45
500–999	142	12	8.45
1000–1999	81	3	3.7
>2000	162	5	3.09
Log-likelihood test: $G_{(\text{Williams correction})_4}$=23.698, *P*=0.00005			
Position			
Periphery	276		20.1
Core	189		10.6
Log-likelihood test: $G_{(\text{Williams correction})_1}$=7.511, *P*=0.0061			

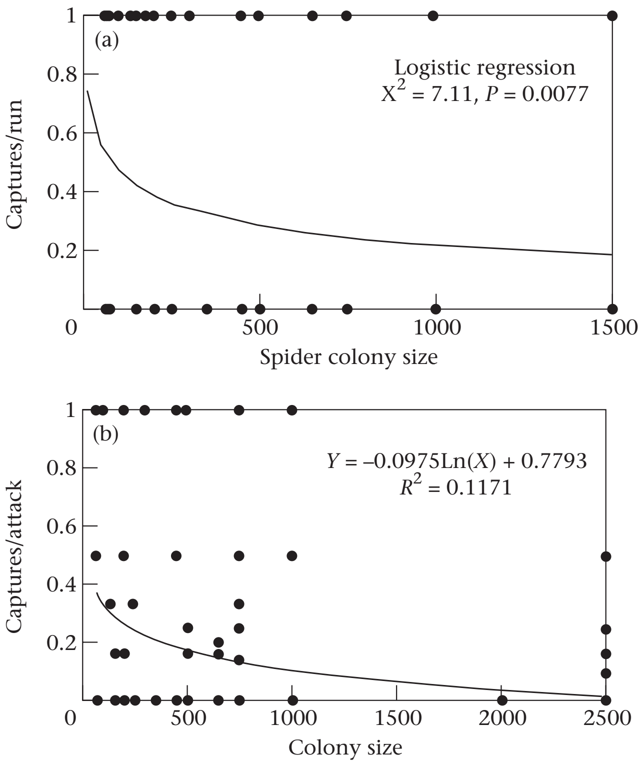

Figure 1. Relationship between wasp capture success and spider colony size, based on logistic regression. (a) Capture success/failure (1/0) of wasps on individual attack runs. (b) Capture efficiency of individual attacks (captures/attack).

We analysed spider behaviour from detailed observations of spiders under attack by wasps (13 wasp attack

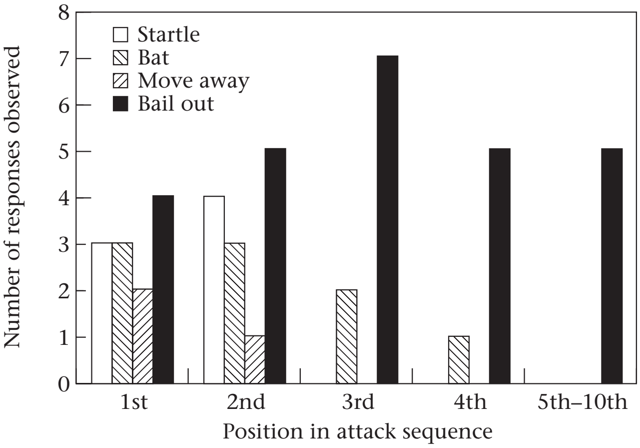

Figure 2. Responses of *Metepeira incrassata* spiders (N=45) recorded during detailed observations of wasp attacks on colonies (N=13) in 1990–1991, as a function of position (rank) within the attack sequence order. Each observation represented indicates the highest level of evasive/antipredator behaviour displayed by an individual spider.

runs involving 45 attacks on individual spiders). Spiders responded to attacks by wasps with four stereotypic behaviours, as reported by Rayor (1997): startle: a simultaneous contraction of all eight legs, indicating a reflexive response to disturbance; bat: spiders swung their forelegs at the wasp; run away: spiders rapidly evacuated their web or retreated and moved away through the colony webbing; bail out: spiders dropped on a dragline of silk from their position at the web hub and retreated into the vegetation or the ground below. Analysis of the frequency of occurrence of these four behaviours (Fig. 2) revealed that behaviour is not independent of the spiders' position (rank) within the order of the attack sequence (log-likelihood test: G=18.05, P=0.034). Spiders attacked later in the wasp attack sequence (3rd–10th) were far more likely to simply bail out of webs and drop to the ground without showing any other response behaviours.

