The Evolution of Sociality in Spiders

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I. Introducing Social Spiders

A solitary lifestyle characterizes the vast majority of almost 40,000 known species of spiders (Platnick, 2007). Thus, the occurrence of group living in spiders begs the question: what is different about these species? Group living has arisen in spiders in basically two different forms. Cooperative or ''nonterritorial permanent-social'' species (sensu Avilés, 1997; also referred to as ''quasi-social,'' Buskirk, 1981) are the main focus of this chapter. These species have family-group territories consisting of communal nests and capture webs, which they inhabit throughout the entire lifetime of the individual, and colony members cooperate in foraging and raising young. In many ways, these species resemble the ''primitively eusocial'' wasps and bees and the cooperative breeders in vertebrate societies, where the family forms the basic unit of sociality (Brockmann, 1997; Whitehouse and Lubin, 2005). Another form of group living in spiders has been termed colonial or communal-territorial (Avilés, 1997: ''territorial permanent-social'' species). Colonial species occur in aggregations, but individuals in the colony generally forage and feed alone and there is no maternal care beyond the egg stage; thus, they lack the cooperative behaviors described below for nonterritorial permanent-social species (reviewed in Uetz and Hieber, 1997; Whitehouse and Lubin, 2005). Colonial species have been likened to foraging flocks of birds (Rypstra, 1979) and are described as ''foraging societies'' by Whitehouse and Lubin (2005). Colonies range from temporary aggregations under favorable conditions to large, long-lived structures. Groups are formed parasocially, by aggregation of individuals, and their composition is variable (Lubin, 1980; Uetz and Hieber, 1997). Although colonies may include related individuals, there is no evidence of inbreeding (Uetz et al., 1987), a trait that distinguishes

them from nonterritorial permanent-social species (see below). Coloniality is the more common form of group living in spiders: Whitehouse and Lubin (2005) list 53 species in 12 families, including both web building and non-web building species, which exhibit temporary or permanent coloniality. The list greatly underestimates the number of colonial species, as most occur in tropical and subtropical regions, and the habits of most tropical species are totally unknown.

Nonterritorial permanent-social spiders (henceforth referred to as "social" spiders) inhabit colonies that last for up to a few generations, and adjacent, interconnected colonies may form a colony cluster (Avilés, 1997). Marques et al. (1998) defined a colony as "a group of individuals that occupy a single web (colonial web) which was spun and maintained by these same individuals," but there are also some social species lacking capture webs. Within colonies, individuals cooperate constructing the capture web and communal nest or retreat and in capturing prey. Young remain in the colony and accrue tasks as they mature; a proportion of females may act as helpers, but there is no division of labor in the sense of social insect castes (Franks, 1987). Unlike the vast majority of cooperatively breeding vertebrates and social insects, which have outbred mating systems, in the social spiders mating occurs within colonies among individuals of the same cohort, and adult, mated females disperse from the mother colony singly or in groups to establish new colonies. Regular inbreeding is in fact a key characteristic of this type of sociality in spiders. Exceptions may be found to one or several of the above traits in different species, but on the whole, the constellation of all or most of these traits characterizes social spider species from a wide range of families.

Social species are rare, even by comparison with colonial species: fewer than 25 species are known to be social (Agnarsson et al., 2006; Avilés, 1997; Table I). Despite the small number, social species are widely distributed across taxonomically distinct families, with social representatives found in nine genera in six families [Table I; one species, *Delena cancerides*, has been redefined as subsocial, making one less family and genus by comparison with Agnarsson et al. (2006)]. They are also widely distributed geographically: social species occur in the tropics and subtropics of every continent, with a particularly high concentration in the Amazonian region of South America (see Avilés, 1997). Furthermore, there is now evidence to support as many as 18 independent origins of sociality (Agnarsson et al., 2006). The majority of social species are found within the family Theridiidae, which contains 11–12 social species in 3 genera representing 9 independent origins of sociality (Agnarsson, 2006; Avilés, 1997; Avilés et al., 2006). The second most abundant group, the Eresidae, contains three independent origins of sociality all found within the genus *Stegodyphus* (Johannesen et al., 2007; Kraus and Kraus, 1988). Thus, social spiders can be viewed as an ideal evolutionary experiment with independent replicates both within and

TABLE I

BEHAVIORAL AND LIFE-HISTORY CHARACTERISTICS OF SOCIAL SPIDERS

Family	Species	Colony composition[a]	Colony foundation[b]		Mode[c]	Sex ratio[d] (% males)
			Females	Males		
Agelenidae	*Agelena consociata*	mf,y	a; all stages (inferred)	?	**f**	8–18%[b]
	A. republicana	mf,y	?	?	f	16.5–22%[b], 0–30%[b]
Dictynidae	*Aebutina binotata*	mf,y	pa,a	pa,a	**f, g**	8.5%[a]
	Mallos gregalis	mf,y	a?	?	?	0–18.5%[b] (captive colonies)
Eresidae	*Stegodyphus dumicola*	mf,y	a (pm)	a(rare?)	f,p, **s**,g	17%[a], 12%[b]
	Stegodyphus mimosarum	mf,y	a (pm)	a	f,p, s,**g**	9%[b]
	Stegodyphus sarasinorum	mf,y	y?, a (pm)	?	f,p s,g	22%[a], 8.5–33%[b]
Oxyopidae	*Tapinillus* sp. 1[*]	mf,y	pa,a?	pa,a?	f	50%[a]
Theridiidae	*Achaearanea disparata*	mf,y	?	?	?	?
	Achaearanea vervoorti	mf,y	?	?	?	5%[b]
	Achaearanea wau	mf,y	a (pm)	a (rare)	f,p, **g**	12%[a]
	Anelosimus domingo	mf,y	?	?	?	11%[b], 8%[a]
	Anelosimus dubiosus	mf,y	pa,a	a?	s,g	31%[b]
	Anelosimus eximius	mf,y	a (pm)	no (rare?)	f,p **s,g**	8%[a]
	Anelosimus guacamayos	mf,y	?	?	?	Yes
	Anelosimus lorenzo	mf,y	?	?	f?	c.2%[b]
	Anelosimus oritoyacu	mf,y	?	?	?	?
	Anelosimus puravida	mf,y	?	?	?	14%[b]
	Anelosimus rupununi	mf,y	?	?	f	8%[b]
	Theridion nigroannulatum	mf,y	a?	?	s?,g?	11%[b]
Thomisidae	*Diaea megagyna*	mf,y	?	?	s?	20%[a]
	Diaea socialis	m + y,y	a (pm)	?	s?	28%[a]

(*Continued*)

