

## A New Independently Derived Social Spider with Explosive Colony Proliferation and a Female Size Dimorphism<sup>1</sup>

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### ABSTRACT

Permanent cooperative sociality is rare in spiders. Here we describe sociality in a cobweb (Theridiidae) genus with no other known social species. In five areas of eastern Ecuador, we found nests of *Theridion nigroannulatum* containing from a single to several thousand adults living together in a communal web. Spiders cooperated in prey capture and shared their food. Subadult to young adult sex ratios were highly female biased, suggesting a strongly subdivided population structure as in other permanent-social spiders. Unusual aspects of *T. nigroannulatum*'s biology include the existence of adult females of two discrete sizes, an extreme boom and bust pattern of colony growth, and the presence, within larger colonies, of populations of a predatory spider (*Faiditus* spp., Argyrodinae) that may play the role of a colony-level parasite. The existence of females of two sizes may be the result of alternative female reproductive strategies, intracolony competition for resources, or an incipient caste system in this species. A redescription and phylogenetic analysis corroborate the placement of this species in *Theridion*, indicating that sociality has evolved independently in at least three theridiid genera.

### RESUMEN

El comportamiento social permanente es muy poco usual en arañas. Aquí describimos comportamiento social en un género de la familia Theridiidae en el que no se conocen otras especies sociales. En cinco áreas del Oriente Ecuatoriano encontramos nidos de *Theridion nigroannulatum* que contuvieron en un nido común desde unas pocas hasta varios miles de arañas adultas. Las arañas cooperaron en la captura de la presa y compartieron su alimento. La proporción de sexos entre individuos subadultos y adultos jóvenes fue altamente desviada en favor de las hembras, sugiriendo una población altamente subdividida, como en otras arañas de socialidad permanente. Entre los aspectos novedosos de la biología de *T. nigroannulatum* se encuentran la existencia de hembras adultas de dos tamaños discretos, un patrón de crecimiento explosivo de las colonias, y la presencia en colonias grandes de una araña predadora (*Faiditus* spp., Argyrodinae) que parece jugar el papel de un parásito intracolonia. La existencia de hembras de dos tamaños diferentes puede ser el resultado de estrategias reproductivas alternativas, competencia intracolonia por recursos, o un sistema de castas incipiente. La redescipción y análisis filogenético confirman la ubicación de esta especie en *Theridion*, demostrando que la socialidad ha evolucionado independientemente en por lo menos tres géneros de Theridiidae.

*Key words:* dispersal; Ecuador; female size dimorphism; kleptoparasitism; reproductive skew; predator–prey dynamics; sociality; Theridiid phylogeny; *Theridion nigroannulatum*.

COOPERATIVE PERMANENT SOCIALITY IS KNOWN in slightly over 20 out of the approximately 39,000 described species of spiders (Avilés 1997, Platnick 2006, Agnarsson 2006b). The social spiders are distributed in seven to eight spider families and 10–11 genera, with nearly half of the species belonging to the cobweb (theridiid) genera *Anelosimus* (seven species) and *Achaearanea* (three species) (Darchen 1968; Levi *et al.* 1982; Lubin 1991; Avilés 1997; Agnarsson 2004, 2005; Agnarsson & Kuntner 2005) (note that we do not include *Argyrodes flavipes* in this category, as it is aggressive towards conspecifics (Whitehouse & Jackson 1998)). Most social spiders live in long-lasting (multigenerational) colonies where colony members typically cooperate in prey capture, nest maintenance, and brood care (Kullmann 1972, Buskirk 1981, D'Andrea 1987, Avilés 1997). In most species, new generations of spiders replace parental generations within the nests, with offspring being produced through internal recruitment following mating between colony members. Colonies that reach relatively large sizes may give rise to daugh-

ter colonies by either budding, fission, or the production of small propagules (Avilés 1997, 2000). Colonies at different stages of their life cycle may also go extinct. The highly female-biased sex ratios characteristic of most of the social species (*e.g.*, Avilés & Maddison 1991; Rowell & Main 1992; Avilés *et al.* 1999, 2000) suggest that little, if any, gene flow occurs between colonies at any stage in their lifecycle (Avilés 1993, 1997; Smith & Hagen 1996). This inbred mating system, along with an absence of division of labor within the colonies (Lubin 1995, Avilés 2000) make social spiders unlike many of the more complex eusocial arthropods such as ants or termites. In particular, all females in social spider colonies have the potential to reproduce, although not all may do so due to competition for resources within the colonies (Vollrath 1986, Rypstra 1993, Lubin 1995, Avilés & Tufiño 1998, Ulbrich & Henschel 1999).

Here we describe cooperative permanent-social behavior in a third theridiid genus, in the species *Theridion nigroannulatum* Keyserling. Levi (1963) already speculated that this species might be social, as collection vials usually contained numerous specimens. Avilés (1997) and Avilés *et al.* (2001) confirmed this in brief notes about this species. Here we provide a more complete description of

<sup>1</sup> Received 7 October 2005; revision accepted 30 January 2006.

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this species' social system, comparing aspects of its biology with that of other social spiders. In particular, we report the discovery of an adult female size dimorphism that hints, among other possibilities, to the existence of an incipient caste system in this species. We also redescribe *T. nigroannulatum* and estimate its phylogenetic position based on a parsimony analysis of morphological characters.