Simulated Predator Studies

The distance at which spiders responded to the simulated predator stimulus varied significantly with colony size, position and age/sex of the spider (three-way analysis of variance (ANOVA): colony size: $F_{5,144}=41.42$, $P<0.001$; position (core/periphery): $F_{1,144}=51.88$, $P<0.001$; sex/age: $F_{2,144}=20.16$, $P<0.001$). All age/sex categories displayed similar behaviours across the range of colony sizes, responding at greater distances as colony size increased (Fig. 3a, b, c). Within each colony size category, adult female spiders (with or without egg sacs) in core positions surrounded by webbing responded at greater distances than those on the periphery (Fig. 3a, b). Adult females (with or without eggs) responded to the simulated predator vibration at distances nearly double that for juveniles in all but the smallest colonies (Bonferroni comparison of means: $P<0.05$), while immature spiders showed no difference with position (Fig. 3c).

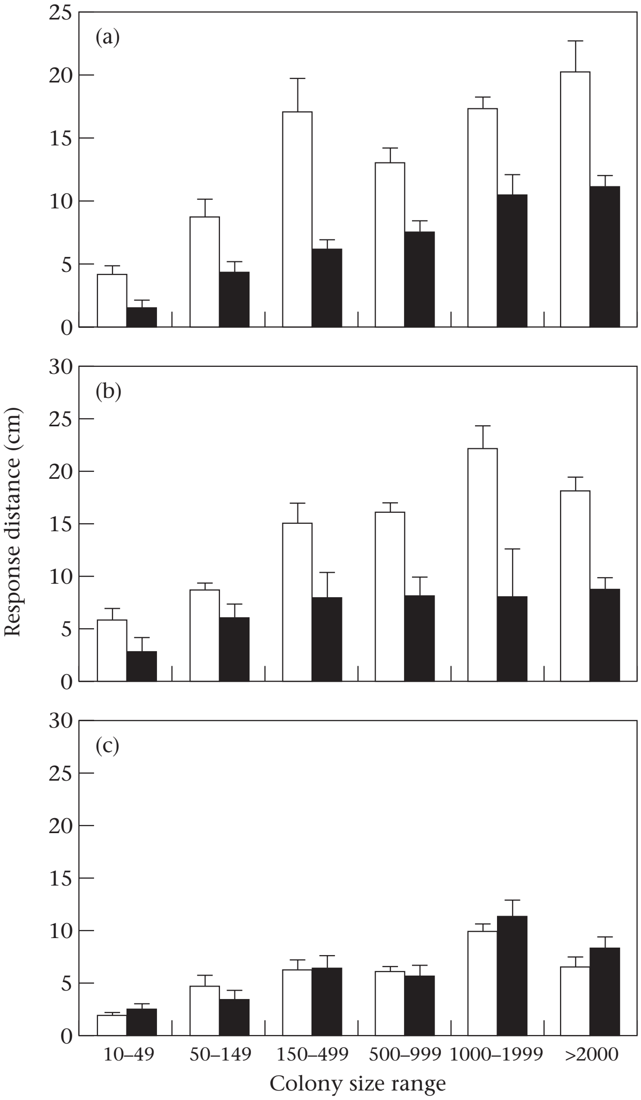

Figure 3. Mean distance (±SE) at which spiders in colonies of various size categories responded to the simulated predator stimulus with evasive/antipredator behaviour. □: Spiders in the central core of colonies; ■: spiders on the periphery of colonies. (a) Female spiders with egg sacs; (b) females without egg sacs; (c) immature spiders.

A two-way ANOVA of latency of response time (s) for evasive behaviours revealed that the time to spiders' response varied significantly with position (rank) in the order of the simulated attack sequence ($F_{4,120}=17.68$, $P<0.001$), but not with colony size ($F_{3,120}=0.74$, $P=0.549$), and so we pooled these data (Fig. 4a, b). The first spiders attacked in this manner often appeared to be caught off-guard, and were more likely to bat at the stimulus (Fig. 4a). However, the second–fifth spiders in the sequence responded by running away or bailing out of their web into the vegetation below (Fig. 4a). Latency to response decreased across the sequence of attack, with the third–fifth spiders in the sequence responding on average in 2 s or less (Fig. 4b).