TABLE I (*Continued*)

| Family | Species | Group activities | | Aggression[g] | Mating behavior | | Reproductive skew[j] |
		Cooperation[e]	Helping[f]		Mating[h]	Sexual competition[i]	
Agelenidae	*Agelena consociata*	w,p	?	0	?	c?	?
	A. republicana	w,p	?	0	?	?	?
Dictynidae	*Aebutina binotata*	w,p	e,p	0	?	c?	1
	Mallos gregalis	w,p	?	0	?	rare	?
Eresidae	*Stegodyphus dumicola*	w,d,p	e,p,r,g	0	f,s,m	c,f	about 3
	Stegodyphus mimosarum	w,d,p	e,p,r,g?	0	s,m	?	?
	Stegodyphus sarasinorum	w,d,p	e,p,r,g?	0	s,m	c,f	?
Oxyopidae	*Tapinillus* sp. 1	w,d	?		f?	?	?
Theridiidae	*Achaearanea disparata*	w,p	e	0	?	?	?
	Achaearanea vervoorti	w,p	p	?	?	c,f	?
	Achaearanea wau	w,p	e,p	0	f,s,m	c,f,o	1.25
	Anelosimus domingo	p	r?	0	?	?	?
	Anelosimus dubiosus	w,p	e,p,r	0	?	?	?
	Anelosimus eximius	w,d,p	e,p,r	0	?	c	about 4
	Anelosimus guacamayos	?	?	?	?	?	?
	Anelosimus lorenzo	w,p	p	0	?	?	?
	Anelosimus oritoyacu	?	?	?	?	?	?
	Anelosimus puravida	?	?	?	?	?	?
	Anelosimus rupununi	w,p	e (sac clusters)	?	?	?	0.7–1
	Theridion nigroannulatum	p	e	?	?	?	?
Thomisidae	*Diaea megagyna*	w	?	?	?	?	?
	Diaea socialis	w,p	?	0	s?	?	?

Family	Species	Sources
Agelenidae	*Agelena consociata*	Darchen, 1978; Riechert *et al.*, 1986; D'Andrea, 1987; Riechert and Roeloffs, 1993; Avilés, 1997
	A. republicana	Darchen, 1967; Darchen, 1976; D'Andrea, 1987, Avilés, 1997
Dictynidae	*Aebutina binotata*	Avilés, 1993a, 1997, 2000; Avilés *et al.*, 2001
	Mallos gregalis	Jackson, 1978; Jackson and Smith, 1978; Jackson, 1979
Eresidae	*Stegodyphus dumicola*	Avilés, 1997; Avilés *et al.*, 1999; Henschel *et al.*, 1995a; Henschel, 1998; Lubin and Crouch, 2003; A. Maklakov, personal communication; M. Salomon, personal communication
	Stegodyphus mimosarum	Wickler and Seibt, 1986; Seibt and Wickler, 1988a; Crouch *et al.*, 1998
	Stegodyphus sarasinorum	Jacson and Joseph, 1973; Avilés, 1997; Seibt and Wickler, 1988a
Oxyopidae	*Tapinillus* sp. 1	Avilés, 1994
Theridiidae	*Achaearanea disparata*	Darchen, 1968; Darchen and Ledoux, 1978; Buskirk, 1981
	Achaearanea vervoorti	Levi *et al.*, 1982; Lubin, 1991
	Achaearanea wau	Lubin, 1982, 1986, 1991, 1995; Lubin and Crozier, 1985; Lubin and Robinson, 1982
	Anelosimus domingo	Rypstra and Tirey, 1989; Aviles, 1997; Aviles *et al.*, 2001
	Anelosimus dubiosus	Marques *et al.*, 1998
	Anelosimus eximius	Christenson, 1984; D'Andrea, 1987; Avilés, 1997; Avilés and Tufiño, 1998; reviewed in Agnarsson, 2006; Vollrath and Windsor, 1983
	Anelosimus guacamayos	Agnarsson, 2006; Agnarsson *et al.*, 2006a
	Anelosimus lorenzo	Fowler and Levi, 1979; Agnarsson, 2006
	Anelosimus oritoyacu	Agnarsson, 2006; Agnarsson *et al.*, 2006a
	Anelosimus puravida	Agnarsson, 2006; Agnarsson *et al.*, 2006a
	Anelosimus rupununi	Avilés, 1997; Aviles and Salazar, 1999; Agnarsson, 2006
	Theridion nigroannulatum	Avilés, 1997; Avilés *et al.*, 2001; Avilés *et al.*, 2006

(*Continued*)

TABLE I (*Continued*)

Family	Species	Sources
Thomisidae	*Diaea megagyna*	Evans, 1995; Avilés, 1997
	Diaea socialis	Main, 1988; Evans and Main, 1993; Avilés, 1997

[a]Overlapping stages: m + y = mother and young, y = young, and mf = multiple females (males are not included).

[b]Dispersal stage: a = adult, pa = preadult, and y = young. Premating or postmating adult dispersal: am = premating and pm = postmating.

[c]Colony foundation (the predominant mode is shown in bold): fission (budding, splitting, or translocation) = f and propagule dispersal = p. Propagule size: g = group and s = solitary.

[d]Sex ratio: a primary or juvenile sex ratio, b subadult or adult sex ratio.

[e]Cooperation: w = web building, d = defense, and p = prey capture.

[f]Helping (allomaternal): c = communal brood chambers, e = guard eggsacs or young, p = bringing prey to nest, r = regurgitation, and g = gerontophagy.

[g]Aggression among adults: 0 = no aggression to foreign females, n = adult nestmates, and f = foreign females.

[h]Mating: f = foreign males, s = sib mating, and m = multiple mating.

[i]Sexual competition: c = male courtship, f = male aggression or fighting, and o = opportunistic mating (during female molt or feeding).

[j]Reproductive skew: number of females per eggsac.

[*]Species considered intermediate-social are noted by *.

across several families. Because of these repeated evolutionary events, social spiders provide a remarkable system to examine the causes and consequences of inbred sociality. The main question motivating this chapter is, why has inbred sociality arisen in spiders so many times independently, and yet there are so few social species?

The generally accepted hypothesis is that nonterritorial permanent-sociality in spiders is derived evolutionarily from a subsocial state (Avilés, 1997: nonterritorial periodic-social; Wickler and Seibt, 1993). Subsocial behavior with respect to spiders refers specifically to the occurrence of two traits: (1) an extended stage of maternal care of offspring prior to their dispersal and (2) a stage of cooperation among young within the brood, usually continuing after the mother dies or leaves the nest (Avilés, 1997). A third characteristic that distinguishes nonterritorial periodic-sociality from permanent-sociality is the obligatory dispersal of young or of adults of one or both sexes before mating, such that regular inbreeding is avoided (Avilés and Bukowski, 2006; Bilde *et al.*, 2005; Powers and Aviles, 2003). In the following sections, we review the characteristics of social species and their subsocial congeners and discuss the evidence for this transition scenario.

Finally, the designation of species as nonterritorial permanent-social and nonterritorial periodic-social applies to groups of traits that generally occur together. Some species do not fit comfortably in a single category, and these exceptions often provide insight into important adaptive and evolutionary processes. Recently, there have been renewed attempts to find a terminology of social organization that can be applied widely across animal taxa (Costa, 2006; Costa and Fitzgerald, 2005; Crespi, 2005; Wcislo, 2005) and to define the nature of social interactions more inclusively (Rayor and Taylor, 2006; West *et al.*, 2007). We have not attempted to fit spider sociality into these schemes, as the jury is still out as to which method will prove most durable over time. We feel that the categories erected by Avilés (1997) suit the diversity of social organization in spiders, first because they are useful descriptors of the temporal and spatial nature of the groups in each case and second, because they imply neither function nor hierarchy and, therefore, are not teleological [a valid criticism of the classic social insect-based terminology, in Costa and Fitzgerald (2005)]. However, as this terminology is also somewhat unwieldy, for convenience we revert to the commonly used shorthand designations of social and subsocial, for nonterritorial permanent-social and territorial periodic-social, respectively.

