LIFE CYCLE AND BEHAVIOR
OF THE KLEPTOPARASITIC SPIDER,
ARGYRODES ULULANS (ARANEAE, THERIDIIDAE)

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ABSTRACT

This study investigated the life cycle and behavior of *Argyrodes ululans* which is a specialist kleptoparasite in the communal webs of its social spider host, *Anelosimus eximius*. Observations of natural and enclosed colonies of *An. eximius* revealed that large *An. eximius* colonies maintain steady populations of high numbers of differently aged *Ar. ululans* individuals whereas small colonies contain fewer kleptoparasites less predictably. Adult female *Ar. ululans* forage almost exclusively by stealing newly captured prey directly from their hosts and were never observed to prey on host spiders. Although male and juvenile *Ar. ululans* will sometimes steal prey from *An. eximius*, they tend to scavenge more and feed on prey scraps abandoned by their hosts.

INTRODUCTION

Spiders in the genus *Argyrodes* conduct nearly all of their activities in the webs of other spiders rather than building webs of their own (Exline and Levi 1962; Gertsch 1979). *Argyrodes* can exist in a variety of relationships with their host spiders (as commensals, kleptoparasites, predators) depending on factors such as relative size of host and *Argyrodes*, morphology of host web, and host feeding rate (Wise 1982; Larcher and Wise 1985). Although specific relationships for certain *Argyrodes*-host systems have been determined (Exline and Levi 1962; Smith Trail 1980; Tanaka 1984; Larcher and Wise 1985), the life cycle and foraging behavior of only a few *Argyrodes* species have been studied in any detail (Vollrath 1979, 1987; Larcher and Wise 1985; Whitehouse 1986).

Argyrodes ululans Cambridge is a specialist kleptoparasite in the communal webs of its host, *Anelosimus eximius* Simon, which lives in the undergrowth of tropical rainforests in Peru. In this paper I describe some aspects of the natural history and behavior of *Argyrodes ululans*, including its relative abundance in *Anelosimus eximius* colonies, general activity, reproductive behavior, and foraging behavior. Comparisons are drawn with other *Argyrodes* species that have solitary and/or temperate-zone hosts.

METHODS

This research was conducted in the Tambopata Reserved Zone, 35 km southwest of Puerto Maldonado, Madre de Dios, Peru. The reserve is located

within a region of subtropical moist forest described in detail elsewhere (Erwin 1985).

Anelosimus eximius, 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 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. Colonies at Tambopata average 68.86 cm ± 50.28 cm (range 10-290 cm) in length (the longest dimension of the three-dimensional bowl) and contain from 5 to approximately 2,500 spiders (Rypstra, unpublished data), most of which are female as in other colonies of this species (Aviles 1986; Vollrath 1986). *Anelosimus eximius* individuals cooperate in prey catpture, feeding, colony construction, web 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*, that specializes in stealing prey from its social host. *Ar. ululans* spends its entire life cycle within the barrier portion of *An. eximius* webs where it forages, mates, and lays egg sacs.

Surveys of colonies.—*Anelosimus eximius* colony length and the number of *Argyrodes ululans* individuals inhabiting the colonies were determined approximately every month. I recorded the total number of female, male, and juvenile kleptoparasites within each colony. For two of the colonies (#883 and #885), these data were collected every one to two weeks from September 1 to November 10, 1988.

General activity.—The activity of individual kleptoparasites (adult females, adult males, and juveniles) was monitored for periods of 1 to 4 hours between 0600 and 2300 for a total of 125 spider-hours (one spider observed for 1 hour). Approximately 30-40 individual kleptoparasites in six different natural colonies were observed. Data were collected from August 26 to November 10, 1988.

Mating and reproduction.—*Natural colonies*: During observations of general activity and stealing behavior, 19 matings were observed. I recorded the details of the courtship behavior and the duration of copulation. Some life history and reproductive characteristics of four female *Argyrodes ululans* individuals in natural colony #885 were recorded every day from September 1 to November 10, 1988. I recorded the date of molt from penultimate to adult, date first egg sac was laid, date of hatching, and date second egg sac was laid. For each female I recorded daily whether it was in an active state, inactive and gravid, or guarding an egg sac.