## METHODS

**STUDY SITES AND COLONIES.**—Numerous individual webs and colonies of *T. nigroannulatum* were encountered at five locations in Ecuador: (1) just north of Laguna Grande in the Cuyabeno Nature Reserve (CNR-LG) (Sucumbios Province, 0.0012°S 76.1715°W, elevation 230 m, L. Avilés and W. Maddison, July 1988, July–August 1989); (2) near the Cuyabeno River, upstream from the Tarapoa-Tipishca bridge, in the CNR (CNR-CR) (Sucumbios Province, 0.03°S 76.33°W, elevation 200–300 m, L. Avilés and G. Cañas, October 1994–December 1995); (3) at the Yasuni Biological Station in the Yasuni National Park (YNP) (Orellana Province, 0.671°S 77.400°W, elevation 200 m, G. Cañas, September 1995); (4) 6.6 km north of Limón on highway to Méndez (Morona Santiago Province, S 2.9227 W 78.4079, elevation 1000 m, rain forest, W. Maddison, I. Agnarsson, G. Iturralde, P. Salazar, 14 July 2004); and (5) at the Estación Biológica Jatun Sacha (Napo Province, 1.067° S 77.617°W, elevation 400 m, rain forest, W. Maddison, I. Agnarsson, G. Iturralde, P. Salazar, 21–24 July 2004). Behavioral and life history observations were conducted on colonies encountered at locations (1) and (2), including the first colony encountered in July 1988 (designated CNR-LG 88-1), a large colony (designated CNR-LG 89-A) and a complex of small colonies (designated CNR-LG 89-B) encountered in July 1989, and a complex of small colonies encountered in April 1994 (designated CNR-CR-94). We collected the entire contents of five medium-sized nests (CNR-LG: 88-1, 89-B64, -B65, -B67; Limón LM1), samples from the large CNR-LG 89-A nest and from two Limón nests (LM2, LM3), and samples, or the entire contents, of ~24 small nests. In the preserved samples, adult females were identified by the presence of a sclerotized epigynum and measured (tibia plus patella of leg pair I) to a 0.1 mm precision under an Olympus SZ61 dissecting microscope (Olympic America Inc., Center Valley, PA, U.S.A.). Egg sacs were opened, and the number of eggs or embryos counted. Voucher specimens are deposited in the National Museum of Natural History, Smithsonian Institution (Washington DC).

**PHYLOGENETICS.**—*Theridion nigroannulatum* was added to the phylogenetic analysis of Agnarsson (2006a, see also Agnarsson 2003b, 2004), and the analysis rerun with the same parameter settings (see Agnarsson 2004 for detailed methodology and justification). Character coding for *T. nigroannulatum* was as follows:

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00010000-00001111120000000001-111—10020000000110000
010??000000001000000110-100000000 000000001100000110
0210100010000001000001000001000100011-1101111000100
00111110101??1-1-00021101111000000111001100001??000??
0111?1????0301??00??110??????0
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## RESULTS

In the sections that follow, we provide evidence that *T. nigroannulatum* is a cooperative nonterritorial permanent-social spider (*sensu* Avilés 1997) while highlighting unusual aspects of its biology, such as the presence of an adult female size dimorphism, an extreme “boom and bust” pattern of colony growth, and the existence within colonies of large populations of a predatory spider that may play the role of a colony-level parasite.

**ECOLOGY.**—*Nests.* At the five study locations, *T. nigroannulatum* colonies typically occurred near small streams of the forest interior or on their valleys' slopes. The species cannot be found reliably in any particular area, however, because its colonies appear highly volatile (see below) and are patchily distributed. With the exception of the largest colony seen, its nests occurred under short forest understory plants (*e.g.*, at the CNR-CR-94 site, mean = 0.4 m, range 0.1–0.8 m,  $N = 15$ ), with the spiders congregated on the underside of leaves. The webs consisted of fine sticky lines that extended from those leaves to the ground below (Figs. 1A–I and 2). Nests containing a single female or small groups typically bent the leaf or leaves they occupied into small tents using silk strands (Fig. 1B, F). Larger colonies did not bend their leaves (Fig. 1A, C). The largest colony found (CNR-LG-89A, Table 1) occupied the leaves of a 2-m tall tree and a few adjacent plants, with webbing extending 3.5 × 2.5 m horizontally × 4 m vertically.

*Predators and parasites.* Inside several of the nests at two sites (CNR-LG-89 sites A and B) we found an argyrodine theridiid spider *Faiditus* sp. (an undescribed species close to *F. subdolosus*), which we observed preying upon *T. nigroannulatum*. At site B (Fig. 2), the predatory spider comprised 23 percent of the spider population within four central nests (24 female and seven male *Faiditus* along with 104 adult *Theridion*). At this site, which contained nests ranging in size from 1 to 42 females (Table 1), the presence of the predator was significantly more likely in intermediate and large nests than in small nests (logistic regression  $\chi^2 = 10.8$ ,  $df = 1$ ,  $P = 0.001$ ,  $N = 54$ ). We also found *Faiditus* within the huge CNR-LG 89A nest when first seen in July 1989. After this colony had undergone a massive dispersal event (see below), we identified among its remnants 11 *Faiditus* individuals cohabiting with the remaining 129 *T. nigroannulatum* females (Table 1). *Faiditus* egg sacs could also be seen suspended within the nests and nearby vegetation at both sites. We did not observe *Faiditus* in smaller colonies or solitary webs.

Other parasites included larvae attached to the abdomen of some females (likely polysphinctine ichneumonids; Nielsen 1932, W. G. Eberhard, pers. comm., see also Gauld *et al.* 1998). We also observed a 2.5-cm unidentified wasp attacking a colony of 37 subadult individuals from which it removed two spiders.