II. SOCIAL AND SUBSOCIAL SPECIES: A SURVEY OF BEHAVIORAL TRAITS

Tables I and II outline behavioral traits that describe the degree of social integration in the colony or nest of social and subsocial species, respectively. In assigning species to the tables, we have followed the designations of

TABLE II
BEHAVIORAL AND LIFE-HISTORY CHARACTERISTICS OF SOME SUBSOCIAL SPECIES

Family	Species	Group composition[a]	Dispersal[b]			Sex ratio[d] (% males)
			Females	Males	Mode[c]	
Agelenidae	*Coelotes terrestris*	m + y	y	y	s	?
Amaurobiidae	*Amaurobius ferox*	m + y	y	y	s	?
Desidae	*Phryganoporus candidus[i]*	m + y	pa,y	a (am)	s,f	57%[a]
Eresidae	*Stegodyphus lineatus*	m + y	y	y	s	No bias
Scytodidae	*Scytodes socialis, S. fusca, S. pallida*	mf,y	y	y	s	No bias
Sparassidae	*Delena cancerides*	m + y,y,mf	a?(am)	a?	s?,g?	48%[a]
Theridiidae	*Anelosimus arizona* (formerly *A. jucundus* or *A.* cf. *jucundus*)	m + y	pa,a (am)	pa,a (am)	s	53%[b]
	Anelosimus baeza (formerly *A. jucundus*)	m + y, y, mf?	pa	?	s	No bias
	Anelosimus jabaquara[*]	m + y,y,mf	pa,a (am, pm)	pa?,a?	s,g	36%[b]
	Anelosimus jucundus	m + y, y	pa	pa	s	No bias
	Anelosimus studiosus (United States- southern populations)	m + y,y	y,pa	a?	s	48%[a]
	Anelosimus studiosus (United States-some northern colonies)[*]	mf, y	pa,a	a?	s	17–24%[b]
	Anelosimus cf. *studiosus* (Uruguay)[*]	m + y,y,mf	pa,a?	pa	s	37%[b]
	Helvibis thorelli	m + y	?	?	?	?
	Theridion pictum	m + y	y	y	s	29–36%[b]
Thomisidae	*Diaea ergandros*	m + y,y	a (pm)	a? (am)	s?	No bias

Family	Species	Group activities		Aggression[g]	Mating behavior[h]	Source
		Cooperation[e]	Maternal care[f]			
Agelenidae	*Coelotes terrestris*	p	r,p,t	?	?	Krafft *et al.*, 1986; Gundermann *et al.*, 1991
Amaurobiidae	*Amaurobius ferox*	p	r,p,t,m	?	?	Kim, 2000; Kim and Horel, 1998; Kim *et al.*, 2005a,b; Kim and Roland, 2000; Kim, Roland and Horel, 2000
Desidae	*Phryganoporus candidus*	w,p	?	?	f,m	Downes, 1993, 1994a, 1994b
Eresidae	*Stegodyphus lineatus*	w?,p	r,p,m	n,f	f,s (rare),m (both sexes),c	Schneider, 1997; Lubin *et al.*, 1998; Schneider and Lubin, 1998; Bilde *et al.*, 2005 and references therein
Scytodidae[c]	*Scytodes socialis, S. pallida, S. fusca*	p	?	?	?	Bowden, 1991; Li *et al.*, 1999; Li and Kuan, 2006; J. A. Miller, personal communication
Sparassidae	*Delena cancerides*	p	p	an (adult sisters)	f,s,m	Rowell and Aviles, 1995; Aviles, 1997; L. Rayor, personal communication
Theridiidae	*Anelosimus arizona* (formerly *A. jucundus* or *A.* cf. *jucundus*)	w,p	Yes—no details	?	f,s?	Aviles and Gelsey, 1998; Bukowski and Avilés, 2002; Powers and Aviles, 2003; Aviles and Bukowski, 2006
	Anelosimus baeza (formerly *A. jucundus*)	p	p,r?	?	?	Aviles *et al.*, 2001; Agnarsson *et al.*, in press; Agnarsson, 2006

TABLE II (*Continued*)

Family	Species	Group activities		Aggression[g]	Mating behavior[h]	Source
		Cooperation[e]	Maternal care[f]			
	Anelosimus jabaquara	w,p	r,p, a?	n, f	f,s?,m (both sexes)	Marques *et al.*, 1998; Gonzaga and Vasconcellos-Neto, 2001
	Anelosimus jucundus	p	yes	?	?	Aviles *et al.*, 2001; Nentwig and Christenson, 1986; Agnarsson, 2006
	Anelosimus studiosus (United States-southern populations)	p	r,p	n,f (adult females)	f?	Brach, 1977; Agnarsson, 2006; Aviles, 1997
	Anelosimus studiosus (United States-some northern colonies)	p	r,p,a		?	Furey, 1998; Jones *et al.*, 2007

	Anelosimus cf. studiosus (Uruguay)	w,p	r,p	n	f	Ghione et al., 2004; Viera et al., 2005, 2007a, 2007b
	Helvibis thorelli	p	?	?	?	Coddington and Agnarsson, 2006
	Theridion pictum	w,p	p, r?	?	?	Ruttan, 1990
Thomisidae	Diaea ergandros	w	m	n (rare), f (females)	f,s?,m	Evans, 1998, 2000; Evans and Goodisman, 2002

[a]Overlapping stages: m + y = mother and young, y = young, and mf = multiple females (males are not included).

[b]Dispersing stage: a = adult, pa = preadult, and y = young. Adult dispersal: am = premating and pm = postmating.

[c]Dispersal mode: b = budding, f = colony fission, g = group dispersal, and s = solitary dispersal.

[d]Sex ratio: a = primary or juvenile sex ratio and b = subadult or adult sex ratio.

[e]Cooperation: w = web building, d = defense, and p = prey capture.

[f]Maternal care: e = guard eggsacs or young, p = bringing prey to nest, r = regurgitation, t = trophic eggs, and m = matriphagy.

[g]Aggression among adults: 0 = no aggression to foreign females, n = adult nestmates, and f = foreign females.

[h]Mating: f = foreign males, s = sib mating, m = multiple mating, and c = sexual competition.

[i]We follow Agnarsson et al. (2006a) in assigning Phryganoporus candidus (Dictynidae) to the subsocial group (contrary to Whitehouse and Lubin, 2005).

*Possible subsocial-social transition species are noted by *.