Enclosed colonies: Female *Ar. ululans* that had laid egg sacs in enclosed colonies of *An. eximius* (maintained in screened field enclosures, 30 × 30 × 30 cm, for use in other experiments, Cangialosi 1990b) were used for observations of egg sac guarding behavior. Egg sacs were removed from two females in separate cages and the reaction of each female was recorded. For one of the females, an egg sac of a different female was placed in the cage with her 30 min after the original one had been removed. This was done to see whether the female could recognize her own egg sac and distinguish it from an egg sac of another female.

Foraging behavior.—Detailed observations of the foraging behavior (including prey stealing) of *Ar. ululans* were recorded for adult females, adult males, and
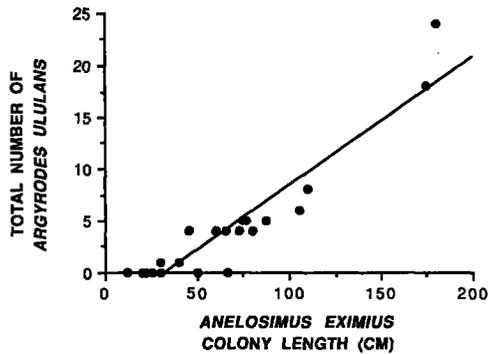
Figure 1.—Linear regression of total number of *Ar. ululans* on *An. eximius* colony length (cm). Equation for the line is $y = -3.99 + 0.124x$; $R^2 = 0.88$.

juveniles foraging in natural colonies of *An. eximius*. Observations were made for both naturally entering insects and those that were introduced purposely by dropping or gently throwing them into the colonies.

RESULTS

Abundance of *Argyrodes ululans*.—Colonies of *An. eximius* contained from zero to 24 individuals of *Ar. ululans*. The number of *Ar. ululans* per colony increases with increasing host colony size (Fig. 1). The relative proportions of females, males, and juveniles that comprise the total population of *Ar. ululans* living within a colony is dependent upon the size of the colony and changes during the course of a season (Fig. 2). In colony #885 (medium sized; 87-93 cm), the number of juveniles decreased steadily from five to zero between September 1 and October 8 and remained at zero until an egg sac hatched on November 5 (Fig. 2a). The number of adult females and males in colony #885 remained constant after the disappearance of the juveniles (from maturation or dispersal). In colony #883, which was larger than #885 (175-188 cm), there was a consistently high number of juveniles and the number of mature females increased from September 1 to November 10 (Fig. 2b). Adult males remained relatively low in comparison to the number of females in this colony.

General activity and behavior.—Eight behavioral activities of *Ar. ululans* were recognized and recorded: (1) rotary probing (rotating the first pair of legs at the coxatrochanter joint, Cangialosi 1990a); (2) feeding (extracting food from prey); (3) folded (resting or inactive position in which the spider remains motionless in the web with the legs folded up near the body, Fig. 3a); (4) still (also an inactive state in which the spider sits in the web motionless with the legs outstretched, Fig. 3b); (5) grooming (cleaning legs by passing them through the chelicerae); (6) mating (courtship and copulation); (7) stealing behaviors (including leg waving, web shaking, and clearing silk); and (8) walking (locomotion on the webbing).

