Behav Ecol Sociobiol (1990) 27:77–85

Behavioral Ecology and Sociobiology

Trade-offs in foraging success and predation risk with spatial position in colonial spiders

Linda S. Rayor and George W. Uetz

Department of Biological Sciences, University of Cincinnati, Cincinnati, OH 45221-0006, USA

Received September 6, 1989 / Accepted February 18, 1990

Summary. Colonial web-building spiders respond to trade-offs between selective forces relative to spatial position within colonies and thus provide support for the selfish herd theory. The size distribution of spiders within colonies of *Metepeira incrassata*, a colonial orb-weaver (Araneae: Araneidae) from tropical Mexico is nonrandom; larger (mature) spiders and females guarding eggsacs are more prevalent in the center, whereas more small (immature) spiders are found on the periphery. Experimental field studies with spiders of selected size classes show that larger spiders actively and aggressively seek protected positions in the center of the colony webbing, even though prey availability and capture rates are significantly higher on the periphery. Attacks by predatory wasps, other spiders, and hummingbirds are more frequent on the periphery than in the core of the colony. Reproductive females on the periphery are at greater risk because they are captured more often than smaller spiders, and if their egg sacs consequently remain unguarded, chances of cocoon parasitism are increased. As a result, spiders in the core of the colony have greater reproductive success, producing more egg sacs with greater hatching frequency. Colonial spiders thus appear to be making a trade-off between foraging and protection from predation and show a spatial organization predicted by the selfish herd theory. The influence of such trade-offs on individual fitness and the structure of colonies is discussed.

Introduction

Food resources and predation risk are not uniformly distributed in space; therefore, the way animals space themselves may have profound effects on individual fitness. Because not all individuals within a group experience the benefits and costs of the social environment equally, this is a particular problem for social animals. Ecological costs and benefits that accrue relative to spatial position have been demonstrated in schooling fishes and flocks of birds (Milinski 1977; Jennings and Evans 1980). Individuals on the periphery of groups may be at greater risk of predation (Horn 1968; Coulson 1968; Tenaza 1971; Gross and MacMillan 1981). The selfish herd theory (Hamilton 1971) predicts that animals in social groups can decrease individual risk and increase fitness by attempting to maneuver to a central position where conspecifics are between them and predators, although recent evidence suggests this is not always so (Parrish 1989).

Animals make trade-offs in their foraging behavior to reduce predation risk by shifting foraging locations or by altering activity patterns or movement (Stein and Magnuson 1976; Milinski and Heller 1978; Sih 1980; Werner et al. 1983; Fraser and Huntingford 1986; Gilliam and Fraser 1987; Dill 1987; Werner and Hall 1988; Pitcher et al. 1988; Abrahams and Dill 1989). However, the nature of a species' social organization may place constraints on decision-making options with regard to spacing within a group. Individuals within mobile schools or flocks are able to change their relative spatial position rapidly in response to perceived threat. Colonial nesting species, which have fixed nest sites, experience differential cost relative to position (Horn 1968; Tenaza 1971; Hoogland and Sherman 1976; Major 1978; Gross and MacMillan 1981; Foster 1989). However, in colonial nesting species, where individuals guard or incubate eggs at the nest site, they forego foraging or leave to forage elsewhere. Although differences in predation risk between regions of some colony types are well documented (Tenaza 1971), the effect of spatial position on foraging success and the interaction of the two in shaping group structure are less understood in other social animals (Major 1978; Rypstra 1979).

The spacing of colonial web-building spiders makes them uniquely suited for examination of the effects of spatial position on the trade-off between prey capture and predation risk. Since web-building spiders are "sit-and-wait" predators, colonial groups constitute non-

---

Offprint requests to: G.W. Uetz

mobile foraging "flocks" (Rypstra 1979; Uetz 1986, 1988a, b). In these flocks, individuals occupy temporarily fixed foraging locations relative to one another in three-dimensional space (Uetz and Cangialosi 1986). Although position can be changed on a daily basis when webs are rebuilt and spacing may change with food availability (Uetz et al. 1982), the spiders' locations are usually fixed for several days in succession. Hence, colonial spiders offer a decided advantage over more motile species in examining trade-offs between foraging success and predation risk. In this study, we investigate trade-offs in spacing behavior of colonial web-building spiders (*Metepeira incrassata*) in response to conflicting selection pressures: (1) how spiders' spatial positions within the colony effect their foraging success as well as their predation and parasitization risk and (2) how these trade-offs affect the size-structure of the spider colony.

Methods

Field observations of *Metepeira incrassata* (Araneidae) colonies were made in Fortin de las Flores, Veracruz, Mexico, for 11 months between July and December 1987 and between August and December 1988. These time periods encompassed the end of the rainy season (July–August) and the beginning of the dry season (September–January). Fortin de las Flores is in a region of montane tropical rainforest, now largely agricultural (information on habitat is available in Benton and Uetz 1986 and Uetz and Hodge (1990)). The spider colonies observed were on a coffee plantation and hotel grounds, typically suspended between vegetation in open sunny spots near flower beds and mulch piles. Seven colonies had between 250 and 450 individuals, three others had between 750 and 1500 individuals. Five of the colonies were artificially created in spider "pens" erected in the coffee plantation; the others formed naturally. The pens consisted of four 2-m high external poles (in a 3 m × 3 m square) and four internal poles (in a 1 m × 1 m square) with nylon rope tied between the poles, which gridded the pen into 18 subdivisions (1 m^3 each). The pens were entirely open, which allowed free and normal flow of insect prey through the colony. Although the spiders were free to leave, once webs and colony frame lines were established spiders remained in pens.