Agnarsson *et al*. (2006) (see also Whitehouse and Lubin, 2005): *social species* (Plates 1 and 2) are those in which juvenile dispersal is lacking and multiple adult females breed within the colony. Thus, social species should show an inbred population structure, and this is often associated with a female-biased primary sex ratio (Avilés, 1986; Hurst and Vollrath, 1992). *Subsocial species* (Plate 3) are those with premating dispersal. Extended maternal care and some cooperation in foraging or nest activities among young prior to dispersal distinguish subsocial from solitary species (Agnarsson *et al*., 2006). Data on cooperative activities of young in the nest are not available for all species listed; the prolonged stay of juveniles in the maternal nest, however, can be taken as evidence of group foraging. Species that exhibit both subsocial and social traits are noted as "transition species" in either Tables I or II and are discussed below.

Colony composition indicates the developmental stages that overlap and interact within the colony. In most of the social species, all stages overlap; in the subsocial species, usually only the mother and her young are present together (we ignore males here). Some subsocial species, however, have multiple breeding females and their offspring (the two Scytodidae species, *Anelosimus jabaquara* and some populations of *Anelosimus studiosus* and *Anelosimus* cf. *studiosus*).

Colony foundation (Table I) and *dispersal* (Table II) refer to the dispersal stage involved in establishment of a new colony (social species) or nest (subsocial species), whether by juveniles or by males or females
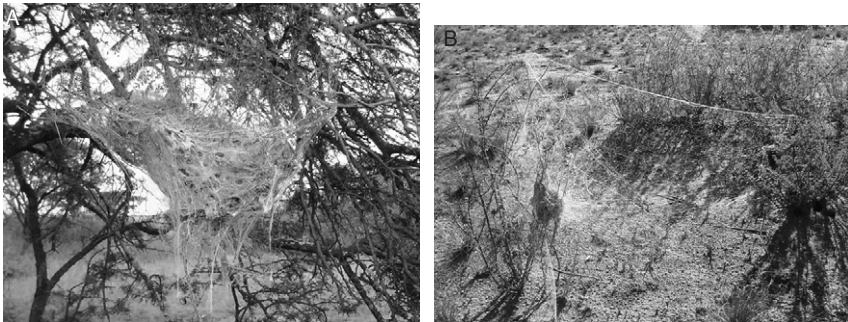

PLATE 1. Social *Stegodyphus* (Eresidae): (A) Large colony of *Stegodyphus mimosarum*, Spioenkop Nature Reserve, KwaZulu Natal Province, South Africa. The nest is at the tip of a branch of an *Acacia* tree located near water. Sticky, cribellate silk covers the surface of the nest and multiple openings are visible leading into the nest. (B) Colony of *Stegodyphus dumicola* (Eresidae) in a small *Acacia* shrub in dry savanna at Seeis, Namibia. Maximum colony size is smaller than *S. mimosarum*. The central nest has undergone fission to produce two smaller daughter nests (one on either side), which remain connected to the mother nest by extensive cribellate capture webs. Photos: T. Bilde.
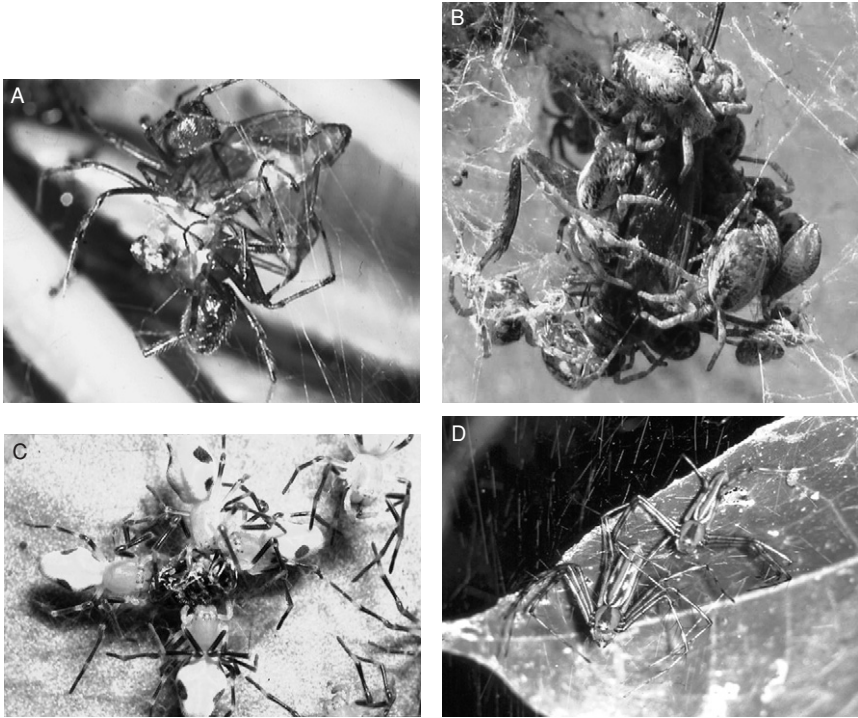
PLATE 2. Foraging groups of social spiders: (A) Females of *Anelosimus eximius* (Theridiidae) feeding together on a small insect, in tropical rainforest at Cuyabeno Nature Reserve, Ecuador. Photo: L. Avilés (published in Avilés *et al.*, 2001; reprinted with the author's permission). (B) Group of subadult females of *Stegodyphus dumicola* (Eresidae) feeding together on insect prey at Seeis, Namibia. The spiders are in the cribellate web below the communal nest. Photo: Y. Botner and M. Salomon. (C) Group of *Aebutina binotata* (Dictynidae) feeding together on prey at Cuyabeno Nature Reserve, Ecuador. The spiders are brightly colored yellow with dark markings and rest on a layer of silk beneath leaves of tropical forest trees. Photo: L. Avilés (published in color in Avilés, 1997; reprinted with the author's permission). (D) Two female *Tapinillus* sp. 1 (Oxyopidae) sitting on a leaf in ambush position, Cuyabeno Nature Reserve, Ecuador. *Tapinillus* sp. 1 builds a loose, irregular mesh web at the tips of leaves. Photo: L. Avilés (published in Avilés, 1994 and Avilés *et al.*, 2001; reprinted with the author's permission).