**DEMOGRAPHY.**—*Colony size and age structure.* Table 1 summarizes the range of colony sizes and their age structure, as seen at different times at the five study locations. Within colonies, spiders were synchronized in their phenology as nests contained either (1)

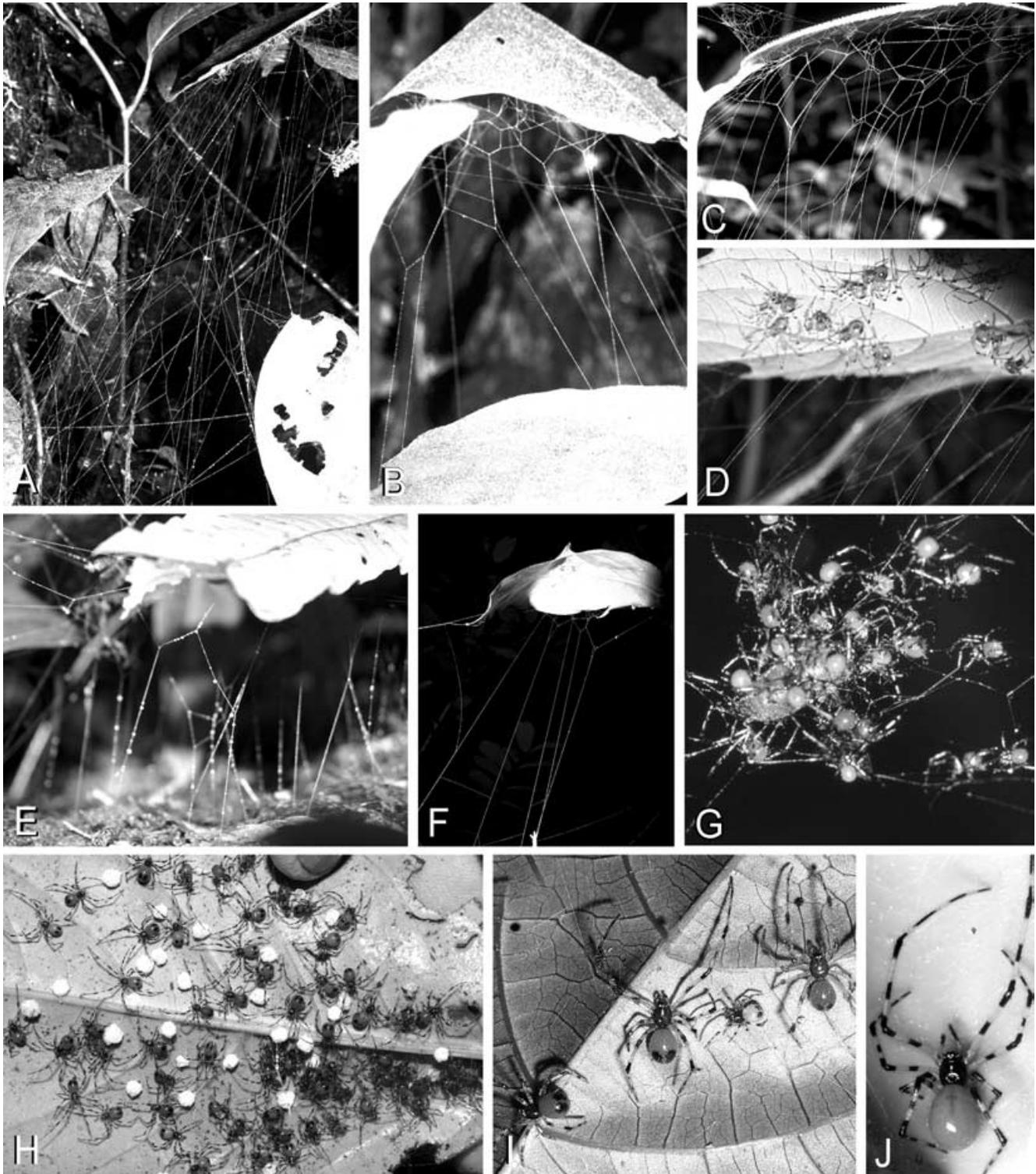


FIGURE 1. Photographs of *Theridion nigroannulatum* colonies. (A) Social web; (B, C) solitary web; (D) adult females resting underside a leaf, the web consists of lines suspended from the leaf; (E) base of sticky lines of web, glue may be found on the entire length of the line, including the very tip (as in typical theridiid gumfoot lines); (F) sticky lines of a solitary web; (G) communal prey capture; (H) females guarding egg sacs on the underside of a leaf; (I) females from Limón, note paired dots on abdomen; (J) female from Cuyabeno, abdomen without dots.

TABLE 1. The range of colony sizes and their age structure, as seen at the five study sites.

Location	Date	No. of colonies	No. of adult females	Median	Contents
CNR-LG 88-1	June 1988	1	163		163 adult females, 24 adult males, 50 juveniles
CNR-LG-89A, prior to proliferation	July 1989	1	~3100		~3100 adult females, ~900 adult males, no egg sacs, no juveniles. <i>Faiditus</i> .
remnants after proliferation:					
propagules	August 1989	1	129		129 adult females, 11 <i>Faiditus</i> .
	August 1989	27	1–5	1	Adult females, egg sacs
CNR-LG-89B	July 1989	54	1–42	2	Adult females either alone, with egg sacs or with small-to-medium juveniles, except in sub area with larger nests (see text).
CNR-CR-94	April 1994	17	1–13	1	Adult females, some sacs/young juveniles; two nests large juveniles/young subadults
	September 1994	17	1–3	1	See text
YASUNÍ, prior to expansion	September 1995	1	378		378 adult females, 8 adult males, 78 sacs
LIMÓN	July 2004	3	68–209	107	Adult males and females; females with sacs; or females with juveniles
JATUN SACHA	July 2004	A few	1	1	Adult females

adult females by themselves; (2) adult females with either egg sacs, small juveniles, or medium/large juveniles; (3) large juveniles and subadults by themselves; (4) or subadult to young adult males and females. This situation held even in the huge CNR-LG 89A colony, which contained only adult and subadult males and females.

In contrast, within sites even colonies found in close proximity to one another could be in different stages of their life cycle. Among the 17 colonies seen at the CNR-CR-94 site in September 1994, for instance, one contained a single adult female; three, females with egg sacs; five, females with young juveniles; two, females with older juveniles; two, juveniles/subadults by themselves; and two, nearly fully grown subadult and adult spiders prior to mating and dispersal. Only two nests at this site had a mixed age structure—one containing three subadult males plus young juveniles; the other containing three adult females, one by herself, another with an egg sac, and the third with young juveniles. The three colonies at the Limón site, found within 100 m of one another, were in three different stages of their life cycle (Table 1) (a nest of  $\sim 30 \times 20 \times 20$  cm contained 68 adult females, 7 adult males, and 5 large juveniles; a nest of  $21 \times 13 \times 38$  cm contained 107 adult females and 39 sacs; a nest of  $110 \times 40 \times 37$  cm contained 209 adult females and ~900 juveniles. Exceptions to the lack of synchronization among nests occurred at the CNR-LG-89A site, where following a colony proliferation event (see below) nests contained only adult females by themselves or with egg sacs, and at CNR-LG-89B site, where small nests contained adult females by themselves or with small-to-medium juveniles (Table 1; Fig. 2).