Overall, the proportion of time allocated to the different categories of behavior is not independent of the time of day for adult females (3 × 8 contingency table, $\chi^2 = 80.78$, $P < 0.001$), adult males (3 × 7 contingency table, $\chi^2 = 48.13$, $P < 0.001$) or juveniles (3 × 7 contingency table, $\chi^2 = 140.98$, $P < 0.001$). Females are more likely to be in a folded rest state from 0600 to 1100 hours, feeding from 1101 to 1600, and in a still position from 1601 to 2300 (Fig. 4a). Males spend most of their time in a still position but are less likely to do so from 0600 to 1100
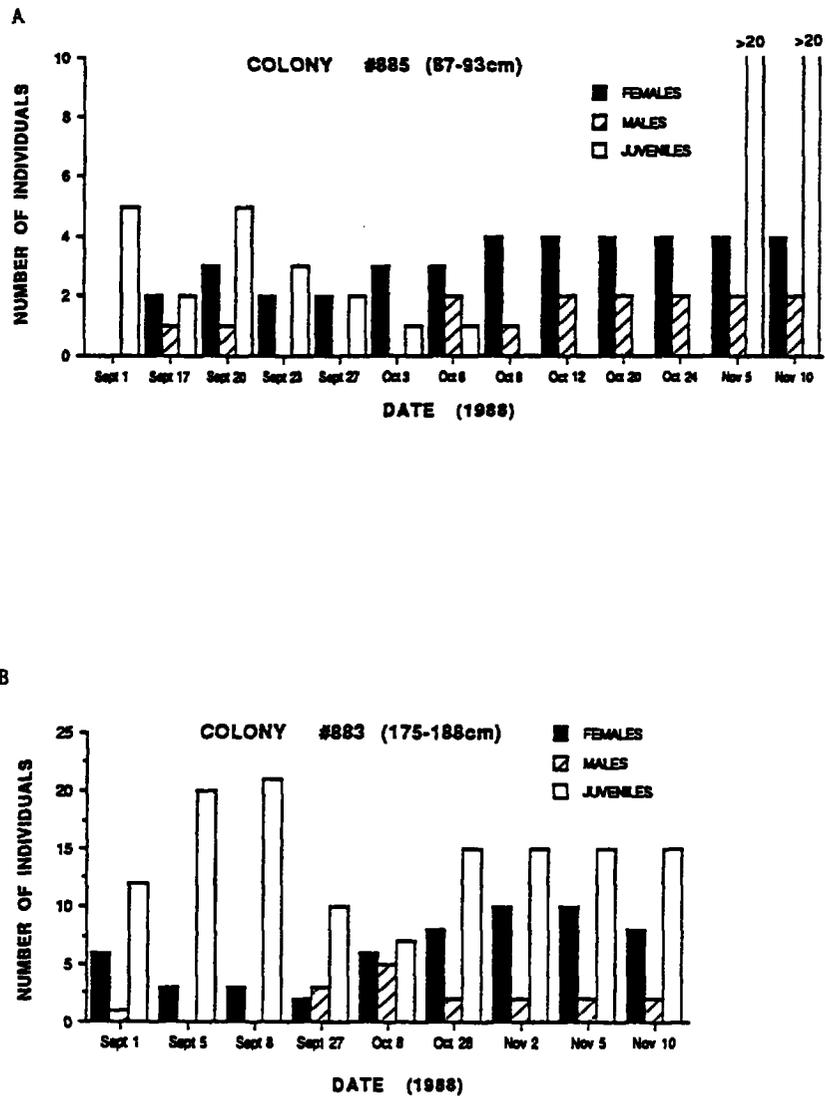
Figure 2.—Total number of female, male, and juvenile *Ar. ululans* in *An. eximius* colonies for dates in Sept and Nov, 1988. A, colony #885 (87-93 cm); B, colony #883 (175-180 cm).

(Fig. 4b). Rotary probing for males is more common from 0600 to 1100 and from 1601 to 2300 (Fig. 4b). No adult males were observed feeding during these observations. For juveniles, a folded rest state is more likely from 0600 to 1100 and a still position is more common later in the day (Fig. 4c). Similar to adult females, juveniles also spend most of their time feeding from 1101 to 1600 (Fig. 4c).