During observation and/or experimentation, determination of spider position was conservative. Spiders were considered to be in the core of the colony only if their webs were entirely enclosed by 2–3 layers of other webs; webs designated as peripheral were limited to those that had free access to the outside. Based on regular censuses of spider position, approximately 60% of the spiders in colonies of 250–1000 individuals are found on the periphery. These disparities in spider numbers in the core and periphery were corrected for in statistical tests when appropriate. In the case of prey capture data, no correction was needed, as equivalent areas with approximately equal spider density were observed. Observations of parasitoid attacks on egg sacs were corrected differently since approximately 60% of the sacs were found in the core.

Colony structure. To determine the relative position of spiders of different size-classes within colonies, previously undisturbed colonies were disassembled ($n=5$). All spiders were collected, and the body length of individuals (measured from the anterior edge of the cephalothorax to the posterior tip of the abdomen) was measured and recorded. In *Metepeira incrassata*, size is an accurate reflection of age; larger spiders were older (Uetz, unpublished). The spider's position from the central core area of the colony and the presence of egg sacs were recorded.

These first studies of colony size structure suggested three hypotheses concerning mechanisms to account for the observed size structure during colony formation. The null hypothesis (H_0) is that spatial position is independent of spider size; the size structure of colonies is random. An alternative "expansion" hypothesis (H_1) suggests that the colony structure is a product of expansion around the initial, large foundresses. In this scenario, the spatial position of older spiders is progressively enveloped by the webs of younger spiders. A "behavioral" alternative (H_2) suggests that colony structure is a product of behavioral interactions; large spiders actively move into the core, displacing smaller individuals toward the periphery.

A series of experiments tested these hypotheses by introducing marked spiders of a given size-class on sequential days to the pens and determining the resulting size structure of the newly created colony. Over 300 individuals in three size classes, in equal proportions (similar to those of each size-class found in the disassembled colonies) were introduced into each pen. All spiders were placed on the rope surrounding the central-most grid. In all experiments, the position of the spiders was recorded on day 4 after the first introduction.

In the first experiment on mechanisms of colony formation, all size-classes (approximately 300 spiders in similar proportions of disassembled natural colonies) were introduced in a random order on day 1. This tested the null hypothesis (H_0), which predicts a random size distribution. In a second experiment utilizing approximately the same number of spiders, large spiders (6–10 mm) were added on day 1 and allowed to build webs; medium spiders (4–5.9 mm) and small (1–3.9 mm) spiders followed on days 2 and 3, respectively. This tested H_1, the colony expansion hypothesis, which predicts that large spiders form a core and smaller individuals build around it. In a third experiment, replicated three times, small spiders were added on day 1, followed by medium and large spiders on subsequent days. This experiment discriminated between the colony expansion (H_1) and behavioral interaction (H_2) hypotheses in structuring the colonies. If small individuals formed the core, it would support the colony expansion hypothesis; if large spiders moved into the core, it would suggest that behavioral interactions mediate the size structure.

Prey capture. Prey capture success was assessed by direct observation of insects captured after flying within 1 m^3 of either the periphery of the core of a colony during half-hour intervals. The density of spiders is approximately the same in both locations (40 spiders/m^3). From previous research (Uetz et al. 1982; Uetz 1989), we have determined that 30 min is an optimum amount of time for uninterrupted observation (because of the unique visual problems associated with observing 3-dimensional colonial webs). Observations in all locations were made with equal frequency throughout daylight hours to accurately reflect capture rates of these diurnally active spiders.

Prey data were collected in two ways: (1) observations of locations and colonies were alternated on different days in order to eliminate successive observation of the same spiders (a total of 28.5 h on the periphery and 28 h in the core of four different colonies and (2) simultaneous (paired) observation of peripheral and core spiders (sometimes by two observers) at different time periods alternated among four different colonies (for a total of 26 h).

Predation, parasitism, and reproductive success. In a separate set of observations, colonies were observed for 397 h for attacks by predators and egg sac parasites. For each wasp, spider, or avian predator, the number of unsuccessful attacks and successful catpures, along with the size and position (core or periphery) of the spider, were recorded. For each egg sac parasitoid, attacks (close approaches and harrassment) and spider position were recorded. Because flies usually attack several spiders in succession, the number of attacks that occurred during a single bout ("run") of attacks in the periphery or core of a colony was calculated.

Females sit upon and actively guard their egg sacs from the time they are laid until the young emerge 4–6 weeks later (at which time they abandon the sac). Representative samples of egg sacs both guarded by females ($n=145$) and hanging unguarded in the colony ($n=161$) were collected from core and peripheral locations.

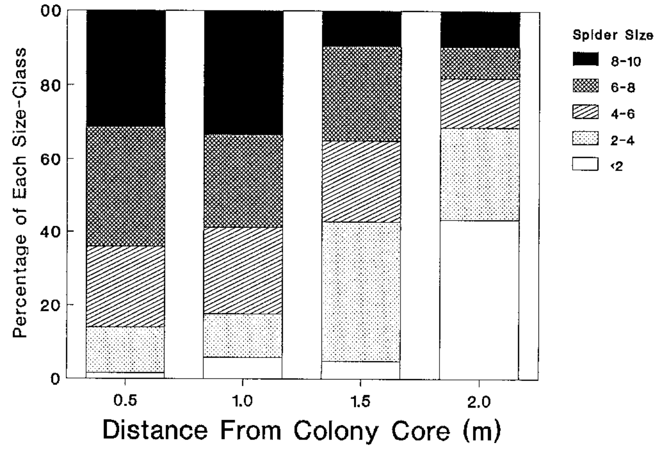

Fig. 1. Size structure of a representative *Metepeira incrassata* colony of approximately 400 individuals. The percentages of spiders of each size-class in 0.5 m zones relative to distance from the center of the colony are shown

In a separate data set, each egg sac laid in the pen colonies ($n = 342$) was located and observed through development (until abandoned or young emerged). For these egg sacs, data were recorded on the date each was laid, its spatial location (core or periphery), whether or not it was guarded, and if and when the sac was abandoned. As soon as an egg sac was abandoned by the female, it was collected, and the number of young or the egg parasitoids that emerged from it were counted.