**Colony dynamics and proliferation.** Observations at three sites point to fairly rapid colony growth followed by explosive disintegration of large colonies into small propagules: (1) The colony seen at Yasuní in September 1995 grew from  $0.5 \times 0.5 \times 0.6$  m to  $2.0 \times 2.2 \times 1.7$  m during a 7-mo period following which several newly founded nests with one to several adult females surrounded it. (2) The 4000-

spider colony seen at the CNR-LG-89A site measured  $3.5 \times 2.5 \times 4$  m when first seen in July 1989; 3 weeks later it was reduced to  $1.0 \times 1.0 \times 1.5$  m while surrounding it, at distances of 4–16 m (median = 7.8 m), were 27 newly founded nests with one to five adult females (median = 1). (3) The spatial distribution and size of colonies at the CNR-LG-89B site in July 1989 (Fig. 2) was suggestive of a recent colony proliferation event: All intermediate-sized colonies in the area, which contained between 10 and 42 adult females plus large juveniles, were clustered in a small elevated area ( $\sim 10 \times 5$  m) while, scattered in the slopes below, were 55 small colonies containing from one to six adult females, either by themselves, with egg sacs, or with small-to-medium juveniles (Fig. 2). Four of the intermediate-sized colonies, but none of the small ones, were infested with the predatory spider *Faiditus* (see above and Fig. 2).

Explosive proliferation of large colonies, however, may not be the only method of colony establishment in this species, as we also observed smaller colonies loose members at rates greater than might have been expected due to mortality alone (e.g., a 13-adult female colony seen at the CNR-CR-94 site became reduced to four females within a week of its first sighting).

**Adult female size dimorphism.** Examination of collected samples in the laboratory confirmed our impressions from the field that adult females occur in two discrete size classes (Fig. 3) (tibia plus patella of leg pair I length, mean  $\pm$  95% ci, large females:  $3.99 \pm 0.046$  mm; small females:  $3.01 \pm 0.032$  mm,  $t = 34.4$ ,  $df = 240$ ,  $P < 0.0001$ ). The ratio of large to small females varied among areas and colonies, from 29 percent large females in a sample of 292 spiders from the 55 colonies in the CNR-LG-89B site to 68 percent large females in the 4000-spider (CNR-LG 89A) colony. At the former site, there was significant heterogeneity among colonies in the proportion of large females they contained (likelihood ratio  $\chi^2 = 76.0$ ,  $P < 0.0001$ ), with a nonsignificant trend for larger colonies to contain a smaller

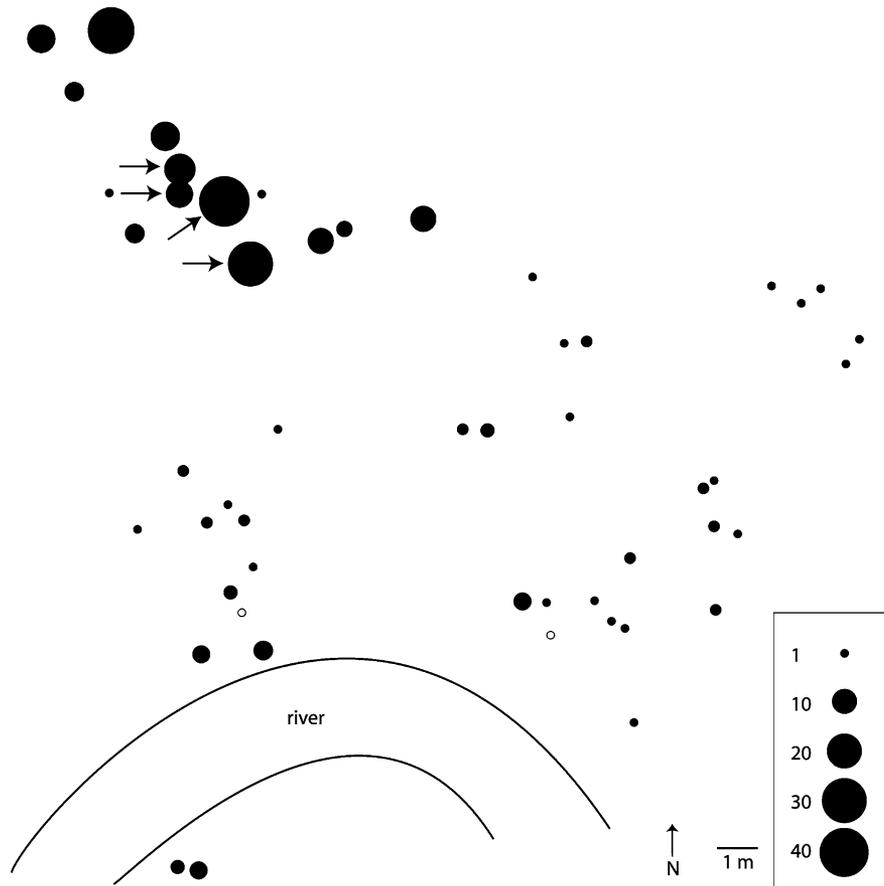


FIGURE 2. A map of relative position and size (number of adult females) of colonies in CNR-LG site B (see Methods). Size of circles is proportional to colony size, ranging from 1 to 42 adult females. Open circles indicate colonies with juveniles only, arrows indicate colonies where the predatory *Faiditus* was present.

proportion of large females ( $F_{1,26} = 3.6$ ,  $P = 0.07$ , test performed on arcsine-transformed proportions, with data points weighted by the number of females in the nest; nests with only one female excluded). There was also a wide spread in the number of embryos—8 to 24 (median 14)—contained within 25 egg sacs examined from various colonies. Unfortunately, we could not match egg sacs with the females that laid them to determine whether larger females laid larger clutches.