Mating and reproduction.—Compared to many other spider species, the courtship behavior of *Ar. ululans* is relatively short and simple. Within the barrier webbing of the *An. eximius* colony, a rotary probing male slowly approaches a female until he almost contacts her. Unreceptive females drop or walk away from the male. A receptive female also begins to rotary probe directly facing the male. After just a few seconds, copulation commences and continues
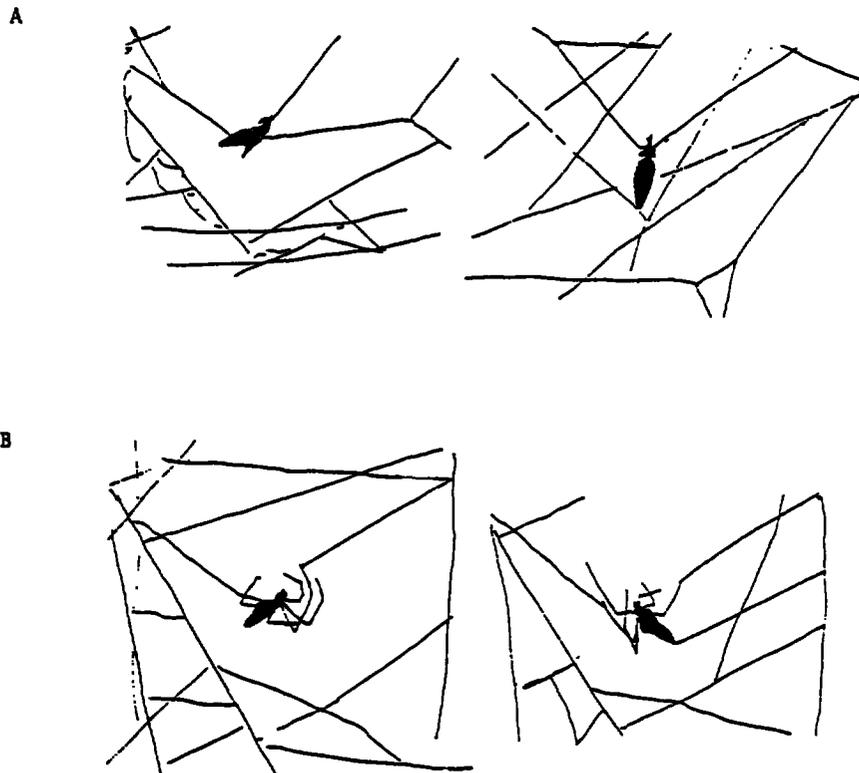
Figure 3.—Diagrams of rest positions of *Ar. ululans* in *An. eximius* webbing. A, legs folded against body. B, legs outstretched. (Drawings by Rebecca Ellis).

from 2 to 15 min ($N = 19$) until the pair breaks apart and the spiders resume other activities. After separating, two of the males observed approached another female and also mated with her.

The females observed in colony #885 took from 14 to 19 days to lay their first egg sac after reaching maturity (Table 1). One of the females produced a second egg sac 12 days after the first (Table 1). Two to four days before laying eggs, gravid females assume an inactive folded position high in the *An. eximius* colony barrier and do not forage. An adult female *Ar. ululans* suspends its egg case in the barrier web at night and guards it until hatching. A guarding female spends almost all of her time in a folded position near the egg sac. When it is threatened by another spider or an insect approaching nearby, it becomes alert and shakes the web and egg sac sharply, which causes the intruder to flee. Guarding females only stray away from their egg sacs in order to drink water from the silk strands within a 5-10 cm radius around the egg sac; they do not forage or feed. The guarding/hatching time for three of the females in colony #885 was 17 to 18 days (Table 1). Mean hatching time (time since egg sac is first laid until the young emerge; not guarded since females were removed from egg sacs placed in vials) for egg sacs laid in the cages was 22.8 days (SD = 2.32, $N = 6$, range 20-27).

