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Social spider defense against kleptoparasitism

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Summary. Because of the large amount of webbing they provide, social spider colonies often host other satellite spider species referred to as kleptoparasites or food stealers. Such kleptoparasites may take advantage of increased prey capture rates associated with large spider aggregations. This study investigated the relationship between a cooperatively social spider species, *Anelosimus eximius* (Araneae: Theridiidae), which lives in the undergrowth of tropical rainforests in Peru, and its kleptoparasite, *Argyrodes ululans* (Araneae: Theridiidae), which specializes in foraging in *An. eximius* webs. Although large aggregates of spiders may be more attractive to kleptoparasites, the benefits of group defense may offset this cost. Natural colonies were observed, and enclosed field colonies containing fixed numbers of host spiders were manipulated in order to determine whether kleptoparasite success is affected by the number of social spiders that are available for defense. Prey was less likely to be stolen by *Ar. ululans* when a greater number of host *An. eximius* spiders were involved in prey capture. When hosts detected a kleptoparasite earlier and chased it more often, prey was more likely to be successfully defended. *Ar. ululans* was more successful in stealing small prey items in all colonies and gave up more readily on very large prey (> 11 mm). I conclude that communal living and group defense in *An. eximius* confer protection from the kleptoparasite *Ar. ululans.*

Introduction

Kleptoparasites are organisms that forage by stealing food procured by other organisms (Brockmann and Barnard 1979), which presumably reduces or eliminates searching and handling costs (Curio 1976). Many spiders in the genus *Argyrodes* are adapted for a kleptoparasitic lifestyle. Rather than building their own webs, they live within the webs of other spiders and steal their captured insect prey (Exline and Levi 1962; Gertsch 1979). Although these kleptoparasites are common and probably have detrimental effects on their hosts (Rypstra 1981; Vollrath 1984; Cangialosi 1990), little is known about the defense mechanisms that host spiders may have coevolved in response to *Argyrodes.*

Some ecological and behavioral conditions that favor kleptoparasitism are: (1) high host concentration, (2) large quantities of available food, (3) spatial or temporal predictability of food availability, and (4) food detectability (Brockmann and Barnard 1979; Barnard 1984). Social spider colonies, usually located in insect rich tropical areas, apparently provide prime conditions for a large variety of kleptobionts since they attract many of these satellite species including kleptoparasitic *Argyrodes* (Christenson 1984; Vollrath 1987; Griswold and Meikle-Griswold 1987). Smith Trail 1980) and Elgar (1989) both found that communal groups of spiders contain a greater number of *Argyrodes* individuals than spiders in solitary webs. This increased attractiveness to enemies is often cited as a disadvantage of living in a communal group (Wilson 1975; Wittenberger 1981). However, groups of individuals may be better equipped for defense against enemies than solitary individuals as a result of increased efficiency in detecting intruders (mutual vigilance, Wittenberger 1981; Pulliam 1973; Pulliam and Caraco 1984) or improved direct behavioral defense by a greater number of defenders (mobbing, Wittenberger 1981 and references therein). In his review of scrounger strategies, Barnard (1984) lists three types of strategies that hosts use to reduce kleptoparasitism: (1) evasion – avoiding attack, (2) retaliation – deterring the kleptoparasite and reclaiming stolen items, and (3) tolerance/compensation – tolerating losses or compensating for them in other ways. All of these strategies may be more efficiently utilized by animals operating in a group.

This study investigated the relationship between a cooperatively social spider, *Anelosimus eximius* (Araneae: Theridiidae), and its kleptoparasite, *Argyrodes ululans* (Araneae: Theridiidae), which specializes in foraging in *An. eximius* webs. The objective of this study was to determine whether the impact of kleptoparasitism is affected by the relative number of social spiders in a colony available for defense. Kleptoparasite success (percentage of food stolen by *Ar. ululans* of total prey attempted) and behavioral defense by *An. eximius* were compared in natural and enclosed colonies.

Methods

Study site and species. This study was conducted in the Tambopata Reserved Zone, 35 km southwest of Puerto Maldonado, Madre de Dios, Perú. The reserve is located within a region of subtropical moist forest, which is described in detail elsewhere (Erwin 1985). Data were collected in the latter part of the rainy season (March to May 1988) and throughout the dry season (June to August 1987; June to November 1988).

