A New Independently Derived Social Spider with Explosive Colony Proliferation and a Female Size Dimorphism

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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 intracolinal. La existencia de hembras de dos tamaños diferentes puede ser el resultado de estrategias reproductivas alternativas, competencia intracolonial por recursos, o un sistema de castas incipiente. La redescrición 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 Acheaeranaea (three species) (Darchen 1968; Levi et al. 1982; Lubin 1991; Avilés 1997; Agnarsson 2004, 2005; Agnarsson & Knutner 2005) (note that we do not include Argyrodex 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-

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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-Tipíshca 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 Yasuní Biological Station in the Yasuní 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, rainforest, 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, rainforest, 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-A and from two Limón nests (LM2, LM3), and samples, or the entire contents of five medium-sized nests (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 (designated CNR-CR-94). We collected the entire contents of five medium-sized nests (CNR-LG: 88-1, 89-A 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 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.

**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:

00010000-00001111120000000001-111—10020000000110000 01000000001000000110-00000000000000110000110 021010001000000100000010000001000011-1101111000100 001111110101111-1-1-000211011110000001110011000012-00010001111111010101010101010101000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000
Theridion nigroannulatum, a Social Spider

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.
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 30 × 20 × 20 cm contained 68 adult females, 7 adult males, and 5 large juveniles; a nest of 21 × 13 × 38 cm contained 107 adult females and 39 sacs; a nest of 110 × 40 × 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 × 0.5 × 0.6 m to 2.0 × 2.2 × 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-spicder colony seen at the CNR-LG-89A site measured 3.5 × 2.5 × 4 m when first seen in July 1989; 3 weeks later it was reduced to 1.0 × 1.0 × 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 (∼10 × 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 ± 95% ci, large females: 3.99 ± 0.046 mm; small females: 3.01 ± 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

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

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


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

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

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
form of social behavior in the Theridiidae, a family with two other genera, *Anelosimus* and *Achaearaneae*, 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
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, Wilson & 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

![Cladogram Diagram](image-url)
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 among 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.

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LITERATURE CITED