(pre- or postmating); the mode of colony establishment, by fission involving short-range displacement, or propagule dispersal over larger distances; and if dispersal and colony foundation are performed by single individuals or in groups. Dispersal and colony foundation by postmating adult females, singly or in groups, is the rule in social species, whereas juveniles or premating males and females disperse singly in subsocial species.
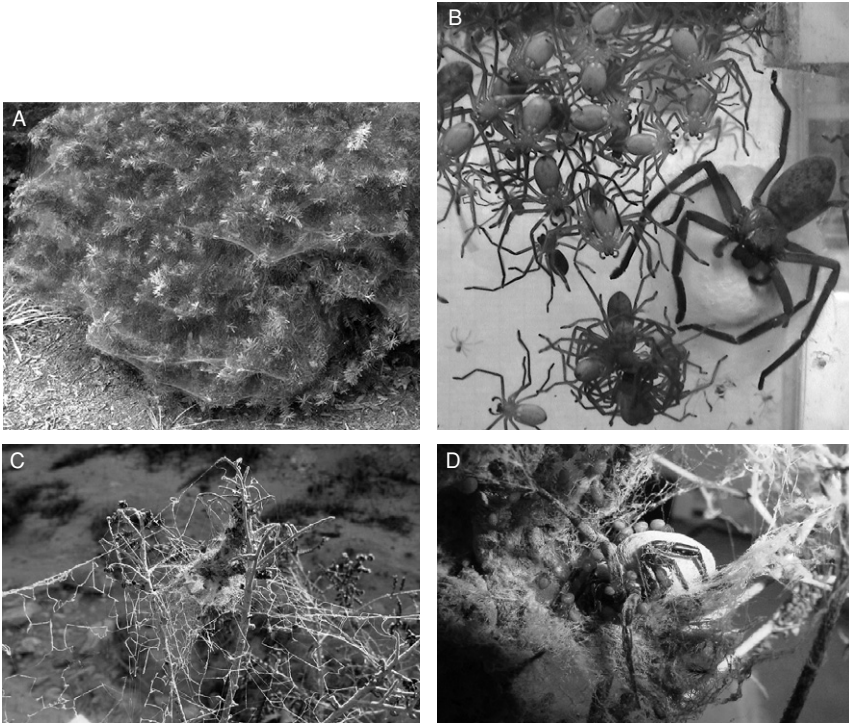
PLATE 3. Subsocial spiders: (A) Large colony of *Anelosimus studiosus* (Theridiidae) in Knox County, eastern Tennessee, USA. The colony measured 28,280cm3 and was composed of clusters of multiple females with their eggsacs and brood and interconnected silk capture webs. Spiders from different clusters moved through the connected webs. Photo: S. E. Riechert. (B) Female huntsman spider from Australia, *Delena cancerides* (Sparassidae), guarding an eggsac attached to the substrate. Below the female, a group of young feed together on a fly. Young from at least two cohorts are visible above the female. Photo: L. Rayor. (C) Nest and capture web of the subsocial spider *Stegodyphus lineatus* (Eresidae) in the Negev Desert, Israel. The nest is conical and is covered with plant debris and prey remains; the cribellate silk web captures mainly flying insects. Photo: T. Bilde. (D) Female *Stegodyphus lineatus* (Eresidae) on her nest with her offspring in the Negev Desert, Israel. The mother feeds her young by regurgitation for 2–4 weeks, after which the young kill and consume her (matriphagy). Photo: T. Bilde and M. Salomon.

The *sex ratio* bias indicates whether nestmates inbreed regularly. Dispersal and the sex ratio define the breeding structure of populations of each of the species. Juvenile and primary sex ratios are highly female biased in the social species with the exception of *Tapinillus* sp. 1, which is apparently outbreeding.

Group activities are cooperative if performed by multiple individuals in the colony. Colony nest and web construction include laying of silk lines and removal of debris by several individuals simultaneously. Communal

defense behaviors against arthropod and vertebrate predators have been described in a few social species; these involve silk production and biting. In all of the social species, several spiders attack large prey jointly and feed together on it, and juveniles of subsocial species behave similarly during the stage they are together in the maternal nest. Maternal care in subsocial species may involve both feeding and defense of the brood. Cooperative brood care in the social species includes behaviors such as defense of eggsacs or young and feeding of young performed by multiple females in the nest. The helpers may be breeding females (allomaternal care) or individuals that do not produce young themselves. Subsocial species with multiple breeding females have some degree of cooperation, either in feeding young or in protection of the nest, and this differs among the species.

Aggression toward nestmates as well as foreign females has been observed in multiple female colonies of subsocial species, for example, during eggsac guarding. In social species, direct aggression is generally lacking.

Under *mating behavior*, we recorded whether females mate with nest-mates or with foreign males, if multiple mating occurs, and the existence of competition among males for access to females. These are traits that deter-mine the potential for outbreeding by means of sexual competition or mate choice, but there are very few observations of mating behavior in any of the social or subsocial species. Some form of male–male competition is recorded in five to seven of the social species, and fighting among males in four species. Finally, reproductive skew, that is, the proportion of repro-ducing females in a colony, reflects the balance of cooperative and compet-itive interactions in the colony. Three of the five species for which data are available have 1.25 to 4 females per eggsac. We suggest that this reflects skewed reproduction as females in the social species are thought to produce a single clutch in their lifetime.

The exceptions to the general patterns of social and subsocial traits are illuminating. We followed Agnarsson *et al*. (2006) in assigning *Tapinillus* sp. 1 to the social species, as multiple cohorts of females and young occur together in a colony and the colonies last for more than a single generation, traits that are typical of the social species. However, dispersal is by groups of subadult or adult males and females, and the lack of a primary sex ratio bias toward females was taken as evidence of outbreeding (Avilés, 1994). Avilés (1997) assigned *D. cancerides* to the social species, but we have moved it to the subsocial category, as groups with multiple breeding females seem to be less common than single females with their brood (L. Rayor, personal communication). Nest persistence alone, however, is not a sufficient descriptor of sociality, as the social crab spider *Diaea socialis* (and perhaps *Diaea megagyna*) may also have colonies that last for a single

generation, yet they have an inbred mating system as evidenced by the presence of female-biased sex ratios (Avilés, 1997; Evans, 1995; Evans and Main, 1993; Main, 1988).

Among the subsocial species (Table II), a few species (notably, *A. studiosus* in North America, *A.* cf. *studiosus* in Uruguay, and *D. cancerides* in Australia) are known to have multiple breeding females in a colony, but apparently lack regular inbreeding (*A. studiosus*: T. C. Jones and S. E. Riechert, personal communication; but, see Furey, 1998; *A.* cf. *studiosus*: Ghione *et al.*, 2004; *D. cancerides*: Rowell and Avilés, 1995; L. Rayor, personal communication). *A. studiosus* from North America and *A.* cf. *studiosus* from Uruguay are presently regarded as a single species (I. Agnarsson, personal communication), and if this is the case, the species has an extraordinary latitudinal range across the Americas. Populations studied in Uruguay by Ghione *et al.* (2004) and Viera *et al.* (2007b) as well as those studied in North America (Brach, 1977; Furey, 1998; Jones and Parker, 2000, 2002; Jones *et al.*, 2007) have a variable social structure, from single-female nests to multiple breeders. Most North American populations of *A. studiosus* have predominantly single-female nests (Furey, 1998; T. C. Jones and S. E. Riechert, personal communication), and there is a latitudinal gradient in the frequency of multiple female colonies, with a higher frequency occurring in lower latitudes (see Section V.C). Furthermore, in some populations, sex ratios are moderately female biased, which suggests the possibility of inbreeding (Table II).

There are other species that may be transitional, but data are lacking to be able to characterize their social structure adequately. *A. jabaquara* from Brazil has a female-biased sex ratio comparable to the social *Anelosimus* but exhibits low tolerance of female nestmates during the breeding stage and dispersal at the subadult stage, indicating possible outbreeding (Table II; Gonzaga and Vasconcellos-Neto, 2001; Marques *et al.*, 1998). The Australian thomisid *D. megagyna* also has a female-biased sex ratio (Evans, 1995; Table I), and Avilés (1997) includes it among species at the transition from subsocial to social as the colonies do not persist for more than one generation. In *Stegodyphus tentoriicola* in the Karoo region of South Africa, most nests were of single females and brood, but a small percentage of nests contained multiple adult females and males or multiple females and their broods (not included in the tables; Y. L. and T. B., personal observations). Thus, this species too may be at the transition from subsocial to social.