Female *Ar. ululans* with egg sacs become active foragers only if the egg sac is lost, or after the egg sac hatches. Female #3 in natural colony #885 lost its egg sac 6 days after laying (cause unknown) and resumed foraging that same day.
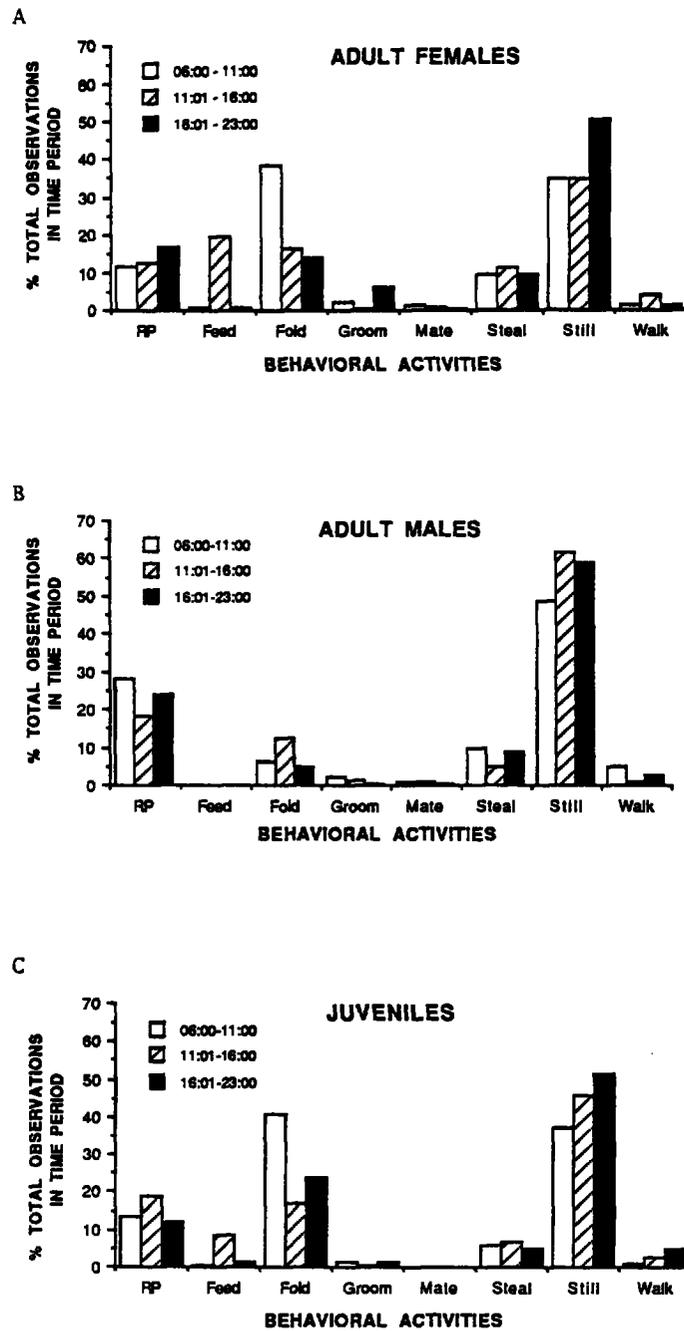
Figure 4.—General activity of *Ar. ululans*. Percentage of total observations of different behavioral activities in three time periods, 0600-1100, 1101-1600, 1601-2300. RP = rotary probing; Feed = feeding; Fold = folded position; Groom = grooming; Mate = mating; Steal = web shaking, silk clearing, and leg waving; Still = still position; Walk = walking. A, adult females, B, adult males, C, juveniles.

Table 1.—Some life history characteristics for four female *Ar. ululans* individuals. Time units are days. (a = egg sac lost).

Female	Penultimate to adult	Maturation molt to 1st egg sac	Guarding time (hatching time)	Time to 2nd egg sac
1	—	—	17	12
2	16	15	18	—
3	—	19	6[a]	29
4	16	14	18	

After removing an egg sac from its owner (which was laid in a cage 3 days earlier), the female immediately started to search for the egg sac, wandering around the area rotary probing and moving further and further away from its original position for 105 min until she became inactive (folded). This female did not attempt to steal prey that day or the following day, but was successful in stealing a prey item two days after the egg sac had been removed. Removing an egg sac from a second female in another cage produced similar searching behavior. For this second female, an egg sac laid by a different female was placed in the cage in the vicinity of the original egg sac after 30 min of searching. The female investigated the egg sac for 5 min, moving around it and touching it with her first pair of legs. She then became inactive and folded near the egg sac. By the next day, this female had attached this new egg sac to the colony webbing and was guarding it in the usual way.

Foraging behavior.—*Females: Ar. ululans* females feed primarily by stealing prey freshly captured by its host. It specializes in *An. eximius* webs as it was never found in webs of any other spider species examined on the study site including all located colonies (8 total) of two other *Anelosimus* species (pers. observ.). A Peruvian arachnologist involved in making a comprehensive collection of the spider fauna at the site examined virtually every spider web that could be located for a month in 1987 and a month in 1988. This investigator found no *Ar. ululans* in any of the spider webs (other than *An. eximius*) that she examined (D. Silva pers. comm.).