Anelosimus eximius Simon (Araneae: Theridiidae), a highly social spider, is common in this area. These spiders build large communal webs usually within understory vegetation. The webs consist of a dense bowl-shaped sheet or capture surface from which strands of tangled silk extend vertically upward, sometimes for several meters, to form a barrier. Dead leaves and other debris are incorporated into the bowl of the web as retreats. The barrier is less visible to insects and is used to ensnare prey. Average colony size at Tambopata is 68.86 cm ± 50.28 cm (range 10–290 cm) in length containing from 5 to approximately 2500 spiders (Rypstra, unpublished data) most of which are female (Aviles 1986). *Anelosimus eximius* individuals cooperate in prey capture, feeding, web construction and maintenance, and care of young (Christenson 1984; Vollrath and Rohde-Arndt 1983).

The barrier webbing of *An. eximius* colonies frequently houses a kleptoparasite, *Argyrodes ululans* Cambridge (Araneae: Theridiidae), that specializes in stealing prey from its social host. *Ar. ululans* spends its entire life within the barrier portion of *An. eximius* webs where it forages, mates, and lays egg sacs (Cangialosi 1990). Most *An. eximius* colonies contain between one and ten *Ar. ululans* individuals (Table 1).

Natural colony observations. I observed the foraging behaviors of *An. eximius* and *Ar. ululans* in natural colonies for periods of 1–5 h for a total of approximately 100 h. I recorded the size and order of insect prey, both natural and introduced, that entered the colonies. Observations were made of 193 prey capture sequences by *An. eximius* during which *Ar. ululans* attempted to steal 88. For each stealing attempt, I recorded the time it took *An. eximius* to detect and chase the intruder, the number of times *Ar. ululans* was chased by *An. eximius*, the total number of *An. eximius* involved in the interaction, and whether or not *Ar. ululans* was successful in stealing the prey.

Enclosure experiment. An. eximius were collected from natural colonies not being used in other observations and were maintained in screened field enclosures (30 x 30 x 30 cm). Nine enclosures were divided into three treatment groups, of three enclosures each, containing 10, 30, or 60 individuals. I maintained them throughout the experiment within 5 spiders of those numbers by periodically adding spiders. In order to keep the spiders at constant hunger levels, they were fed one insect per day, 10–14 mm in length, for every 10 spiders. Adult female *Ar. ululans*, collected from natural *An. eximius* colonies, were kept separately in vials and fed dead insects.

Table 1. Number of *An. eximius* colonies and number of *Ar. ululans* present; observed over a 2-month period in 1987 and a 6-month period in 1988

Year	Number of colonies observed			
	Total	With zero kleptos	With 1–10 kleptos	With >10 kleptos
1987	14	7	4	3
1988	12	3	8	1

Prior to experimentation, an *Ar. ululans* individual was starved for 2 days in order to elicit feeding behavior; afterwards, it was introduced into a colony. There was never more than one kleptoparasite per cage. The kleptoparasite was given 1–2 h to acclimate to the host web. I then added an insect to the enclosed colony and recorded the prey capture sequence of the host spiders and the response of the kleptoparasite in the same manner as for the natural colonies (as just described). Insect prey in experiments were restricted to two size categories: small (4–8 mm in length) and large (10–14 mm in length). All of the insects used were dipterans (houseflies) or hymenopterans (wasps or sweatbees), which are common prey of both spider species on the site. I recorded the details of the 152 stealing attempts that occurred out of 226 prey (109 small and 117 large) that I introduced in this manner in all cages. Observations were terminated when a kleptoparasite was successful in acquiring the prey and began to feed or when it gave up and no longer attempted to steal the prey. The duration of stealing attempts ranged from 2 min to 2 h.

I controlled kleptoparasite consumption by removing them from the enclosures at various times. Unsuccessful kleptoparasites were removed from the cage and placed in a vial where they were fed a dead insect and then starved for another 2 days. Successful kleptoparasites were allowed to feed to satiation in the host web and then were placed in a vial to starve for 2 days. Afterwards, both groups of kleptoparasites were returned to the cages for subsequent trials. Kleptoparasites were rotated among cages. I replaced kleptoparasites if they laid an egg sac (at which time they stop feeding to guard) or if they died.