The distinguishing characteristic of subsocial species is a prolonged period of maternal care, with the potential for interactions among the young in the maternal nest. However, many solitary species exhibit some maternal care, and the distinction between subsocial and solitary species with maternal care is somewhat arbitrary, depending mainly on the length of the

communal stage after the end of maternal care (see above). Additionally, we lack information on most species with maternal care. Aviles (1997) indicates 16 families showing some form of maternal care of offspring beyond the egg stage. The list of subsocial species in Table II is clearly incomplete, with only seven families represented. We have included mainly those species with social congeners, and for which some behavioral information is available. Agnarsson (2006) reviewed the New World *Anelosimus* and indicated additional subsocial species, and collections made in Madagascar revealed several likely subsocial *Anelosimus* (Agnarsson and Kuntner, 2005). Observations of some of these species suggested both extended maternal care and joint prey capture and feeding by juveniles in the maternal nest. Extended maternal care and delayed juvenile dispersal occur in many other comb-footed spider (Theridiidae) genera (e.g., *Theridion, Achaearanea*; Agnarsson, 2004), in all Eresidae that have been studied to date (*Dorceus, Eresus, Seothyra, Stegodyphus*; D'Andrea, 1987; Henschel and Lubin, 1992; Kraus and Kraus, 1988; Kullmann, 1972; Y. L., personal observations), in the Amaurobioidea families Agelenidae (*Amaurobius, Coelotes*; Avilés, 1997 and references therein) and Desidae (*Phryganoporus candida*; Table II), and in the crab spiders, Thomisidae (*Diaea ergandros*; Table II). These groups need further study in order to reveal the environmental and demographic conditions that favor family-group living and the transition to inbred sociality.

III. INBRED SOCIALITY IN SPIDERS

How similar are the different social spider species, spread among seven different families, in their behavioral, life-history, and demographic characteristics? The social insects and cooperative-breeding vertebrates each demonstrates a wide diversity of social traits, with cooperation taking different forms, reproductive patterns ranging from multiple breeding females to single breeders with helpers, and various types of dispersal and group establishment patterns (Brockmann, 1997). The constellation of traits that characterize social systems provide a window onto the selective processes that promote and maintain sociality. What traits characterize the social spiders, how variable are they, and what are the underlying mechanisms that maintain them? These questions are discussed in the next sections.

A. COOPERATION VERSUS COMPETITION: A BALANCING ACT

Nest construction, web building, foraging, defense, and brood care are all behaviors that give the appearance of being ''cooperative.'' Cooperative activities can be defined as collective activities of individuals that interact

over a period of time, and where the cooperating individuals obtain fitness benefits from their activities (Whitehouse and Lubin, 2005; see also Downes, 1995). For example, colony members cooperate in web building and removal of debris (*Anelosimus eximius*: Christenson, 1984; *Achaearanea wau*: Lubin, 1995). Cooperation, however, does not necessarily imply coordination among interacting individuals. As demonstrated in a number of studies, apparent coordination of an activity such as web building or prey capture can be obtained by means of similar responses of individuals to stimuli, with further individual adjustment of behavior in response to local information (Sendova-Franks and Franks, 1998). Information provided in silk, pheromones, and web vibrations may thus amplify the group response (Burgess, 1979; Saffre *et al.*, 1999; Vakanas and Krafft, 2001).

One form of apparent group coordination is the synchronization of movement of individuals on the nest or web, which has been observed in several of the social species. During nest building, late instar females and males of *Tapinillus* sp. 1 (Oxyopidae) participate in laying silk and their "bouts of activity and quiet appeared to be synchronized" (Avilés, 1994). *Stegodyphus dumicola* individuals move in unison toward prey trapped in the sticky capture web, starting and stopping suddenly in a synchronized, rhythmical manner (personal observations) and similar behavior was observed in *A. eximius* (Krafft and Pasquet, 1991). A likely explanation of this behavior is that during group prey capture, synchronized movement enables spiders to distinguish prey vibrations from those of conspecifics and thus to locate the source of prey vibrations on the web (Krafft and Pasquet, 1991). Such movements might be defensive as well, preventing potential predators from focusing on a single individual (Bertram, 1978).

Group foraging occurs in all of the web building social spiders, and in all social species individuals share prey. The Australian social crab spiders, *D. socialis* and *D. megagyna*, which do not construct webs, forage individually (Main, 1988), while *D. cancerides*, a group-living huntsman spider, cooperates in prey capture (Rowell and Avilés, 1995). By hunting in a group, spiders can capture larger prey and save on per capita costs of silk production (reviewed in Avilés, 1997). They may also benefit from sharing digestive enzymes, though here, as well as in prey capture, the question arises whether cheating occurs, in which some individuals exploit the efforts of others. While there is no direct evidence for cheating, contests over access to prey have been noted in several social species (*A. eximius*: Christenson, 1984; *Agelena consociata*: Riechert, 1985; *Stegodyphus mimosarum*: Ward and Enders, 1985). Competition may be over a feeding site on the prey. Willey and Jackson (1993) found in *Stegodyphus sarasinorum* that the first spider to begin feeding could feed on the thorax, which is the preferred site on the prey, and thus obtain more food. In *S. dumicola*, large individuals had a competitive advantage over smaller ones: they excluded smaller

individuals from prey and ingested more food (Whitehouse and Lubin, 1999). Some spiders that fed in a group did not increase in mass and even lost mass, hinting at the additional possibility of enzyme exploitation by dominant individuals (Amir *et al.*, 2000; Whitehouse and Lubin, 1999). Competition increased with feeding group size (Ward and Enders, 1985; Whitehouse and Lubin, 1999; but see Pasquet and Krafft, 1992), and the mean body mass of individuals in the colony and the proportion of breeding females were negatively correlated with colony size—likely outcomes of competition (Avilés and Tufiño, 1998; Bilde *et al.*, 2007; Seibt and Wickler, 1988b; Ward and Enders, 1985). Differential feeding success due to competition for prey is a likely mechanism underlying the variation among individuals in body size and reproduction in large colonies (Seibt and Wickler, 1988b; Ulbrich and Henschel, 1999; Ulbrich *et al.*, 1996; Vollrath and Rohde-Arndt, 1983; Ward and Enders, 1985).

Competition may occur not just for energy, but possibly also for specific nutrients (M. Salomon, unpublished observation). Lipids are a source of energy for growth and maturation and are also presumed to be required for oogenesis (Anderson, 1978; Pulz, 1987). Field colonies of *S. dumicola* containing large juveniles were supplemented with lipid- or protein-rich crickets. More females matured to adult, and the adults were heavier in lipid-supplemented colonies. The proportion of adult females in protein-supplemented colonies actually decreased with increasing colony size, suggesting that lipids were a limiting resource in these colonies. These results were supported by a laboratory experiment in which individual spiders were given crickets that were kept on standard cricket diet: during the first 2 h of a feeding bout, they extracted mostly lipids from the prey (M. Salomon, personal communication).