Results

Colony structure

Since naturally occurring colonies varied in number of spiders and size dimensions, each colony was analyzed separately. For each of the five disassembled colonies, the size distribution of spiders within colonies is nonrandom (G test; $P < 0.001$). Larger, more mature, spiders are concentrated in the core, whereas more small, immature spiders are found toward the periphery (Fig. 1). The largest individuals comprise more than 30% of the spiders in the core, but less than 10% on the edge. Spiders less than 4 mm in size constituted approximately 15% of the individuals found in the core, but an increasingly large component (over 70%) on the periphery.

Only mature females of 6 mm or larger lay eggs. Although the number of egg sacs and the precise egg sac distributions varied between colonies, differences within colonies were significant (G test; $P < 0.05$). Most females guarding sacs were concentrated in the core and relatively infrequent on the periphery. For example, in the colony shown in Fig. 1, 42% of the 42 sacs were located in the core, 25% and 30% in the more external half-meter areas, and only 6% on the periphery.

When the position of spiders was recorded on the fourth day of each colony formation experiment, the size distribution in all cases was similar to that seen in the disassembled colonies (Fig. 2). In all experiments and replicates, larger spiders were more frequent in the core, with more small individuals on the periphery (G test; $P < 0.05$). Thus, the null hypothesis of independence of spider size and spatial position is rejected; spiders do not acquire spatial positions simply as a function of where they were initially introduced.

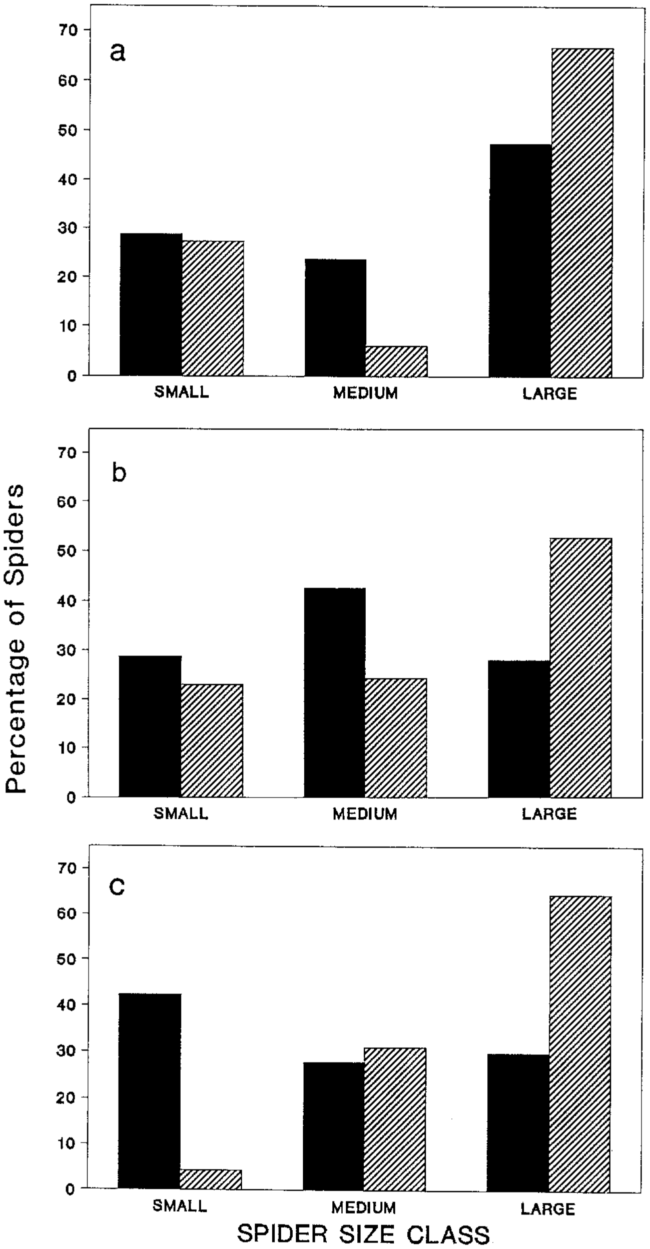

Fig. 2a–c. Percentage of spiders in each size-class found in the periphery (solid) and core (diagonal stripe) at the conclusion of experiments on colony formation. **a** Random introduction of all size-classes on day one. Large spiders were significantly more likely to be in the core (G-test: $G = 5.99$, $P < 0.05$). **b** Large spiders introduced into the pen first. Large spiders were significantly more likely to be in the core ($G = 10.66$, $P < 0.01$). **c** Small spiders introduced into the pen first (pooled data from three replicates not significantly different from each other; Cochran's heterogeneity $\chi^2 = 0.79$, $P > 0.50$). Large spiders were significantly more likely to be in the core ($G = 55.28$, $P < 0.001$)

The results of the third experiment strongly support the behavioral interaction hypothesis over the colony expansion hypothesis (Fig. 2c). Prior to the introduction

Table 1. Summary statistics for prey captured in half-hour observation periods

A. Separate observations:

Colony:	Pen 1	Greenery	Potting	Cortez
Periphery:				
$\bar{x}$	7.8^{a}	8.0^{a}	11.46^{d}	15.89^{e}
(2 SE)	±3.62	±2.37	±2.8	±4.68
N	10	12	28	9
Core:				
$\bar{x}$	3.62^{b}	4.80^{b}	$7.20^{a,c}$	$5.56^{b,c}$
(2 SE)	±0.92	±1.81	±1.90	±2.56
N	13	10	20	9
+	3.74	3.66	6.07	13.5
P	<0.01	<0.01	<0.001	<0.001