The main sequence of events for stealing attempts by adult females is summarized in Fig. 5. (The individual behaviors of the kleptoparasites and of *An. eximius* are described in more detail in Cangialosi 1990a and Cangialosi 1990b). A female *Ar. ululans* locates a prey item in the process of being captured by *An. eximius* be detecting vibrations while rotary probing. The kleptoparasite approaches the prey slowly and waits above it (10-15 cm) in a still position until the prey is subdued by the social spiders. Once the prey is immobilized, the kleptoparasite moves more quickly toward it, either leg waving or clearing silk, and then starts web shaking. The relative frequency of these behaviors varies depending on such factors as the number of host spiders involved and their reaction (Cangialosi 1990a). Once the prey item is cleared of host spiders, the kleptoparasite attaches the prey to itself via a silk line, and transports it up into the barrier web to feed. Females were never observed killing an *An. eximius* individual but were observed feeding on them on five occasions (two adult females, one adult male, one juvenile) in natural colonies. In the cages, the host spiders that were observed eaten by kleptoparasites were those that were accidently killed from prey movements during prey capture ($N = 3$).
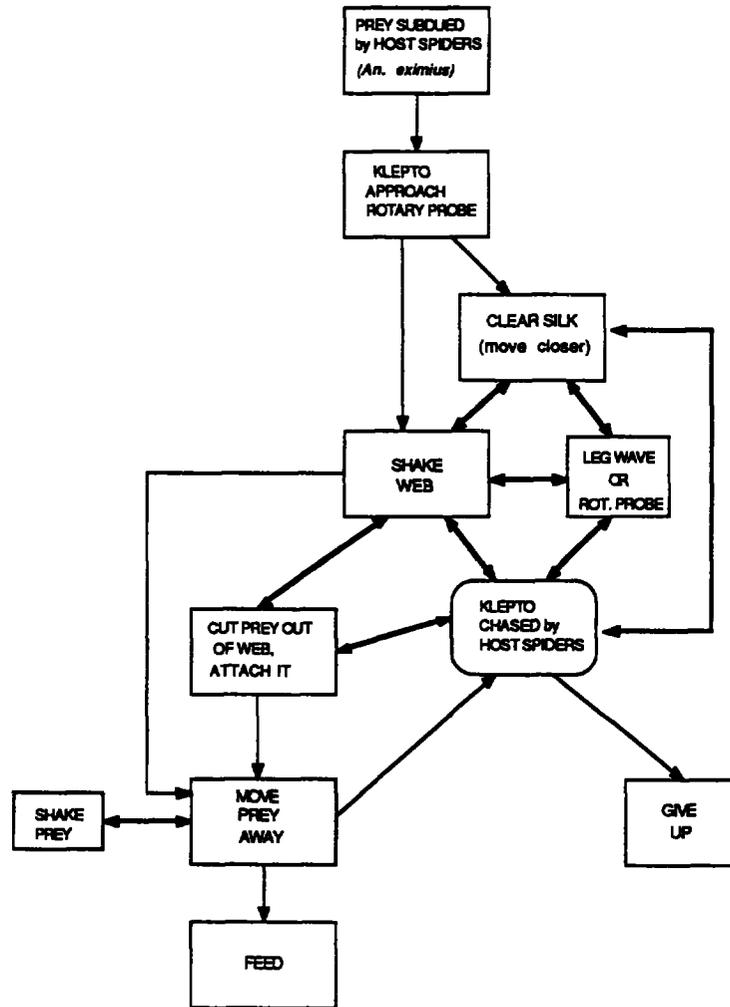
Figure 5.—Ethogram of adult female *Ar. ululans* prey-stealing behavioral sequences.

Males: Adult males spend very little time feeding (Fig. 3). However, males were observed attempting to steal prey six times in natural colonies. Males tend to scavenge more, feeding on prey left in the web by the social spiders and do not usually transport prey. Insects or pieces of insects that have been in the webs for several hours have only a few (if any) host spiders still feeding on them. The kleptoparasite may shake the web and prey to remove these hosts and then feed on the prey without transporting it.

Juveniles: Younger juveniles of both sexes tend to forage similarly to adult males. However, in addition to scavenging for abandoned prey, they sometimes move in and feed with the host spiders on newly captured insects. The hosts apparently do not detect these kleptoparasites since they are able to feed for long periods of time. As they get older, female juveniles begin to behave more and more like adult females and exhibit the same stealing behaviors. Even relatively small, immature kleptoparasites can remove host spiders from prey by web shaking.