Cooperation in rearing young is well known in group-living vertebrates and in social insects, where helpers feed and guard young of other females and often forgo reproduction themselves, either temporarily as in most cooperative breeding birds and mammals (Emlen, 1997) or permanently as in many eusocial insects (Wilson, 1971). In social spiders, all females in a colony are potential breeders. The occurrence of allomaternal brood care has been assumed by most students of social spider biology (reviewed in Avilés, 1997; Whitehouse and Lubin, 2005) but is rarely tested critically. An alternative possibility is that each female cares for her own young only, in which case there is no direct cooperation. So far, allomaternal brood care has been shown unequivocally only in *A. eximius* (Christenson, 1984) and *S. dumicola* (Salomon and Lubin, 2007). For helping to be a viable strategy of cooperation, two conditions must be met, namely, that helpers increase the fitness of the females that they help and that helpers derive benefits from this behavior. Given the high relatedness among individuals within the colony, helpers are likely to gain inclusive fitness benefits from helping to raise young of other

females in their cohort. The costs of helping may be relatively low if helpers are females that are unable to breed due to external causes, for example lack of sufficient food to mature (Ulbrich and Henschel, 1999). Salomon and Lubin (2007) compared the growth of *S. dumicola* young from a single brood in experimental nests containing either a mother alone or a mother together with four or five other females (either subadult or adult). They found that young maintained with a group of females survived better and increased their body mass more than young that were raised by a single female. The young obtained food from helpers both by regurgitation and later by killing and feeding on the helpers (gerontophagy; Seibt and Wickler, 1987) as well as on their mother (matriphagy).

Other forms of helping have been reported. Large juveniles of *Anelosimus dubiosus* fed younger individuals (Marques *et al.*, 1998). *Anelosimus rupununi* females clustered their eggsacs and the clusters were tended by a single female. Avilés and Salazar (1999) observed that on completing the construction of an eggsac, a female moved it to a cluster of sacs and assumed a position near the cluster. They observed several instances of a female moving away from this presumed guarding position and being replaced by another. Clusters of sacs were more likely to be guarded than were individual ones. This behavior has not been recorded in other social species, though eggsac guarding is reported in several (Table I).

B. DO SOCIAL SPIDERS HAVE DIVISION OF LABOR?

Division of labor involves the partitioning of colony tasks among different individuals in the colony and is characteristic of species with strongly skewed reproduction (Fjerdingstad and Crozier, 2006; Oster and Wilson, 1978). Activities may be divided by age (age-based polyethism), phenotype (physical castes), or some combination of these (Wilson, 1971). While social spiders may accrue tasks as they mature, true task differentiation of either sort seems to be lacking. For example, in *A. wau* colonies, young remain in the nest for ∼11 days after emergence from the eggsac and feed on prey brought into the nest by females (Lubin, 1995). They begin to venture out and to participate in nest or web repair activities, first near the nest, and later further away. At 3–4 weeks after emergence, they begin to take part in prey capture. In *A. eximius*, adult females are more likely to execute repairs and remove debris from outer parts of the web than are juveniles (Christenson, 1984). Adult females of *Aebutina binotata* capture most of the prey, with larger juveniles joining, and the young sometimes engaging in web repair (Avilés, 1993b). Overall, there appears to be little differentiation among adults in the tendency to hunt or repair the web (Avilés, 1993b; Lubin, 1995). Adult males are not known to participate in colony activities.

The frequency with which individuals engage in different activities may depend mainly on their hunger state and competitive abilities (Ainsworth *et al.*, 2002; Ebert, 1998; Ward and Enders, 1985), but this requires further study. The South American social theridiid *Theridion nigroannulatum* was found to have two distinct size classes of adult females in its colonies (Avilés *et al*., 2006); this begs the question if different individuals derive benefit from maturing at different instars.

Several studies have addressed the question whether reproductive division of labor, or reproductive skew, occurs in social spiders (Lubin, 1995; Riechert and Roeloffs, 1993; Vollrath, 1986; Vollrath and Rohde-Arndt, 1983). In a classic experimental study, Rypstra (1993) showed that in *A. eximius* colonies, when juveniles were fed large prey, some females obtained more food than others, grew larger, and produced more eggsacs, while others did not obtain enough to mature. When groups were fed only with small prey, most juveniles matured, but few had enough resources to reproduce. Competition of this sort (see Section III.A) can create an unequal distribution of resources among colony members (modeled by Ulbrich *et al*., 1996) and result in differential reproduction within the colony (Ulbrich and Henschel, 1999). M. Salomon (unpublished observation) found that in colonies of *S. dumicola* that were collected at the beginning of the egg-laying period, but after males had largely disappeared from the colonies, on average 40% of the females were adult and the remainder were subadult. Most of these subadults would mature (if at all) too late to acquire mates and reproduce. The range of adult females, however, was very large (10–60%) and was unrelated to overall colony size (number of females). Perhaps there is a threshold group size above which competition results in reproductive skew, while the degree of skew may be density dependent or ''fine-tuned'' by the amount or type of prey available and other environmental factors. Nonbreeding females and subadults may enhance colony productivity through brood care as well as by participation in web repairs and prey capture, while gaining fitness benefits through closely related breeders. Yet, nonbreeders also increase the competition for resources in the colony. Thus, reproductive cooperation increases colony productivity on the one hand, while on the other hand, competition for food will decrease it. These opposite effects can result in unstable colony dynamics (Avilés, 1999), which is discussed further in later sections.

C. Colony Foundation: Propagule Dispersal Versus Fission

Dispersal and establishment of a new colony are critical stages in the life history of social species. In most group-living species, juveniles or young adults of one or both sexes undergo premating dispersal to establish a new

group or to join another group (Emlen, 1991). The nature of dispersal events and the mode of group founding have far-reaching consequences for population genetic structure and dynamics. Social spiders exhibit two substantially different types of dispersal, which we term ''propagule dispersal'' and ''fission.'' These correspond to potentially long-range dispersal or emigration and short-range colony budding or translocation, respectively (Vollrath, 1982).

A colony founded by propagule dispersal begins its existence as a single adult female or a small group of females (*A. wau*: Lubin and Robinson, 1982; *A. eximius*: Vollrath, 1982; *D. socialis*: Main, 1988; *S. dumicola* and *S. mimosarum*: Seibt and Wickler, 1988a; Lubin and Crouch, 2003; *T. nigroannulatum*: Avilés *et al*., 2006). These females are mostly previously mated in the mother colony. Sometimes additional individuals join an incipient colony, and these may be subadult or adult females and occasionally males (*A. wau*: Lubin and Robinson, 1982; *A. jabaquara*: Marques *et al*., 1998; *S. dumicola, S. mimosarum*: personal observation).