**Sex ratio.** The percentage of males among subadult to young adult spiders in four colonies seen at the CNR (LG-89 and CR-94 sites) ranged from 7.1 to 12.8, with no significant heterogeneity among colonies (likelihood ratio  $\chi^2 = 1.43$ ,  $df = 3$ ,  $P = 0.70$ ). The overall 11.3 percent males observed (weighted average) was significantly lower than an expected 50:50 ratio (Fisher’s exact test  $P < 0.0001$ ; Table 2). It remains to be confirmed, however, by means of embryo chromosome preparations (as in Avilés & Maddison 1991), whether this sex ratio bias is already present in developing embryos.

**BEHAVIOR.—Cooperative prey capture and food sharing.** Nine of ten instances of prey capture observed at the CNR-LG sites involved

the participation of more than one spider (median = 5, range: 4–20 among seven cases with exact numbers of spiders recorded). Flying or jumping prey were first trapped by the vertical sticky threads of the nest. The spiders then approached the prey by traveling down the silk lines from their resting spot under the leaves. Spiders attacked the prey by wrapping it with sticky silk and biting it. Prey was then transported back to the resting place, a task that involved from one to several spiders. Typically, a greater number of individuals fed on the prey than were involved in attacking it (e.g., six fed on a 1 cm moth caught by four and transported by one spider; 25 fed on a large tabanid caught by 20 spiders) (Fig. 1G). Prey seen being caught or fed upon by the spiders included a large tabanid, three beetles, one leaf hopper, one 1 cm moth, a 4 cm katydid, a 10 cm mantid, a 3 cm fly, and three smaller flies.

**TAXONOMY AND PHYLOGENETICS.—Description:**

*Theridion nigroannulatum* Keyserling, 1884.

**Types.** Female lectotype designated by Levi (1963: 539) from Amable María, Tarma, Junín Province, Peru, elevation 640 m. In the Polish Academy of Sciences, not examined.

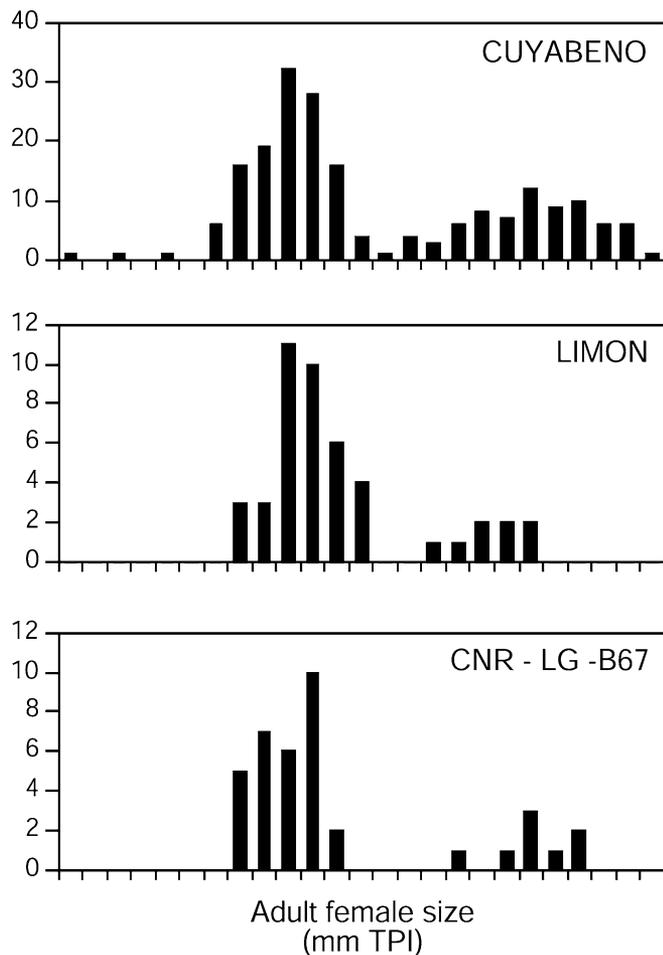


FIGURE 3. Distributions of adult female sizes at the Cuyabeno Nature Reserve - Laguna Grande (overall and colony B67) and at Limón.

*Synonymies.* *Theridion nigroannulatum* Keyserling, 1884: 74, plate 4, fig. 45 (note that listed as *T. migromaculatum* in table on pp. 5, 8).

*Theridion nigroannulatum*; Levi, 1963: 539, figs. 59–63; Platnick 2006.

*Diagnosis.* Both sexes of *T. nigroannulatum* are separated from other *Theridion* by their striking coloration, especially the distinct dark annulations of the legs (Figs. 1H–J). Males differ from other *Theridion* by the shape of the posterior rim of the median apophysis (Fig. 4A), females by the simple epigyna and extremely short copulation and fertilization ducts (Fig. 4C).

*Description.* Medium-sized theridiid spiders, male total body length 3.2–4.1 mm, cephalothorax 1.4–1.7 mm, abdomen 1.8–2.2 mm, femur I 3.4–4.2 mm, leg I total length circa 14 mm, about twice the length of leg II and IV, leg III shortest. Female total body length 3.20–5.40 mm, cephalothorax 1.5–2.1, abdomen 2.8–3.6, femur I 3.2–4.3, leg I total length circa 13 mm, leg IV about 10 mm, II about 8 mm, leg III shortest. Prosoma brown to dark brown, legs long, whitish, with striking dark annulations, about as broad as the distance between them (Fig. 1H–J). Abdomen usually uniformly medium beige with dark areas around spinnerets and pedicel (Fig. 1I), but specimens from Limón with large paired dark spots posteriorly above spinnerets (Fig. 1J). Genitalia as in Figs (4A–D). Males from Limón ( $N = 5$ ) with palpal organs approximately 20 percent smaller than males from Cuyabeno ( $N = 5$ ), but no differences noted in the structure or composition of palpal sclerites. Epigyna of differently sized specimens appear equal in size.