No *Ar. ululans* (of any age or sex) were observed capturing even the smallest prey on their own. In fact, when an *Ar. ululans* individual approaches and touches a still insect that begins to move when contacted, the kleptoparasite will back away from it quickly. This sometimes alerts the host to the insect's presence and they will attempt to subdue it. Afterwards, the kleptoparasite may try to steal the newly captured prey.

DISCUSSION

Abundance and age/sex structure.—Large colonies of *Anelosimus eximius* harbor greater numbers of *Argyrodes ululans* than small colonies. Smith Trail (1980) found a higher number of *Argyrodes fictilium* (Hentz) and *Ar. baboquivari* Exline and Levi in communal groups of *Philoponella oweni* (Chamberlin) compared to solitary *P. oweni*, and no more than one *Argyrodes* was ever found in any solitary web. She presents evidence that suggests that this distribution is due to the fact that *Argyrodes* encounter communal groups more often than solitary webs, and that *Argyrodes* remain longer in communal groups, which probably represent a large source of potential prey to these predatory species of *Argyrodes*. Elgar (1989) found a significant positive correlation between aggregation size of the orb-weaver, *Nephila edulis* Koch and the number of kleptoparasites, *Ar. antipodianus* Cambridge per web (after correcting for *N. edulis* body size). He demonstrated that spiders in aggregations suffered a higher colonization rate of kleptoparasites than spiders in solitary webs, which could explain the kleptoparasite distribution. However, webs of other solitary host species often contain many *Argyrodes* individuals (Robinson and Robinson 1973; Rypstra 1981; Wise 1982; Larcher and Wise 1985).

Although larger colonies of *An. eximius* may have higher kleptoparasite immigration rates, the fact that *Ar. ululans* completes its entire life cycle within host colonies means that new kleptoparasites are added as the older ones reproduce. Larger stable colonies are inhabited by a greater number of kleptoparasites of all ages and reproductive states, and kleptoparasite spiderlings hatch from egg sacs fairly regularly. Hence, the proportion of juveniles in large *An. eximius* colonies stays relatively constant over time, thus maintaining a steady supply of kleptoparasites. In smaller colonies, which might contain a few adult females for only a certain time period, the hatching of juveniles is more sporadic. Thus the presence of kleptoparasites in these colonies is less consistent. Several smaller to medium sized colonies (12-65 cm) often contain no *Ar. ululans* at all.

Although some *Ar. ululans* offspring remain in the natal colony, many newly hatched spiderlings disappear shortly (1-2 days) after emerging. Presumably, some percentage of these aerially disperse to other colonies. It is unclear how random dispersal results in the location of new host colonies. Older juveniles and adult males also occasionally show up in colonies that previously contained no kleptoparasites. The mechanisms, frequency, and patterns of emmigration require further investigation.

General activity.—Most spider species are predominately active either diurnally or nocturnally but not both (Foelix 1982). *Ar. ululans* forages in both the day and night and rests intermittantly. The activity of this kleptoparasite, not

surprisingly, appears to be generally geared to its host which, unlike most spider species, actively forages 24 hours a day (Rypstra unpublished data; pers. observ.). *Ar. elevatus* is day-active and *Ar. caudatus* is night-active when they cohabit *Nephila clavipes* webs (Vollrath 1976). Being active at different times, along with other behavioral and physiological adaptations, allows them to exploit their host in different ways (Vollrath 1976, 1987).

Differences in behavioral activity of *Ar. ululans* among the time periods were mainly due to differences in behaviors not related to prey stealing such as changing from a still to a folded position. The significance of these two rest states is ambiguous. The legs-outstretched still position would seem to be more of an alert state than the legs-folded position; however, *Ar. ululans* quickly switchs from a folded position to active behaviors when responding to prey. Sex differences in timing of behavior may be related to mating activity. Males spend more time rotary probing (probably in search of mates) when females are less likely to be feeding.

Mating and reproduction.—The mating behavior of *Ar. ululans* is very simple and unritualized. Elaborate courtship displays by male spiders generally function to suppress the females' predatory behavior toward the males (Bristowe and Locket 1926; Platnick 1971; Foelix 1982). Because *Ar. ululans* is non-predatory, it is reasonable to assume that the lack of extensive courtship in these kleptoparasites is due to the fact that males are not in danger of being eaten.