Results

When an insect prey lands in the web of *An. eximius*, the social spiders rush out and wrap and bite the insect until it is subdued. They may then feed on the prey at the capture site or carry it to a retreat area to feed. The prey is most vulnerable to an attack by a kleptoparasite just after it is captured. Variables important to the defense of prey include the number of host spiders that react to the prey, the time it takes the social spiders to detect the presence of the kleptoparasite, and the extent to which the social spiders actively defend the prey, i.e., the number of times they chase the kleptoparasite away from the prey capture area.

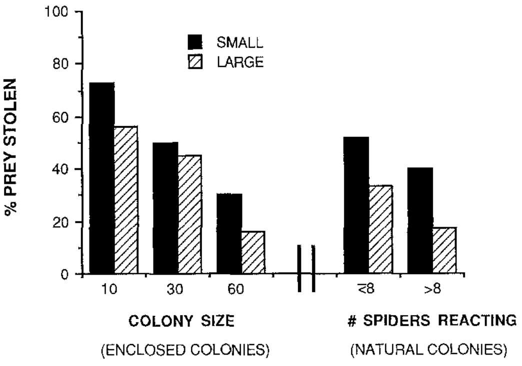

Fig. 1. Percentage of prey stolen of total attempted in enclosed and natural colonies depending on number of host spiders for large and small prey

Table 2. Mean number of social spiders reacting to prey and mean size of prey, for prey stolen and not stolen (but attempted) in natural *An. eximius* colonies

	Prey stolen ($n = 31$)	Prey not stolen ($n = 57$)	t-value	P
Mean # of social spiders reacting (SE)	9.72 (1.62)	19.29 (2.08)	9.91	0.002
Mean size of prey (mm) (SE)	7.00 (0.71)	8.54 (0.52)	3.09	0.082

In the enclosures, I observed a total of 152 stealing attempts of which 65 (42.7%) were successful. A log-linear model for a 3-way categorical analysis indicated that the percentage of successful stealing attempts (prey stolen) differed significantly across both colony size ($X^2 = 65.81$, $P = 0.0001$) and prey size ($X^2 = 10.61$, $P = 0.001$) categories. In the enclosures, the success rate (successful steals/total attempted) of *Ar. ululans* was lower with larger *An. eximius* colony sizes regardless of prey size (Fig. 1). Also, *Ar. ululans* stole a greater percentage of small (4–8 mm) prey items in all colonies (Fig. 1). There was no significant interaction between colony size and prey size ($X^2 = 2.53$, $P = 0.282$).

I observed a total of 88 stealing attempts in natural colonies of *An. eximius*, of which 31 (35.2%) were successful. *Ar. ululans* was less successful in stealing an insect when more of the host social spiders were present at the prey capture (Table 2). Although not significant, the prey that *Ar. ululans* stole was smaller than prey not stolen in these colonies (Table 2). In order to compare the natural colony data with the enclosed colony data, I divided the prey that *Ar. ululans* attempted to steal in natural colonies into "small" (≤ 7 mm) and "large" (> 7 mm) categories, and the number of social spiders reacting into "few" (≤ 8 spiders) and "many" (> 8 spiders) categories. The prey size division was made to correspond roughly to the prey size groupings in the enclosure experiment without losing observations (since there were natural prey in a size range between the two manipulated groupings). The number of host spiders reacting were divided into the two groups based on the approximate mean number of spiders that react in an enclosed colony of 30 individuals ($x = 8.12$). A log-linear model for a 3-way categorical analysis indicated similar results to the enclosure data. *Ar. ululans* had a higher success rate when few spiders reacted ($X^2 = 9.23$, $P = 0.002$; Fig. 1) and when attempting to steal small prey ($X^2 = 19.37$, $P = 0.0001$; Fig. 1). Similar to the enclosure results, there was no significant interaction between number of spiders reacting and prey size ($X^2 = 0.72$, $P = 0.395$; Fig. 1).