The frequency with which spiders responded to simulated sequential predator attacks was not independent of

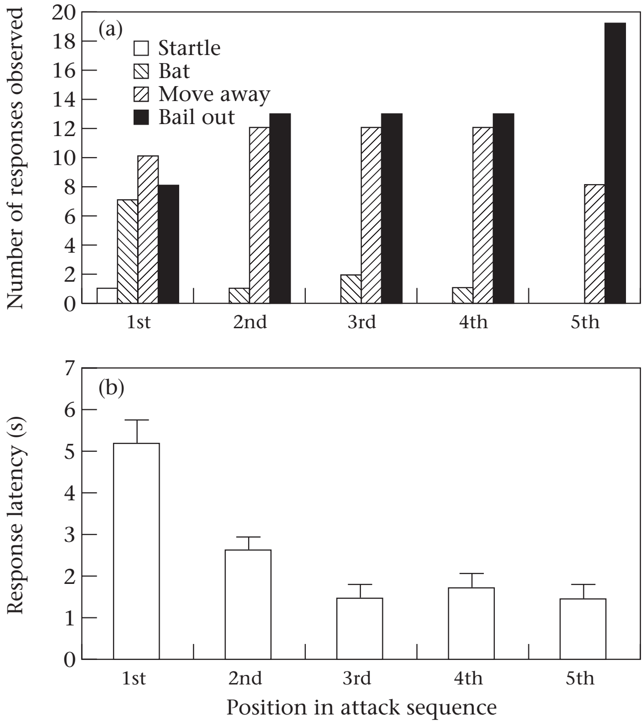

Figure 4. Responses of adult female spiders to sequential 'attacks' (N=5 individuals/attack series) with the simulated predator stimulus (N=150 spiders in 30 colonies) as a function of position (rank) within the attack sequence order: (a) evasive/antipredator behaviours observed; (b) mean latency in seconds (±SE) to evasive response by target individuals.

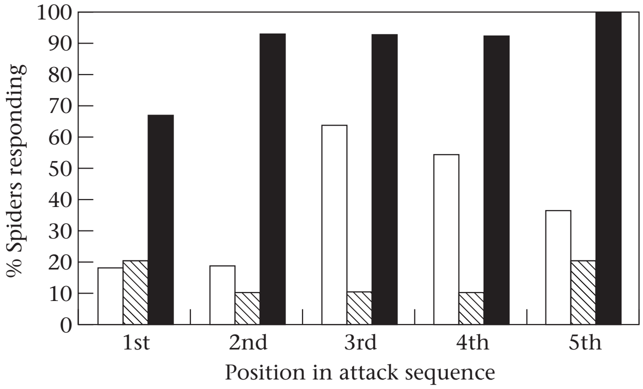

Figure 5. Percentage of adult female spiders (N=240 spiders in 11 colonies) responding with evasive behaviours during sequential 'attacks' (N=5 individuals/attack series) as a function of position (rank) within the attack sequence order. Bars represent responses to different sensory cues from the simulated predator stimulus: web contact only (☐); airborne vibration only (▨); web vibration only (■).

the nature of the vibration stimulus applied (three-dimensional log-linear analysis: G_{22}=137.99, $P<0.0001$). Subsequent analyses revealed that this result was based on significant differences in the proportion of responses by stimulus type (G_{10}=130.234, $P<0.0001$) as well as the position in the attack sequence (G_{12}=26.29, P=0.0097). While the proportion of individuals responding to airborne vibration alone was low and similar across the attack sequence, the proportion of individuals responding to web-borne vibration and web contact were higher and varied across the sequence of attack (Fig. 5). Responses to web-borne vibration were similar to those in the previous experiment, with disproportionately more spiders bailing out as the attack sequence proceeded (increasing from 29.6 to 70.4%). In addition, more spiders responded to web contact alone with evasive behaviours later in the sequence, showing a shift from a majority of startle, pluck and bat behaviours at first (63.4% for first and second spiders) to run away and bail out later (54.6–70.3% for the third–fifth spiders). These results suggest that the early warning mechanism depends almost entirely on web-borne cues, but may involve detection of vibrations caused by the reaction(s) of other spiders as well as vibrations produced by the predator.

DISCUSSION

Our observations confirm that the decrease in an individual spider's risk of capture by wasps when in a larger colony and surrounded by others is attributable to reduced capture success of the predator. This result differs from that expected from the predictions of passive antipredator mechanisms (i.e. dilution and selfish herd effects; Hamilton 1971), which assume a reduction in the probability of capture based solely on population size and spatial arrangement of prey, but a constant capture rate of the predator. Reduced capture success of wasps is not likely to be a result of the impediment caused by more complex webbing in larger colonies, as most of the predatory wasp species in question appear to fly easily within colonies. Success of wasp predators of *M. incrassata* depends instead largely on two factors: (1) an attack strategy incorporating the element of surprise; and (2) the reponse of the spider dropping from the web (bailing out) (Rayor 1997). The spider behaviour discussed above demonstrates that antipredator strategies used by individual spiders vary during the attack sequence of the wasp (i.e. as wasps move from spider to spider in the attack sequence, individuals are more likely to drop from the web). This indicates that as the attack proceeds, the wasp loses the element of surprise because spiders become aware of its presence and take evasive action, which also supports predictions of the early warning hypothesis.