The cessation of foraging during egg sac guarding (17-27 days) implies that egg predation pressure is very strong for *Ar. ululans*. Since foraging resumes within hours of an egg sac being lost, it is important for the kleptoparasites to immediately start gaining reserves to produce a new one. To this end, they apparently undergo quick physiological changes from a fasting state (and from relative inactivity) to an active feeding state. Also, the diligent searching behavior for lost egg sacs indicates that female *Ar. ululans* are sensitive to the presence of their egg sacs. This might imply that abandoned egg sacs have little chance of surviving to the hatching stage.

An. eximius cleans its web regularly (pers. observ.; Ryypstra pers. comm.; Vollrath and Rohde-Arndt 1983; Christenson 1984) and undoubtedly removes unattended *Ar. ululans* egg sacs from their communal web. In spite of this, there may be benefits for *Ar. ululans* associated with suspending their egg sacs in *An. eximius* colonies. *An. caudatus* (Taczanowski) females place their egg sacs away from host webs and guard them until the young hatch, whereas *Ar. elevatus* (Taczanowski) leaves its egg sacs unattended in host webs (Vollrath 1987). The behavior of the host and the nature of its web may determine, in part, the placement and guarding of *Argyrodes* egg sacs. Additionally, *Ar. elevatus* produces more egg sacs (with more eggs per sac) than *Ar. caudatus* (one every 5 days for *Ar. elevatus* compared to one every 30 days for *Ar. caudatus*, Vollrath 1987). Vollrath (1987) suggests that, because of these and other factors, *Ar. elevatus* is a more 'r-selected' species whereas *Ar. caudatus* is a more 'K-selected' species (Pianka 1970). In these respects (low egg sac output and tenacious guarding), *Ar. ululans* is more similar to *Ar. caudatus*. This might indicate that *Ar. ululans* also tends to be more 'K-selected', however other factors such as generation time and mortality need to be considered.

Foraging behavior.—*Ar. ululans* is a host-specific kleptoparasite which takes a substantial portion of its hosts' prey (Cangialosi in press). Males and juveniles

tend to scavenge more and perhaps function as commensals rather than kleptoparasites. Juvenile females switch to stealing newly captured prey directly from their hosts as they age and therefore turn more kleptoparasitic.

Wise (1982) suggested that predation may be more important for temperate *Argyrodes* whereas kleptoparasitism might be more important for tropical *Argyrodes*. This conclusion was based mainly on the fact that most tropical host spiders studied are large orb-weavers (Robinson and Robinson 1973; Rypstra 1981; Vollrath 1979) and that kleptoparasitism is more likely when the *Argyrodes* is much smaller than its host, and predation is more likely when *Argyrodes* is bigger than its host. The temperate *Argyrodes* species studied by Smith Trail (1980) are large compared to their hosts and are primarily predators. Individual adult female *Ar. ululans* and *An. eximius* are roughly equivalent in body size (5-9 mm) and adult *Ar. ululans* are bigger than *An. eximius* juveniles (subordinate). Nonetheless, *Ar. ululans* appears to be nearly exclusively kleptoparasitic. Because it is social, groups of *An. eximius* make this host "bigger" than *Ar. ululans* (and therefore defensively stronger, Cangialosi, 1990b) making kleptoparasitism more likely than predation.

Although direct predation by *Ar. ululans* on *An. eximius* individuals was not observed (even for individuals starved six days, Cangialosi 1990a), *Ar. ululans* were occasionally observed feeding on their hosts. These may have been individuals that were already dead and scavenged by the kleptoparasites. Other *Argyrodes* species have been observed to kill and/or feed on *An. eximius* (Rypstra, unpublished data; Vollrath 1982). Tanaka (1984) found that *Argyrodes fissifrons* O. P.-Cambridge (which is much smaller than its hosts) preys on its hosts when they are molting and therefore motionless. Because *Ar. ululans* does not kill its host, capture its own prey, or cannibalize its mates, it would be interesting to investigate whether they have venom which is capable of immobilizing prey.

ACKNOWLEDGMENTS

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