An. eximius typically defend their prey against *Ar.*

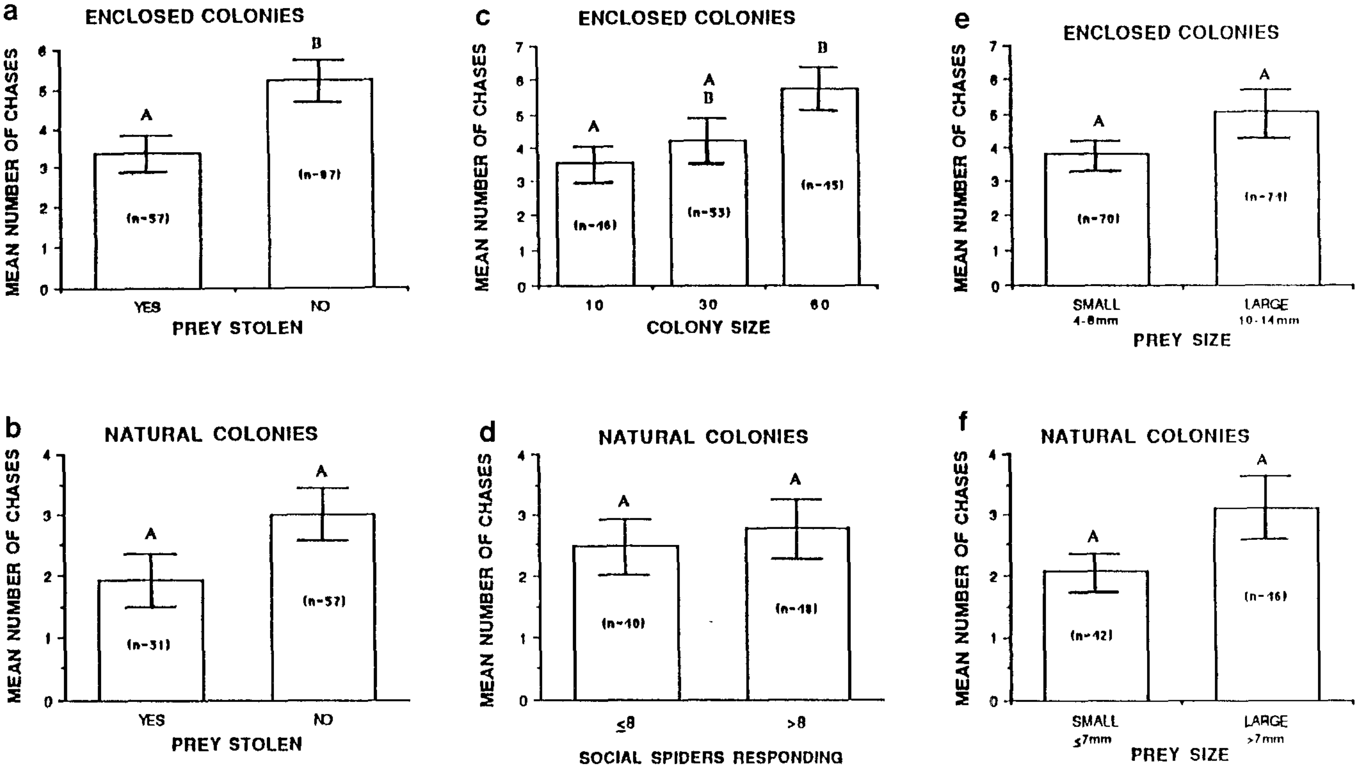

Fig. 2a–f. Mean number of chases by *An. eximius*, **a** for prey stolen and not stolen in enclosed colonies, **b** for prey stolen and not stolen in natural colonies, **c** for different colony sizes in enclosed colonies, **d** for different numbers of host spiders reacting in natural colonies, **e** for large (10–14 mm) and small (4–8 mm) prey in enclosed colonies, **f** for large (> 7 mm) and small (≤ 7 mm) prey in natural colonies. Error bars are standard error of the mean. Different letters within a figure indicate significant differences according to a least squares means comparison at the $P < 0.05$ level

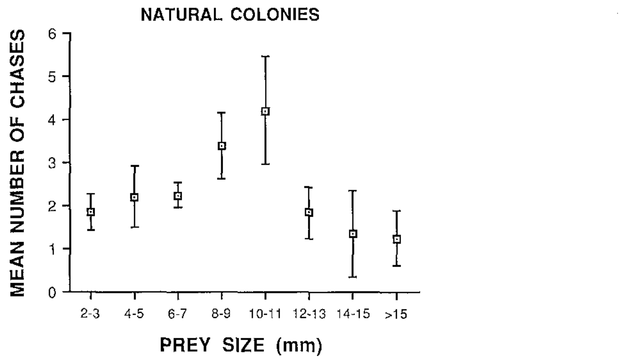

Fig. 3. Mean number of chases for different prey sizes in natural colonies. Error bars are standard error of the mean