*Distribution.* Peru–Ecuador, wet rain forests from altitudes of ca 400–2000 m.

*Phylogenetics.* The cladistic analysis found two most parsimonious trees ( $L = 790$ ,  $CI = 36$ ,  $RI = 73$ ), where *T. nigroannulatum* groups sister to *T. longipedatum* (Fig. 5). The trees are otherwise identical to that preferred by Agnarsson (2004, 2006a) (the strict consensus collapses one clade within Pholcommatinae, as in Agnarsson, 2006a). This result corroborates the placement of *T. nigroannulatum* in *Theridion* (note though, that *Theridion* is not monophyletic), and confirms that sociality has evolved independently in at least three theridiid genera.

## DISCUSSION

Although sociality is rare in spiders, it has arisen independently multiple times (Avilés 1997; I. Agnarsson *et al.*, pers. comm.). Here we have documented an additional independent derivation of this

TABLE 2. Estimates of sex ratios in four colonies of appropriate age (mostly subadults to young adults present).

Location	Colony	Date	Sub ad/ females	Sub ad/ males	Males (%)	Other spiders in nest
CNR-LG	88-1	26 June 1988	163	24	12.8	50 juveniles
CNR-CR	94A377	28 April 1994	26	2	7.1	None
CNR-CR	94A395	26 September 1994	32	3	8.6	Two juveniles
CNR-CR	94A379	26 September 1994	39	4	9.3	One adult female (others subadults)
		Total	260	33	11.3	

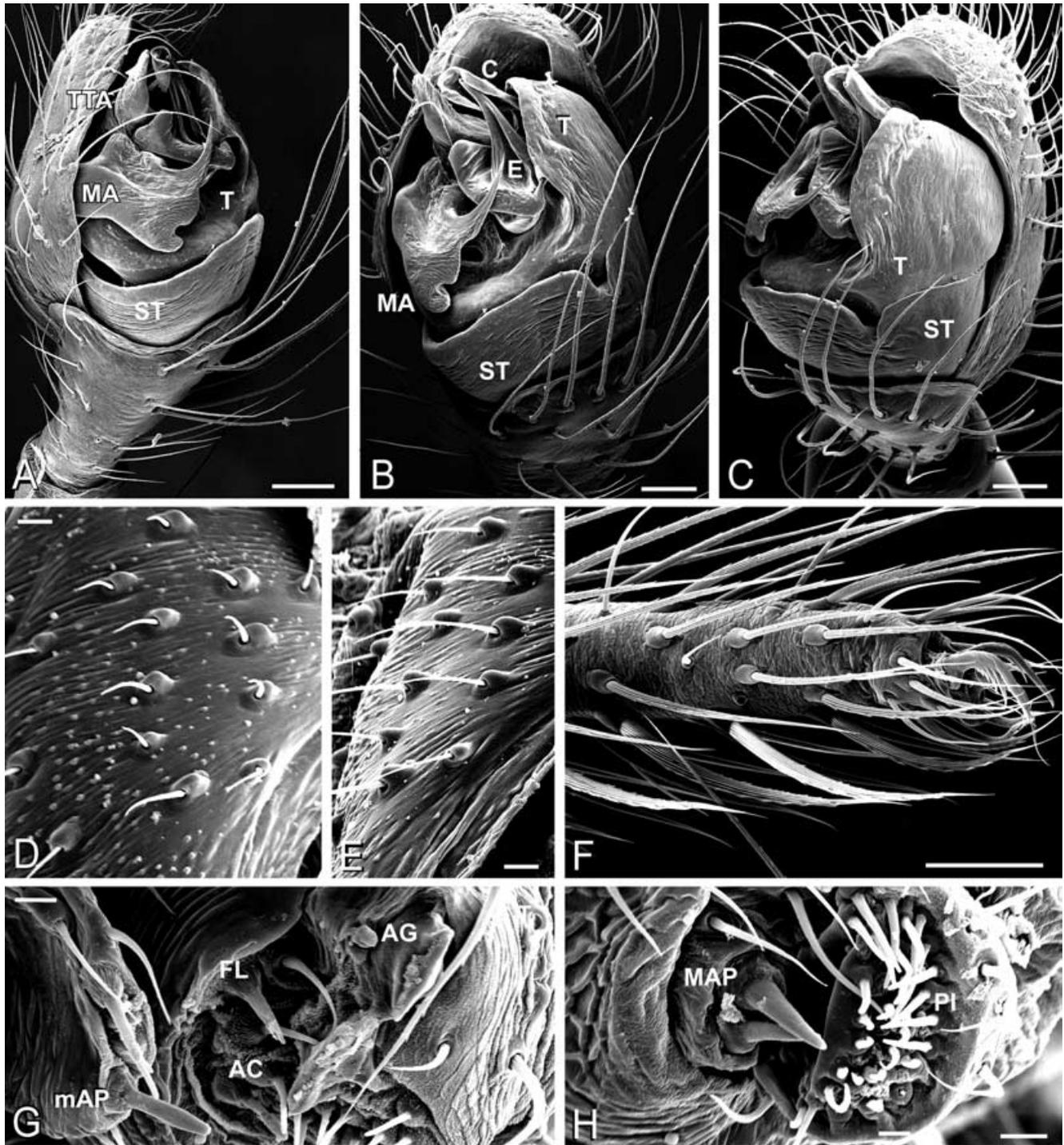


FIGURE 4. Scanning electron microscope photographs of *T. nigroannulatum*. (A–C), male palp: (A) mesal; (B) ventral; (C) ectal. (D, E), Male abdominal stridulatory picks; (F) female tarsus IV; (G) female posterior lateral and posterior median spinnerets; (H) female anterior lateral spinnerets, the presence of two major ampullate spigots (MAP) in the adult stage is very unusual.