[a–e] Different letters indicate means significantly different ($P<0.05$) by multiple range tests (modified Tukey's procedure)

B. Paired (simultaneous) observations:

Colony	Pen 1	Pen 3	Potting	Cortez
Periphery:				
$\bar{x}$	5.55	5.69	19.77	17.13
(2 SE)	±1.15	±1.02	±4.72	±4.61
N	22	13	9	8
Core:				
$\bar{x}$	3.55	4.39	6.22	5.14
(2 SE)	±0.05	±1.46	±2.30	±2.28
N	22	13	9	8
P-value[f]	<0.01	<0.05	<0.005	<0.01

[f] Wilcoxon paired comparison test

Table 2. Two-way ANOVA for half-hour prey capture observations

Source	Sum of squares	df	Mean square	F	*P*
Main effects	1049.03	4	262.26	12.88	<0.001
Colony position	403.32	3	134.44	6.60	<0.001
	611.44	1	611.44	30.03	<0.001
Interaction (colony × position)	248.32	3	82.77	4.06	<0.01
Residual	2117.21	104	20.36		
Total	3414.56	111			

of the large individuals, the small and medium spiders built a dense complex of webs and retreats. Upon their introduction, the large spiders climbed up spider silk into the established webs and promptly displaced or through agonistic interactions took over smaller individuals' webs and/or retreats. The area of webbing taken over by the large spiders became the colony's core as the smaller animals were forced to move and build new webs around those of the larger spiders. These results indicate that during colony formation, aggressive behavior by large spiders moving into the core was a major factor structuring the colony.

Prey capture

In all colonies, in both paired samples and separate observations, more insect prey were caught (per half hour observation period) on the periphery than in the core (Table 1). Statistical significance of differences in prey capture was determined by several different means, to accomodate questions concerning assumptions of randomness and independence of samples.

The most robust and detailed analysis, a two-way ANOVA, revealed significance in the main effects (position and colony), and a significant interaction of colony × position (Table 2). However, since repeated samples were taken of the same colonies and locations within colonies, this may be considered temporal pseudoreplication (Hurlbert 1984), which violates the randomness and independence assumptions of ANOVA. Although temporal pseudoreplication may be unavoidable, for the purposes of this study its effect may be minimal. Since half-hour observations represent small subsamples (< 5%) of the spiders' daily activity and were never taken in the same colony or location in successive time periods on the same day, they may be sufficiently independent to be considered as replicates in a Two-way ANOVA design with colony and location as main effects. Subsequent testing revealed that differences in prey captured/half-hour between core and periphery positions (the primary factor of interest) were significant in all colonies (t test; $P<0.05$).

The significant colony effect was probably due to the fact that colonies differed in both size and in relative habitat quality, which affected mean number of prey caught per observation session (Table 1). Habitat quality was assessed on the basis of flowering vegetation or organic matter (compost) that attracted potential insect prey; increasing prey capture rate is significant in some cases. The "Pen 1" colony of 250–300 individuals was located over small herbaceous vegetation and near coffee trees. The naturally occurring "Greenery" (350–400 individuals) and the "Potting" and "Cortez" (1000+individuals) colonies were located near flowers and over flower beds and a compost pile, respectively. Prey capture observations for the smaller colonies did not differ significantly although differences between smaller and larger colonies were significant, at least on the periphery (Tukey's procedure; $P<0.05$).

As a non-parametric alternative, a Friedman's chi-square analysis, with colonies as blocks and position as the main effect, was done using the mean number of prey captured per half-hour as a single replicate. This alternative, although less revealing than the above ANOVA, does not require any of the statistical assumptions in question. The result is a significant position effect ($\chi^2=4.0$; $P<0.05$). A subsequent multiple comparison test (modified Tukey's procedure; Zar 1984) revealed that peripheral positions had significantly more prey captures ($P<0.05$).

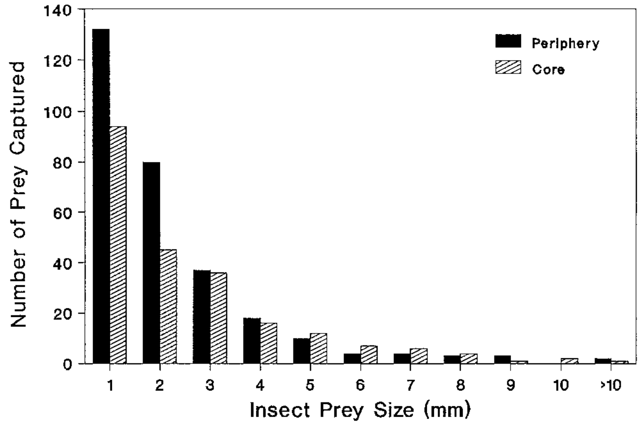

Fig. 3. Size distribution of insect prey captured in peripheral webs (solid) and core webs (diagonal stripe) from a representative *Metepeira incrassata* colony

Because core and peripheral locations are in the same colonies and observations can never be truly independent, we also used a non-parametric paired-sample design and analysis on a separate data set (simultaneous observation of periphery and core). This method also revealed a significant effect of position; prey capture on the periphery was greater in all colonies sampled (Wilcoxon Paired Comparison tests; $P<0.05$).