ululans by chasing them. A kleptoparasite may return repeatedly and be chased away several times (up to 12 times) during one stealing attempt. Chases last only a few seconds as *An. eximius* usually quickly loses track of the kleptoparasite's position. *Ar. ululans* is quite adept at escaping from defending host spiders and uses a number of different behavioral tactics for this purpose (Cangialosi 1990). Even though *Ar. ululans* is rarely captured and eaten by *An. eximius* (I observed this a total of four times in all natural and enclosed observations), chasing is effective at reducing the kleptoparasite's success. In enclosed colonies, prey was less likely to be stolen when *An. eximius* chased the kleptoparasite more often during a stealing attempt (Kruskal-Wallis: $X^2=9.07$, $P=0.003$; Fig. 2a). A similar trend was seen in the natural colony data (Kruskal-Wallis: $X^2=3.59$, $P=0.058$; Fig. 2b).

The number of host spiders responding to a prey item may have influenced the number of chases executed during a stealing attempt. In enclosed colonies, more social spiders reacting to a prey item resulted in more spiders available to chase off kleptoparasites. There was a significant difference in number of chases among the colony sizes in the enclosures (Kruskal Wallis: $X^2=10.97$, $P=0.004$; Fig. 2c). However, there was no difference in the number of chases for "few" and "many" social spiders responding in natural colonies (Kruskal-Wallis: $X^2=0.02$, $P=0.875$; Fig. 2d).

Prey size did not appear to influence the number of chases executed during a stealing attempt. Number of chases did not differ between small (4–8 mm) and large (10–14 mm) prey in enclosed colonies (Kruskal-Wallis: $X^2=1.29$, $P=0.256$; Fig. 2e). In natural colonies, there was also no difference in number of chases between the two prey groups ≤ 7 mm and >7 mm (Kruskal-Wallis: $X^2=0.83$, $P=0.362$; Fig. 2f). However, these results might be explained by the unimodal pattern of number of chases with increasing prey size in natural colonies (Fig. 3). Number of chases increased with prey size up to 11 mm (linear regression on raw data, $F=5.86$, $P=0.018$; Fig. 3). For prey sizes 12 mm and greater, mean number of chases dropped off to where the largest prey are associated with the lowest number of chases (Fig. 3).

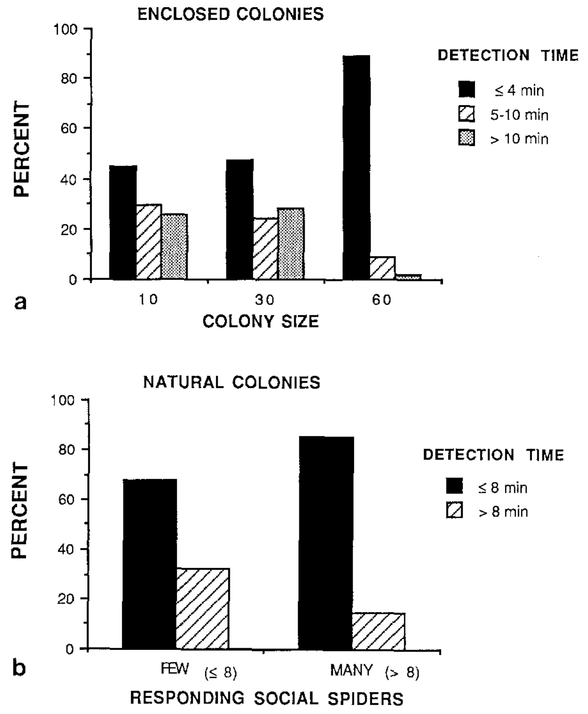

Fig. 4a, b. Percent observations in detection time categories (time until *Ar. ululans* is detected by *An. eximius*), **a** in enclosed colonies of different sizes, **b** in natural colonies with different numbers of responding social spiders