form of social behavior in the Theridiidae, a family with two other genera, *Anelosimus* and *Achaearanea*, with multiple social species (Avilés 1997, Agnarsson 2006b). The discovery of a permanent-social *Theridion* does not come as a surprise given the widespread

occurrence of extended maternal care in this genus (e.g., Gillespie 1990, Ruttan 1990; see also Avilés 1997, Agnarsson 2004). We have shown that *T. nigroannulatum* exhibits key characteristics of nonterritorial permanent-social species, including the formation of

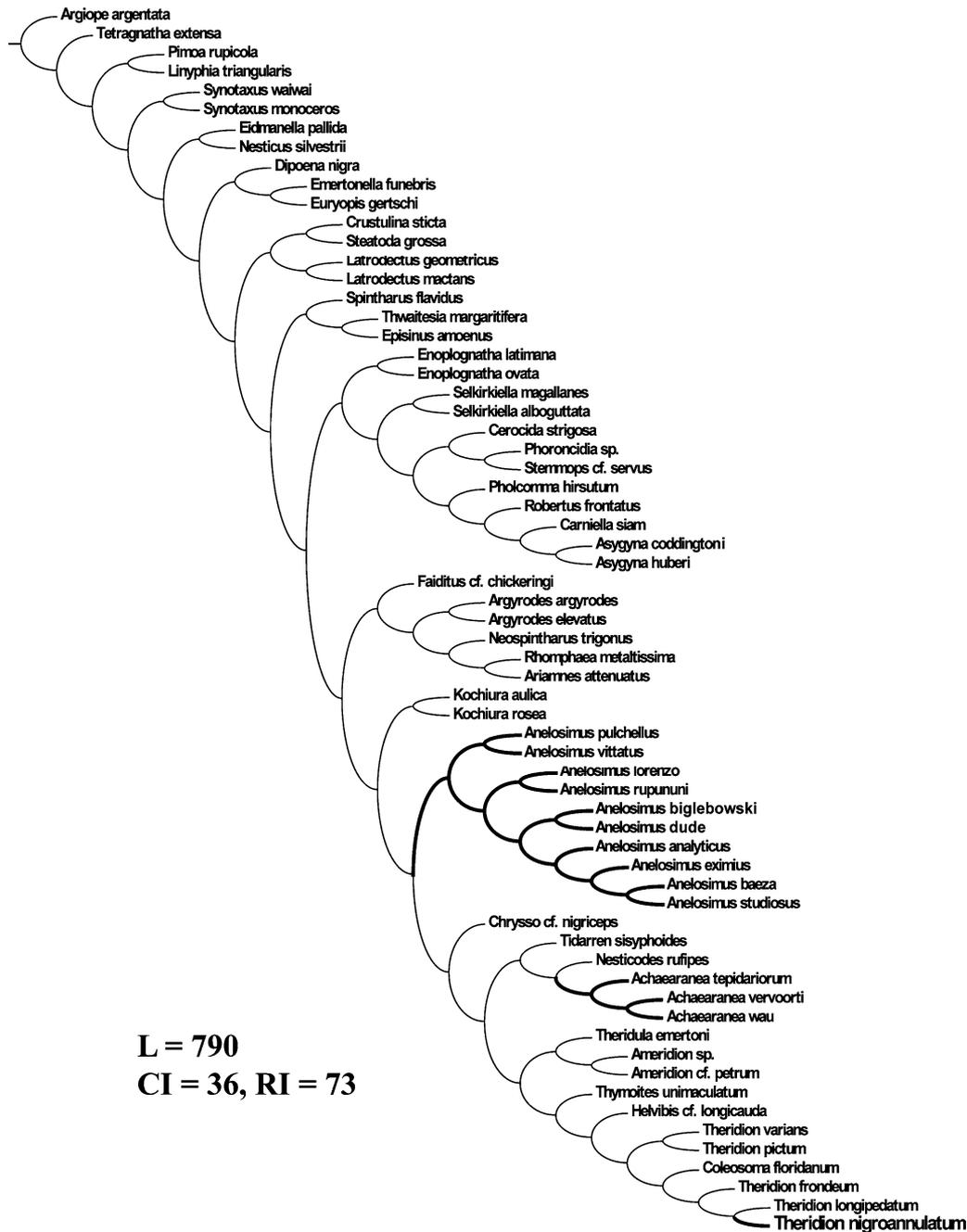


FIGURE 5. The preferred cladogram, indicating the phylogenetic position of *T. nigroannulatum* (in larger font) sister to *T. longipedatum*. The other two genera containing social species are indicated with bold lines in the cladogram.

communal nests with multiple adult females and their offspring, cooperative prey capture and transport, and food sharing. The preponderance of females among subadult and young adult spiders in *T. nigroannulatum*'s colonies is suggestive of a primary sex ratio bias and associated population subdivision, as in most permanent-social spiders (Avilés 1986, 1993, 2000; Lubin 1991; Smith & Hagen 1996). As shown by several authors (Hamilton 1979, Wilsson & Colwell 1981, Charnov 1982, Frank 1986, Avilés 1993),

selection for biased sex ratios among more or less isolated breeding groups may be sufficiently strong to counter to some extent selection within groups for a Fisherian 1:1 sex ratio. Given the positive association between colony size and colony proliferation (reviewed in Avilés 1997), social spider colonies with a greater proportion of females would grow faster and would thus be more successful at producing daughter colonies. Consistent with the implication that colonies may represent more or less isolated breeding groups, in

*T. nigroannulatum* we found that individuals within colonies were largely synchronized in their phenology, but the life cycle stages across colonies, except in areas where a recent colony proliferation event had taken place, were not.