More small prey items than larger items were caught in all colonies (Fig. 3). There was no significant difference in the size distribution of prey captured in the periphery or core of the pens (Kolmogorov-Smirnov test; χ^2 approximately = 5.38, $P>0.10$) or the Greenery colonies (Kolmogorov-Smirnov test; χ^2 approximately = 1.27; $P>0.10$). However, size distributions of prey captured in the core and periphery were significantly different for the Potting Shed colony (Kolmogorov-Smirnov test; χ^2 approximately = 30.06, $P<0.001$) and the Cortez colony (Kolmogorov-Smirnov test; χ^2 approximately = 24.44, $P<0.001$). These differences are the result of a disproportionate number of mid-sized prey captured on the periphery of the Potting colony, and a disproportionate number of mid- and large-sized prey captured in the core of the Cortez colony. There does not appear to be a difference in the capture efficiency of spiders in the core or the periphery; capture efficiency (captures/hits) and position are independent (G test; $P>0.10$ for all colonies). Although some prey of all sizes escape, a greater proportion of prey 8 mm and larger escapes than is captured (69.3% escape). Lepidoptera, large (> 8 mm) Hymenoptera, muscoid Diptera, and Coleoptera escape most frequently. Taxonomic composition of prey captured in core and periphery was significantly different in all colonies (G test; $P<0.05$), but there are no obvious or consistent trends (Table 3).

Table 3. Proportion (%) of major insect prey taxa captured in the periphery vs core of colonies

Taxon	Periphery	Core	G-test	*P*
Cage 1:				
Coleoptera	19.76	7.26	22.7	<0.01
Diptera	43.11	34.68		
Hymenoptera	17.37	14.52		
Other	37.72	43.55		
N	167	124		
Cage 3:				
Coleoptera	19.78	18.48	7.124	<0.05
Diptera	34.07	28.35		
Hymenoptera	6.59	19.57		
Other	39.56	32.61		
N	91	92		
Greenery:				
Coleoptera	18.95	12.73	16.76	<0.01
Diptera	32.63	34.55		
Hymenoptera	16.84	14.55		
Other	31.58	38.18		
N	95	55		
Potting:				
Coleoptera	15.46	19.28	43.65	<0.01
Diptera	43.66	36.32		
Hymenoptera	20.10	5.38		
Other	20.88	39.01		
N	388	223		
Cortez:				
Coleoptera	22.09	20.37	11.18	<0.01
Diptera	54.07	35.19		
Hymenoptera	8.14	7.41		
Other	15.70	37.04		
N	172	54		

Table 4. Predation by wasps, spiders and hummingbirds on *Metepeira incrassata* during 397 h of observation. Significantly more attacks and captures occurred on periphery ($G=7.02$ $P<0.01$)

	Unsuccessful attacks	Captures	Total attacks/h	Captures/h
Periphery	224	58	0.94	0.193
Core	139	17	0.52	0.057

Predation, parasitism, and reproductive success

A total of 438 predatory attacks on *Metepeira incrassata* were observed. Spiders experience predation from a number of wasp species (92.2% of all attacks observed; pompilids: *Poecilopompilus mixtus, Caliadurgus flavidus*, others; sphecids: *Trypoxylon* sp., others; and ichneumonids) other spiders (6.6% of all attacks observed; salticid *Phidippus* sp., theridiid *Argyrodes* sp.), and hummingbirds (1.2% of attacks). Both total attacks and successful captures were significantly more frequent on the periphery (G test, $G=7.015$, $P<0.01$; Table 4). Peripheral spiders were attacked almost twice as often as core individuals, and 77% of the captures occurred on the periphery. Of the 249 predatory attacks observed in 1988, where size of the victimized spider was known, larger spiders were attacked more frequently. Spiders 5 mm and larger received 58.9% of attacks on the pe-

Table 5. Number of egg sacs parasitized: (a) collected while being guarded by female or hanging unguarded in the colony; (b) located in periphery or core of Pen colonies. Different data sets on egg sacs were used for each test

	Parasitized	Not parasitized	G-test	*P*
(a) Guarded	25	120	20.25	<0.001
Unguarded	65	96		
(b) Periphery	57	135	0.042	>0.50
Core	43	107		

Table 6. Parasitoid attacks on spiders with and without egg sacs (where approximately 60% of the spiders are on the periphery) and only on those with egg sacs (where approximately 60% of the eggs are in the core). The number of attacks that occurred on the periphery or in the core during runs of fly attacks

		Periphery	Core	G-test	*P*
All spiders:					
Wasps	1987	63	56	2.43	>0.10
Flies	1987	124	134	14.97	<0.01
Flies	1988	159	99	0.29	>0.50
Egg sacs only:					
Flies	1987	22	43	1.05	>0.10
Flies	1988	71	59	11.28	<0.001
Attacks/run:					
Flies	1987	124/21	131/28	0.50	>0.50
Flies	1988	140/17	93/14	0.15	>0.50

Table 7. Summary of egg sac data (pen colonies)

1987	Periphery	Core	*P* value
$\bar{x}$ egg sacs/female	1.00	1.13	$P<0.05$[a]
(±2 SE)	±0.0	±0.163	
N	24	33	
$\bar{x}$ offspring/sac	28.92	26.86	$P>0.10$[a]
(±2 SE)	±14.46	±6.01	
N	12	22	
% hatch	65.2%	75.75	$P>0.10$[b]
Est. reproductive success (no. offspring hatched/female)	18.85	23.01	
1988	**Periphery**	**Core**	***P* value**
$\bar{x}$ egg sacs/female	1.204	1.394	
(±2 SE)	±0.096	±0.142	$P<0.05$[a]
N	98	66	
$\bar{x}$ offspring/sac	43.44	41.48	$P>0.10$[a]
(±2 SE)	±19.22	±4.87	
N	61	40	
% hatch	62.7%	78.3	$P<0.01$[b]
Est. reproductive success (no. offspring hatched/female)	32.79	45.27	

[a] Mann-Whitney Two-Sample test
[b] G-test

riphery and 72.9% of attacks in the core, although these size classes only comprise 36% to 38% of the spiders within colonies.