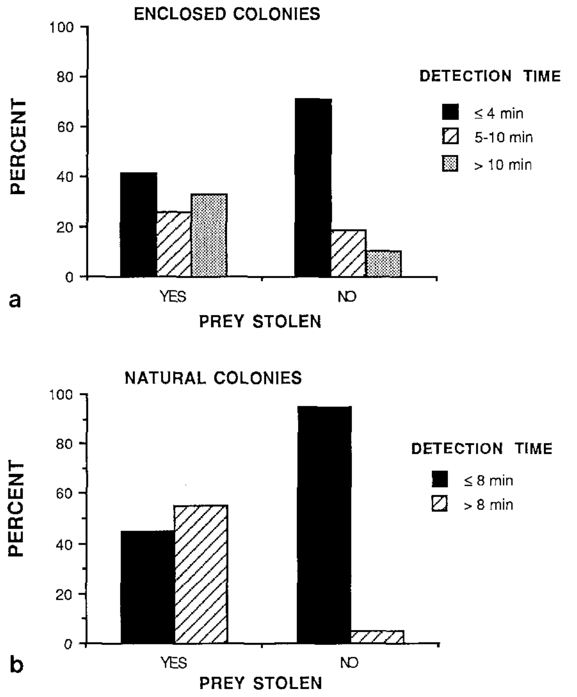

Fig. 5a, b. Percent observations in detection time categories (time until *Ar. ululans* is detected by *An. eximius*) for prey stolen and not stolen, **a** in enclosed colonies, **b** in natural colonies

When more social spiders responded to a prey, kleptoparasites were detected earlier. Detection times were grouped into categories for analysis since several kleptoparasites were not detected at all. "Not detected" data were placed into the longest time category. The categories used for both enclosed and natural data sets were selected in order to keep the length of the categories and number of observations in each roughly equivalent. Kleptoparasites in enclosed colonies of 60 spiders were detected in (≤ 4 min) a significantly greater number of times than kleptoparasites in colonies of 10 or 30 (3×2 contingency table, $X^2 = 24.70$, $P < 0.001$; Fig. 4a). In natural colonies, more kleptoparasites were detected sooner (≤ 8 min) when many (> 8) spiders responded to a prey item (2×2 contingency table, $X^2 = 3.99$, $P < 0.046$; Fig. 4b). For the enclosed colonies, detection time was dependent on the number of social spiders responding even though the undetected kleptoparasites could not be included in this analysis (linear regression, $F = 23.01$, $P = 0.001$). Early detection by *An. eximius* resulted in better defense of prey. Kleptoparasites that were not successful (prey not stolen) were detected in (≤ 4 min) a significantly greater number of times than successful (prey stolen) kleptoparasites in enclosed colonies (2×2 contingency table, $X^2 = 15.20$, $P < 0.001$; Fig. 5a). Unsuccessful kleptoparasites were also detected earlier ($\leq$ 8 min) than successful kleptoparasites in natural colonies (2×2 contingency table, $X^2 = 28.10$, $P < 0.001$; Fig. 5b).

Discussion

The large, stable colonies of *Anelosimus eximius*, which are associated with high rates of prey capture and the relatively long prey-handling times (including capture, transport, and feeding) typical of spiders, provide suitable conditions for the kleptoparasite specialist, *Argyrodes ululans*. *An. eximius* loses 26% of its prey to *Ar. ululans*, Cangialosi 1990). Pressure of this magnitude from kleptoparasites may be strong enough to cause local extinctions or disappearances of colonies. Evidence supporting this possibility is that abandoned *An. eximius* webs usually contain a few to several *Ar. ululans* (personal observation). Barnard (1984) suggested that the substantial negative impact that kleptoparasites have on their hosts is likely to set up a counter-adaptive evolutionary arms race between host and kleptoparasite. Selection acts on hosts to reduce the impact of the kleptoparasite and on kleptoparasites to counter the host and improve their attack efficiency (Dawkins and Krebs 1979; Barnard 1984). However, social groups might already have characteristics (or preadaptations) conducive to kleptoparasite defense.

Protection from enemies is frequently cited as an advantage of group living (Wittenberger 1981; Pulliam and Caraco 1984). The disadvantages to *An. eximius* in providing a living environment favorable to kleptoparasites are perhaps offset somewhat by the advantages that being in a group provide in terms of protection. *Ar. ululans* is less likely to be successful when more *An. eximius* are involved in a prey capture. This represents a definite advantage to living in a social group for *An. eximius*. This advantage is seen in other social animals such as lions. Groups of lions are better able than solitary lions to defend their carcasses against food-stealing hyenas (Schaller 1972). The defense mechanisms that *An. eximius* employs against *Ar. ululans* encompass all three strategy types that hosts use to reduce kleptoparasitism (evasion, retaliation, and toleration/compensation; Barnard 1984) and are related to or enhanced by their social lifestyle.