*Theridion nigroannulatum*, however, also has characteristics shared with few other known permanent-social spiders, including an adult female size dimorphism, volatile colony dynamics, and a high incidence within its colonies of a predatory spider that may play the role of a colony-level parasite. *Theridion nigroannulatum* represents a rare case among social spiders of a bimodal distribution of adult female sizes (Fig. 3). This distribution probably reflects maturation at different chronological instars, as the smaller females were of a similar size as adult males (see Description), which in spiders usually mature an instar earlier than females (e.g., Krauss & Kraus 1988). In contrast, in other social spiders, such as the social theridiid *Anelosimus eximius*, documented variation in adult female body size encompasses a range expected among females belonging to the same chronological instar (Rypstra 1993; Ebert 1998; Agnarsson 2006b). Only among social species in the genus *Stegodyphus* have there been reports of males and females becoming adult at more than one instar (Krauss & Kraus 1988), although it has not been reported whether adults of different chronological instars co-occur within colonies.

Given the well-documented association between female size and fecundity in spiders (e.g., Wise 1979, 1993; Marshall & Gittleman 1994; Simpson 1995; Buddle 2000), and the range of clutch sizes documented here, the co-occurrence of adult females of two sizes in colonies of *T. nigroannulatum* opens a number of interesting possibilities. Smaller females, for instance, may reach reproductive maturity at a younger instar as a strategy to get a head start in reproduction or as a mechanism to secure some reproduction after failing to molt to a larger size due to competition for resources within the colonies. Alternatively, if smaller females combine a reduction in reproduction with greater contribution to communal activities, the female size dimorphism observed may be indicative of an incipient caste system in this species.

Another puzzling aspect of *T. nigroannulatum*'s biology is the volatile nature of its colonies, which appear capable of fast growth to large sizes followed by explosive proliferation. A variety of colony-level life history strategies (*sensu* Avilés 2000) have been documented for social spiders. In species such as *Aebutina binotata*, colonies undergo relatively mild growth for one generation before reproducing by fission (Avilés 2000), while in species such as *Anelosimus eximius* colonies grow to large sizes for several generations before giving rise to many small propagules (Vollrath 1982; Veinticinque *et al.* 1993; see Lubin & Robinson 1982, for an intermediate case). *Theridion nigroannulatum*'s explosive mode of colony proliferation appears an even more extreme case along this continuum. The fast growth of *T. nigroannulatum*'s colonies may be facilitated by the much lighter nature of its webs (Fig. 1A–F), which are presumably cheaper to produce than the dense mesh webs with reinforced basal sheet typical of *Anelosimus* and *Achaearanea*, the two other theridiid genera with social species (see fig. p. 480, in Avilés 1997). The preponderance of small colonies in the distribution of *T. nigroannulatum*'s colony sizes, however, suggest that successful growth to large sizes is either rare or short-lived. Only 7 of 50

marked colonies at one of our field sites (CNR-LG site B) had any remaining spiders when reinspected a month later. Colonies also only rarely remained in the same location from one generation to the next; the Yasuni colony, seen in the same spot after 7 mo, was an exception.

It is tempting to speculate that colony proliferation in *T. nigroannulatum* may occur to some extent in response to a build up of the predatory *Faiditus*, a theridiid spider we found living within larger colonies in substantial numbers (e.g., 23 percent of the population of the four core colonies at CNR-LG site B). Other *Faiditus* species routinely inhabit the social webs of many *Anelosimus* species (e.g., Cangialosi 1990a, b), in addition to webs of large solitary orb weavers (e.g., Elgar 1989, Agnarsson 2003a). These other species, however, are primarily kleptoparasitic, stealing prey items from their host's webs (Cangialosi 1990a, b), rather than predatory. The concentration of the predatory *Faiditus* in large- and intermediate-sized *T. nigroannulatum* colonies, and its absence from small and presumably newly founded colonies, suggests that *T. nigroannulatum*'s explosive proliferation may permit the spiders to escape, albeit temporarily, this colony parasite. In another social spider, *Stegodyphus mimosarum*, wasp parasitoids have been suggested as a likely factor driving colony proliferation (Crouch & Lubin. 2001). The discovery of this host–parasite association opens a number of questions for future exploration. What mechanisms does *Faiditus* employ to locate new colonies and to what extent does it track local colony lineages? What is its impact on the fitness of infected colonies? How long are newly founded colonies able to remain parasite free? Is this a species-specific interaction? And, finally, to what extent is the volatile nature of *T. nigroannulatum*'s colonies driven by this predator–prey interaction?

The discovery of an additional independent derivation of cooperative permanent-sociality in spiders extends the opportunities we have to test hypotheses involving common aspects of social spider biology, such as the association between biased sex ratios and population structure and dynamics (Avilés 1993), the role of predator or kleptoparasite–host interactions in demography and colony dynamics (this paper), the factors that facilitate or drive social evolution, and the consequences that inbred social systems may have had on macroevolutionary patterns (Avilés 1997; I. Agnarsson *et al.*, pers. comm.). At the same time, unusual aspects of *T. nigroannulatum*'s biology may expand our view of what a social spider can be, including the possibility that reproductive castes may be a viable feature of social spider biology after all.

## ACKNOWLEDGMENTS

We are indebted to Herbert W. Levi for original identification of the species, Gustavo Cañas for the observations on the Yasuni colony, and Patricio Salazar for help in collecting the Limón field data. Thanks to Jeff Fletcher, Jessica Purcell, Patricio Salazar, and two anonymous reviewers for comments on the manuscript. Research and collecting permits were obtained through the Instituto Ecuatoriano de Areas Protegidas y Vida Silvestre, with the sponsorship of the Museo Ecuatoriano de Ciencias Naturales and the Department of Biology of the Pontificia Universidad Católica del Ecuador.

Early phases of this research were conducted while LA was affiliated with Harvard University (Organismic and Evolutionary Biology) and WPM with the University of California at Berkeley (Integrative Biology) and then both with the University of Arizona (Ecology and Evolutionary Biology). Research conducted while at the University of British Columbia was funded by grants from the National Sciences and Engineering Research Council of Canada to LA and WPM and a Killam postdoctoral fellowship to IA.

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