In addition to predators attacking juvenile and adult spiders, *Metepeira incrassata* has four major types of egg sac parasitoids: sarcophagid flies (*Arachnidomyia lindae* Souza-Lopez), chalcidoid wasps (subfamily: Tetrastichinae, *Arachnoobius* sp.), ichneumonid wasps (*Tromatobia* spp.), and mantispids (*Mantispa viridis*). Only the sarcophagid flies and inchneumonid wasps were observed harassing the females and attempting to lay their eggs or larva on or in the sac, although all four types emerged from egg sacs. Female *Metepeira* guard egg sacs by sitting upon them and encircling them with their legs, as well as actively defending them against attack by sarcophagid flies and ichneumonid wasps. For example, they flail their legs at the fly, race around the sac to prevent the fly from sitting on it, and carefully groom the sac once the fly has left. The flies persistently return to a recently laid sac during a round of attacks. Unguarded egg sacs were significantly more likely to be parasitized than guarded sacs ($G=20.25$, $P<0.001$), by all types of parasitoids (Table 5).

Parasitoids apparently have no difficulty negotiating their way through the colony and avoiding webs, although the observed attacks on spiders differed between years and the subsample of spiders examined (Table 6). Sarcophagid fly attacks on spiders with egg sacs (with 60% of the eggs in the core) were significantly more frequent on the periphery in 1988 ($G=11.28$, $P<0.001$), but not in 1987 ($G=1.05$, $P>0.5$). The series of fly attacks that occurred during a run were equally distributed in the periphery and core during both 1987 and 1988 (G test, $P>0.10$). Ichneumonid wasps, observed only in 1987, were seen with equal frequency in the periphery and core ($G=2.43$, $P>0.10$). Despite some differences in observed rates of attack, parasitization rates of Pen egg sacs followed through their development did not differ significantly between the periphery and core (Table 5, $G=0.042$, $P>0.10$).

Reproductive success varies with position in the colony (Table 7). There were significant differences in the number of egg sacs produced per female on the periphery and in the core during each year (Mann-Whitney Two Sample test; $P<0.05$), although the number of eggs per sac is not significantly different (Mann-Whitney test; $P>0.10$). Spiders in core positions lay more egg sacs, and (in 1988) have a higher rate of hatching success (G test; $P<0.05$), which leads to a higher estimated reproductive success (no. of offspring hatched per female).

Discussion

The importance of both foraging considerations and predation in the evolution of spider coloniality have recently received considerable attention. Foraging advantages for colonial spiders include increased prey capture efficiency and reduced variance in prey (Gillespie 1987; Uetz 1988a, b, 1989; Rypstra 1989). While a number of studies suggest that coloniality reduces predation risk (Lubin 1974, 1980; Rypstra 1979), others have shown either no such effect (Spiller and Schoener 1989) or the opposite effect – colonies are conspicuous targets for predators or egg sac parasitoids (Lubin 1974; Smith 1982; Hieber and Uetz 1990).

Our studies of the structure of *Metepeira incrassata* colonies suggest that spiders respond to trade-offs between these selective forces relative to spatial position within colonies, and provide support for the selfish herd theory of Hamilton (1971). Spiders on the periphery capture more insect prey, but also experience greater predation. *Metepeira incrassata* colonies have larger individuals concentrated in the core and increasing numbers of smaller individuals located toward the periphery. Results of colony formation experiments suggest that this size-structure is maintained by behavioral interactions, primarily by large individuals establishing webs in the core. Differential fitness relative to spatial position appears to be the driving force behind this, as web sites in the core of the colony allow protection from predation and higher reproductive success.

Natural spider colonies, however, are unlikely to form by the gradual accumulation of different size-classes on subsequent days (as in our experiments or in aggregations of territorial animals subdividing spatial resources – see review by Stamps 1988). Observations of the ways that new colonies are formed in nature suggests that the mechanisms inherent in both the behavioral interaction (H_3) and colony expansion (H_2) hypotheses may interact in colony formation. Unlike some of the other social or colonial spiders that establish new colonies by large groups "swarming" from the natal colony (Lubin and Robinson 1982), most new *M. incrassata* colonies are formed when falling branches or leaves subdivide the original colony or when individuals are blown out of the colony to new areas during exceptionally high winds.

During Hurricane Gilbert, which buffeted the Gulf coast of Mexico in September 1988, one of us (LSR) observed that *M. incrassata* webs were blown one into another until entire portions of the colony were collapsed into one long silken rope of webbing with spiders clinging to it. These silken ropes were blown into new areas where, if sufficient supporting structures were available, the spiders began to build new colonies. Large females always began construction first. Whether due to innate aggregation tendencies and/or protocooperative colony construction (Cangialosi and Uetz 1987), or because the first individuals to build tend to connect framelines and end up closer together, the result is that large spiders build the core of the new colony and smaller individuals that start later build around them. In addition to these dramatic changes in colonies, there is continual turnover in individuals over the long-term existence of colonies. Individuals eventually die and are replaced by their younger counterparts, but the largest individuals continue to predominate in the colony core. These observations suggest that the colony structure is a dynamic equilibrium; mechanisms of colony expansion (H_2) act in the formation of colonies, while behavioral interactions (H_3) serve in the maintenance of colony structure over time.

Although proximate behavioral mechanisms may explain the origin and maintenance of colony structure, the ultimate causative mechanism(s) may be found in the relative distribution of costs and benefits with spatial position within the colony. While foraging benefits are greater on the periphery of colonies, costs – in terms of predation risk – are also much higher there. Increased predation risk on the periphery of spider colonies makes choice of web site an adaptive decision (Rypstra 1979), and thus larger spiders appear to be making a trade-off of reduced food for increased safety from predation, as predicted by the selfish herd theory (Hamilton 1971).