The simulated attacks on spiders in sequence produced responses similar to those seen in naturally occurring attacks, and provide further evidence of spider perception of an advancing attack. These observations support predictions of the early warning hypothesis, suggesting that spiders in larger groups are better able to perceive approaching danger at greater distance, through vibrations in the silk of colony webbing produced by wasp wingbeats or by evasive behaviour of other spiders (Hodge & Uetz 1992). Colony webbing is highly conductive of vibratory signals, and spiders within the largest colonies may perceive vibration up to several metres from the source (R. S. Wilcox & G. W. Uetz, unpublished data).

Risk of capture varies with spider size (age) and reproductive status (Rayor & Uetz 1993). Larger spiders (adult females) are preferred targets, and females with eggs have a reproductive investment that would be vulnerable to parasites if they were killed (Hieber & Uetz 1990; Rayor & Uetz 1990). Therefore, they would be expected to respond to a predator threat at greater distances than mid-sized juveniles (which are less likely to be at risk from wasps). Moreover, escape responses of larger spiders would generate a greater amplitude disturbance in the web, alerting individuals farther away.

Since orb-weaving spiders use vibration as a means of prey detection and communication, the joining of webs in colonial groups has been suggested either as a preadaptation for social living, or an important advantage accruing from group living (Burgess & Witt 1976). The matrix of interconnected webbing in colonies of orbweavers allows individuals to share information, similar in some ways to the 'communication networks' described by McGregor & Peake (2000). However, while this network of webbing primarily benefits receivers, most of the information gained by spiders is not necessarily from comunication or signals per se, but rather from cues (e.g. prey and predator vibrations, behaviours of other spiders). Even so, information from these cues may have both positive and negative impacts on fitness. Spiders in colonies clearly detect the presence of prey in nearby webs or framework webbing, which may have two fitness impacts: (1) increase the opportunity for prey-stealing; and (2) allow spiders to move to a capture-ready position and take advantage of the 'ricochet effect' wherein escaped prey bounce onto other webs (Uetz 1989). These mechanisms may serve to increase individual prey capture rates, and/or reduce variance in capture rate over time (Caraco et al. 1995). Spiders also communicate with each other in both mating encounters and aggressive interactions using web-borne signals (Barth 1986), and there is considerable evidence that this information is shared within colonial spider webs (Buskirk 1975; Burgess & Witt 1976; Uetz & Hieber 1997; R. S. Wilcox, C. S. Hieber & G. W. Uetz, unpublished data). However, the same mechanisms that allow web-building spiders to detect and locate prey and communicate with each other may also serve as an effective means of protection against predators for colonial web builders, as a network for information sharing. The behaviour of colonial spiders indicates an 'early warning system' that involves not only monitoring predator cues but the behaviour of others, a mechanism seen in other taxa (Hodge & Uetz 1992; Eason & Stamps 1993; Lima 1995b). Taken together, our results provide strong support for additional fitness benefits based on a unique 'early warning' mechanism within colonial spider webs. This mechanism incorporates both enhanced sensory detection (the 'many eyes' hypothesis demonstrated in avian flocks by Bertram 1978; Kenward 1978) and information sharing through web vibrations (the 'Trafalgar' effect displayed by ocean skaters; Foster & Treherne 1981; Treherne & Foster 1982).

One question not fully addressed in this study concerns the degree of discrimination and recognition of predatory wasp species by spiders. Spiders are known to be capable of discriminating between various forms of vibration from sources in their environment, based upon sensitivity of sensory organs to specific frequency ranges (Barth 1986). Previous research suggests that *M. incrassata* has egg sac defence behaviours that have coevolved with a predatory fly, *Arachnidomyia lindae* Souza-Lopez, and that spiders recognize the predatory fly by wingbeat frequency (unpublished data). Studies of predatory wasp behaviour by Rayor (1997) suggest that at least one of several wasp species attacking *M. incrassata* (*Poecilopompilus mixtus*, Pompilidae), has exploited bailing out behaviour by inducing spiders to leave webs, then following the spiders to the ground (where the wasp has a capture advantage). A similar strategy has been reported for a mud-dauber wasp (*Sceliphron caementarium* Drury, Sphecidae) attacking solitary orb weavers (Blackledge & Pickett 2000). Given that there are several predatory wasp species from different families attacking *M. incrassata*, variation in the frequency of wingbeats between these species, and low-level selection pressure from any one of them may make specific responses unlikely. However, despite a lack of species specificity in response, fitness gains from a generalized antipredator mechanism like the early warning effect might well be substantial.

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