Since defensive behavior is energetically costly to hosts, its evolution implies the serious detrimental effects of prey loss to kleptoparasites. For instance, lapwings and golden plovers may be forced into long, expensive aerial chases attempting to evade the loss of earthworm prey to black-headed gulls (Kallander 1977; Barnard and Thompson 1985). The orb-weaver *Nephila clavipes* incurs the costs and risks associated with changing web location in response to decreases in food consumption when kleptoparasites are in their webs (Rypstra 1981). An evasive tactic that *An. eximius* exhibits is to move its prey after capture to leaf retreats (Vollrath and Rohde-Arndt 1983; Rypstra, personal communication, personal observation), most likely in order to hide it from potential prey stealers. For larger prey, groups of *An. eximius* can move a prey item to a retreat more quickly than a single individual (Rypstra, unpublished data). This decrease in prey transport time associated with group capture reduces the time frame in which kleptoparasites have to steal prey. Since kleptoparasitism is more likely when food items are easily detectable, long prey-handling times make hosts more vulnerable to attack (Barnard 1984). Some aquatic birds that must manipulate large prey items at the water surface are more susceptible to kleptoparasitism (Grubb 1971; Kushlan 1978).

The successful evolution of retaliation strategies also implies that kleptoparasitism is costly. Two orb-weaving spiders, *Argiope argentata* and *Nephila clavipes*, expend energy plucking their webs vigorously at *Argyrodes elevatus* kleptoparasites in the process of making off with a prey, sometimes causing them to retreat (Vollrath 1979). *Nephila* may rush towards the disturbance in their web and occasionally recover the lost prey (Vollrath 1979, 1984). Retaliation in *An. eximius*, involving detecting and chasing the kleptoparasite, is more effective in larger groups. When more of these social spiders surround a prey item, kleptoparasites are detected sooner since a greater amount of webbing is being monitored for vibrations. This early detection leads to better defense of prey probably because kleptoparasites are either chased more often or forced to give up sooner. Because these results indicate a tendency for an increase in the number of chases with increasing numbers of *An. eximius* present, and because increased chasing leads to lower kleptoparasite success, *Ar. ululans* is more successfully foiled by spiders in larger groups. Hyenas often give up kills to lions, but when the hyenas are in large groups, they tend to retaliate against kleptoparasitic lions (Kruuk 1972). Therefore, retaliation by hosts puts a qualifier on the benefit to kleptoparasites of living in areas of "high host concentration" (Barnard 1984). In addition, the physical presence of many social spiders surrounding a prey actively blocks a kleptoparasite's ability to attack. Because chasing did not seem to increase with the number of *An. eximius* responding in natural colonies, early detection and the mere presence of many social spiders (both causing kleptoparasites to give up sooner) are perhaps the most effective deterrents against kleptoparasitism for *An. eximius*.

By virtue of its sociality, *An. eximius* has other built-in toleration/compensation defense mechanisms against kleptoparasitism. Increased prey capture rates associated with spider colonies (Uetz 1986; Rypstra 1989) probably offset, in part, losses due to kleptoparasitism. High food availability, therefore, may allow an increased tolerance of kleptoparasites. Additionally, since social spiders can capture larger prey than solitary individuals (Buskirk 1981), and because large prey make up an important percentage of their food intake, *An. eximius* may be more tolerant of the loss of the small prey that *Ar. ululans* usually takes. These kleptoparasites presumably give up sooner on the largest prey types because they would waste energy attempting to steal prey they cannot handle. Therefore, chasing by hosts increases with prey size only to an extent. This makes extremely large prey very profitable to the social spiders since there is minimal energy expended for defense by chasing and a large return in food. In this way, kleptoparasitism reinforces the benefits that social spiders receive from their ability to capture prey much larger than themselves.

Kleptoparasitism is common even among solitary web-building spiders (Vollrath 1987). Large aggregates of spiders may be more attractive to kleptoparasites, but other characteristics of social groups make them well-equipped for defense. The results of this study demonstrate that communal living and group cooperation in *Anelosimus eximius* confer protection from the kleptoparasite *Argyrodes ululans*. If the benefits of protection from *Ar. ululans* that *An. eximius* receives from being social outweigh the costs of increased attraction, kleptoparasitism pressure may make sociality even more selectively advantageous for *An. eximius*.

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