If foraging success alone were the sole consideration in where spiders positioned themselves, spiders could maximize fitness by locating where they could obtain as much energy as possible (to reach large adult size and attain maximum egg output). However, because core size increases as the size of the colony increases, the difference in prey capture between the periphery and core is more pronounced in larger colonies (Table 1). With increasing colony size, prey must avoid or crash through more webs to get into the deep core of the colony. Rypstra (1979) has shown that the most prey is captured midway between the outer edge (periphery) and the center (core) of *Cyrtophora citricola* colonies. This may be attributable to the "ricochet effect" where prey that is not captured in the first web it strikes is more likely to become entangled in subsequent webs it hits (Uetz 1986, 1989). In any case, spiders in web locations in the colony core are at a clear foraging disadvantage.

The reduction in prey capture rate (24%–42%) as a consequence of core position may be seen as a measure of the energetic cost of predation risk, as suggested by Abrahams and Dill (1989). A spider on the periphery has a three times greater probability of being attacked and captured by predators. Moreover, predator attacks are not evenly distributed by spider size; the smallest spiderlings and larger spiders are attacked most frequently. Large female spiders with egg sacs are therefore subject to disproportionate predation pressures; not only do they experience greater predation risk themselves, but they must content with the risk to their offspring from egg sac parasitoids and predatory wasps (*Trypoxylon*) specializing on spiderlings.

There is thus a complex trade-off between predation risk, foraging success, and (ultimately) fitness, with spatial position in a colony. A female spider on the periphery has a greater chance of being killed because she is on the edge of the colony and because there are proportionally fewer large spiders in this area. If she is killed and her sac consequently unguarded, it has a much higher chance of being parasitized. Thus, the female could lose not only her life but also her reproductive investment by occupying a web site on the periphery of the colony. Reproductive success is higher for spiders in the core of colonies, as a consequence of more egg sacs laid per female and a greater hatching success. This would suggest that large reproductive (or soon to be reproductive) individuals can maximize fitness by making a trade-off to live where food supplies are poorer, but the chances of surviving longer and producing more egg sacs and viable offspring are improved.

Since there is a larger concentration of egg sacs in the colony core, the majority of hatchlings begin their lives there at a disadvantage. Prey availability is lower, and larger spiders have the advantage in contests over prey items (Uetz and Hodge 1990). Smaller spiders may simply be forced to the edge through behavioral interactions or lack of space deeper in the core, or they may be making a trade-off of greater risk for increased prey. The cost of defending space within the colony may be higher for smaller spiders, and the probability of winning low (size asymmetries are used to settle web contests in *Metepeira*; Uetz and Hodge 1990). In addition, because predators prefer larger-sized spiders or because the smaller size-classes are more abundant, smaller individuals may actually experience somewhat reduced predation risk on the periphery. Thus, their apparent trade-off makes sense – juveniles may take a chance in the peripheral "fast lane" where there is a greater availability of food and where they can grow faster and have better odds of actually reaching sexual maturity.

The structure of *Metepeira incrassata* colonies suggests that spiders respond to trade-offs in ecological factors relative to spatial position in the colonies, and may represent a dynamic optimization process (Mangel and Clark 1988; Werner and Hall 1988). Numerous questions may be raised regarding the behavioral mechanisms inherent in this process. How are spiders able to ascertain their position and determine costs and benefits relative to other positions? It has been suggested that spiders may assess foraging success by gut distension or time since last meal (Vollrath 1987), but how do spiders assess predation risk – through perception of vibrations during predator attacks on neighbors? Further research into these mechanisms as well as the size and age-related costs and benefits is necessary before a realistic dynamic optimization model can be developed.

Acknowledgements. This research was supported by NSF Grant BSR-8615060 and by grants from the National Geographic Society (‰3095-85 to GWU) and the Exline-Frizzell Arachnological Research Fund (to LSR). We thank the Mexican government, Direccion General de Conservacion y Ecologia de los Recursos Naturales, Direccion de Flora y Fauna Silvestres for permission to work in Mexico. We wish to thank Ana Valiente de Carmona and family, Becky Cotera, Loli Alvarez-Garcia, Blanca Alvarez, and LeOra Forbes, for not only their kindness in tolerating and protecting the spiders on their land, but also their friendship. We are also grateful to C. Hieber, M. Hodge, and C. Gilbert, who helped build the spider pens and assisted in various other field work. Spider predators and parasites were kindly identified by H.E. Evans (predatory wasps), H. Souza-Lopez (sarcophagid fly), J. LaSalle (chalcidoid wasps), D. Wahl (ichneumonid wasps), and C. Hieber (mantispids). We also wish to thank E. Linsenmair, A. Rypstra, C. Craig, and an anonymous reviewer for their helpful editorial comments.

References

Abrahams MA, Dill LM (1989) A determination of the energetic equivalence of the risk of predation. Ecology 70:999–1007

Benton MJ, Uetz GW (1986) Variation in life-history characteristics over a clinal gradient in three populations of a communal orb-weaving spider. Oecologia 68:395–399

Cangialosi KR, Uetz GW (1987) Spacing in colonial spiders: effects of environment and experience. Ethology 76:236–246

Coulson JC (1968) Differences in the quality of birds nesting in the centre and on the edges of a colony. Nature 217:478–479

Dill LM (1987) Animal decision making and its ecological consequences: the future of aquatic ecology and behavior. Can J Zool 65:803–811

Foster SA (1989) The implications of divergence in spatial nesting patterns in the geminate Caribbean and Pacific sergeant damselfish. Anim Behav 37:465–476

Fraser DF, Huntingford FA (1986) Feeding and avoiding predation hazard: the behavioral response of the prey. Ethology 73:56–68

Gillespie RG (1987) The role of prey availability in aggregate behaviour of the orb weaving spider *Tetragnatha elongata*. Anim Behav 35:675–681

Gilliam JF, Fraser DF (1987) Habitat selection under predation hazard: test of a model with foraging minnows. Ecology 68:1856–1862

Gross MR, MacMillan AM (1981) Predation and the evolution of colonial nesting in bluegill sunfish (*Lepomis macrochirus*). Behav Ecol Sociobiol 8:163–174

Hamilton WD (1971) Geometry for the selfish herd. J Theor Biol 31:295–311

Hieber CS, Uetz GW (1990) Colony size and parasitoid load in two species of colonial *Metepeira* spiders from Mexico (Araneae: Araneidae). Oecologia 82:145–150

Hoogland J, Sherman PW (1976) Advantages and disadvantages of bank swallow (*Riparia riparia*) coloniality. Ecol Monogr 46:33–58

Horn HS (1968) The adaptive significance of colonial nesting in the Brewer's blackbird *Euphagus cyanocephalus*. Ecology 49:682–694

Hurlbert SH (1984) Pseudoreplication and the design of ecological field experiments. Ecol Monogr 54:187–211

Jennings T, Evans SM (1980) Influence of position in the flock and flock size on vigilance in the starling, *Sturnus vulgaris*. Anim Behav 28:634–635

Lubin YA (1974) Adaptive advantages and the evolution of colony formation in *Cyrtophora* (Araneae: Araneidae). Zool J Linn Soc 54:321–339

Lubin YA (1980) Population studies of two colonial orb-weaving spiders. Zool J Linn Soc 70:265–287

Lubin YA, Robinson MH (1982) Dispersal by swarming in a social spider. Science 216:319–321

Major P (1978) Predator-prey interactions in two schooling fishes, *Caranx ignobilis* and *Stolephorus purpureus*. Anim Behav 26:760–777

Mangel M, Clark CW (1988) Dynamic modelling in behavioral ecology. Princeton University Press, New Jersey

Milinsky M (1977) Do all members of a swarm suffer the same predation? Z Tierpsychol 45:373–378

Milinski M, Heller R (1978) Influence of a predator on the optimal foraging behavior of sticklebacks, *Gasterosteus aculeatus*. Nature 275:642–644

Parrish JK (1989) Re-examining the selfish herd; are central fish safer? Anim Behav 38:1048–1053

Pitcher TJ, Lang SH, Turner JA (1988) A risk-balancing trade off between foraging rewards and predation hazard in a shoaling fish. Behav Ecol Sociobiol 22:225–228

Rypstra AL (1979) Foraging flocks of spiders – a study of aggregate behavior in Crytophora citricola Forskal (Araneae: Araneidae) in West Africa. Behav Ecol Sociobiol 5:291–300

Rypstra AL (1989) Foraging success of solitary and aggregated spiders: insights into flock formation. Anim Behav 37:274–281

Sih A (1980) Optimal behavior: can foragers balance two conflicting demands? Science 210:1041–1043

Smith DR (1982) Reproductive success of solitary and communal *Philoponella oweni* (Araneae: Uloboridae). Behav Ecol Sociobiol 11:149–154

Spiller DA, Schoener TS (1989) Effect of a major predator on grouping of an orb-weaving spider. J Anim Ecol 58:509–523

Stamps JA (1988) Conspecific attraction and aggregation in territorial species. Am Nat 131:329–347

Stein RA, Magnuson JJ (1976) Behavioral response of a crayfish to a fish predator. Ecology 57:751–761

Tenaza R (1971) Behavior and nesting success relative to nest location in Adelie penquins (*Pygoscelis adeliae*). Condor 73:81–92

Uetz GW (1986) Web-building and prey capture in communal orb weavers. In: Shear WA (ed) Spiders: webs, behavior, and evolution. Stanford University Press, Stanford, pp 207–231

Uetz GW (1988a) Risk-sensitivity and foraging in colonial spiders. In: Slobodchikoff CA (ed) Ecology of social behavior. Academic Press, San Diego, pp 353–377

Uetz GW (1988b) Group foraging in colonial web-building spiders: evidence for risk-sensitivity. Behav Ecol Sociobiol 22:265–270

Uetz GW (1989) The "ricochet effect" and prey capture in colonial spiders. Oecologia 81:154–159

Uetz GW, Cangialosi KR (1986) Genetic differences in social behavior and spacing in populations of *Metepeira spinipes* Pickard-Cambridge (Araneae: Araneidae), a communal-territorial orb weaver. J Arachnol 14:159–174

Uetz GW, Hodge MA (1990) Influence of habitat and prey availability on spatial organization and behavior of colonial web-building spiders. Nat Geogr Res 6:22–40

Uetz GW, Kane TC, Stratton GE (1982) Variation in the social grouping tendency of a communal web-building spider. Science 217:547–549

Vollrath F (1987) Growth, foraging, and reproductive success. In: Nentwig W (ed) Ecophysiology of spiders. Springer, Berlin Heidelberg New York, pp 357–370

Werner EE, Hall DJ (1988) Ontogenetic habitat shifts in bluegill: the foraging rate-predation risk trade-off. Ecology 69:1352–1366

Werner EE, Gilliam JF, Hall DJ, Mittelbach GG (1983) An experimental test of the effects of predation risk on habitat use in fish. Ecology 64:1540–1548

Zar JH (1984) Biostatistical analysis. Prentice-Hall, Englewood Cliffs NJ