Several modes of propagule dispersal have been observed in social species, including single or small numbers of females bridging on silk threads or mass movement of large numbers of females across the substrate and on silk-bridging threads (*A. eximius*: Vollrath, 1982; Avilés, 1997 and references therein; *S. mimosarum*: Crouch *et al*., 1998) or along silk ''highways'' (*A. wau*; Lubin and Robinson, 1982). Ballooning of adult females during midday thermal updrafts was observed in several species of *Stegodyphus*: Jacson and Joseph (1973) noted aerial dispersal, but did not distinguish it from bridging behavior, in adult females and fourth to eighth instar young of *S. sarasinorum*; Wickler and Seibt (1986) observed ballooning of a single adult female *S. mimosarum*; and Schneider *et al*. (2001) recorded the ballooning of multiple females of *S. dumicola* in Namibia. This behavior is surprising, as the body mass of a social *Stegodyphus* female (80–150 mg) far exceeds the estimated maximum spider mass that can be lifted on a silk line (Henschel *et al*., 1995b; Suter, 1991). We speculated that these cribellate spiders release multiple silk lines from the cribellum and thus acquire greater lift; indeed, ballooning *S. dumicola* females appeared to sail up on a broad veil of silk lines (Schneider *et al*., 2001).

Propagule dispersal occurs at a distinct stage in colony development, when postmating females are present in the nest and before egg laying commences (*A. wau*: Lubin and Robinson, 1982; *A. eximius*: Vollrath, 1982; *S. mimosarum*: Seibt and Wickler, 1988a; *S. dumicola*: Schneider *et al*., 2001). In most species, the generations within a colony are discrete and development is rather synchronous. Thus, a large colony may contain numerous postmating females that will undergo dispersal over a short time period of a few days, as seen in swarming in *A. wau, A. eximius,*

S. mimosarum, and *S. dumicola*. Indeed, only large colonies give rise to dispersers (reviewed in Avilés, 1997; Schneider *et al.*, 2001). Mass dispersal has been seen in several species, both from a single colony and synchronously from many colonies in a population (Table I; see Section III.F). Consequently, a large number of small nests containing a single female or a small number of females appear suddenly in the population. These dispersing propagules have many predators and the probability of survival is low (Avilés and Tufino, 1998; Avilés *et al.*, 2006; Bilde *et al.*, 2007; Henschel, 1993, 1998; Lubin, 1991; Vollrath, 1992).

Colony fission (we include colony splitting or fission, budding and translocation under the general category of ''fission''; Table I) also leads to the establishment of new nests. This may be accidental, for example when falling branches or winds damage the nest or when large mammals move through the forest understory (Riechert *et al.*, 1986). In *A. binotata*, the only recorded method of dispersal is by colony fission, which takes place when the colony grows and individuals expand the web onto nearby vegetation (Avilés, 2000). The transient nature of *Aebutina* colonies may be related to the ephemeral quality of their two-dimensional nests, consisting of a thin sheet of silk laid on the surfaces of leaves (Avilés, 2000).

Fission can occur at any stage of development, but is most prevalent when the colony expands in space during later growth stages of the young and when competition for food is likely to be greatest (Bilde *et al.*, 2007). In *A. wau*, nests split at the stage of large juveniles and subadults, as the web is expanded to additional supports and many new leaf nests are added to the structure. Connections between parts of the nest may then be severed by wind or branch-falls or, when spiders mature and begin to reproduce they cease to repair the web, movement between the subdivisions is reduced and the connections are discontinued (unpublished observations). In laboratory conditions, Bodasing *et al.* (2001) found that fission in *S. mimosarum* was most likely to occur in the spring when larger juveniles were present in the nest, but that the feeding regime did not influence dispersal tendency.

Both dispersal and colony fission can lead to clustering of incipient nests, but only propagule dispersal produces long-range migrants as well (but, see exceptions below). Daughter colonies established by fission have a greater chance of surviving owing to their larger size, but the greater number of individuals in such a daughter colony will also increase the amount of within-colony competition for food. Furthermore, fission colonies contain individuals of an assortment of ages, similar to the parent colony, whereas a dispersal propagule consists of one or a few mated females ready to oviposit. Thus, for a propagule colony, the clock is reset, so to speak, and the subsequent generation will be synchronized in its development, while a fission colony is subject to the same developmental asynchrony as the

original parent colony. Synchronous egg laying in propagule colonies will produce young of similar size and age, thus lessening the variance in growth rate due to asymmetric contests over prey (Ulbrich and Henschel, 1999), and perhaps increasing the benefit of cooperating in colony activities (see Avilés, 1999; Section III.E). The consequence should be that most offspring in the first generation of a propagule colony will mature and reproduce and colony growth will be maximized. By comparison, fission colonies will be subject to competition between spiders of differing sizes, colony growth rate will be retarded, and there should be a greater chance of colony failure. Data are needed to test these predictions.

Propagule foundation may have other beneficial effects on colony growth and survival, such as escape from parasites or disease by dispersers (Boulinier *et al*., 2001; Hamilton, 1987) or access to a better habitat (Danchin *et al*., 2001). Avilés *et al*. (2006) suggested that by undergoing ''explosive'' dispersal and propagule formation, the social *T. nigroannulatum* rids itself of predatory inquilines [*Faiditus* spp. (Argyrodinae)]. These inquilines were abundant in medium-sized and large colonies, but absent from small ones. Several of these ''guests'' are also predators of the host spiders, as were the unidentified Argyrodinae in colonies of *A. wau* (Lubin and Robinson, 1982), *Argyrodes projiciens* in *A. eximius* nests in Panama (Vollrath, 1982), and members of several spider families found in nests of *A. studiosus* (Perkins *et al*., 2007). *A. wau* colonies suffered increasing kleptoparasite (Argyrodinae) loads with increasing colony population size and nest dimensions (Lubin and Robinson, 1982), while kleptoparasites were rarely found in propagule nests (Y. L., unpublished observations).

Most of the social spiders studied to date exhibit both modes of dispersal at different life stages. The apparent exceptions are *A. binotata* and *A. consociata*, both of which form daughter colonies only by fission (Avilés, 2000; Riechert *et al.*, 1986). Riechert *et al*. (1986) suggest that segments of *A. consociata* colonies in equatorial African forests are carried accidentally on large mammals that disrupt the nests and disperse the spiders as they move. *Aebutina* undergoes repeated translocations of the entire colony [Aviles (2000) refers to a nomadic phase] at the stage of newly matured males and females (thus at the same stage that propagule dispersal should occur) in movements that can cover several hundred meters over a period of several weeks. These long-distance translocations may compensate for the lack of propagule dispersal. In both of the above species, colony translocation is unusual in that it can result in long-range dispersal, and thus differs from the typical budding or splitting of a colony, which produces a cluster of daughter colonies separated by only short distances of a few meters. Thus, these exceptions may prove the rule that a long-distance

dispersal stage is an essential component of social spider life history. We return to this theme in discussing the transition from subsocial to social group living.

D. Female-Biased Colony Sex Ratios: Primary and Operational Sex Ratios

The social spiders are characterized by female-biased sex ratios with one to two males produced for seven to eight females (Table I; reviewed in Avilés, 1997). Such a marked departure from the Fisherian sex ratio of equal numbers of males and females in diplo-diploid species raises questions concerning both the mechanism of the sex ratio bias and the nature of the selective forces acting on the trait (see Section V.B). Chromosomal studies of developing embryos in several species show that the female-biased sex ratio is caused by an overproduction of female embryos, showing a strong bias in the primary sex ratio. In *S. dumicola*, females appear to have control over the mean sex ratio—17% males—but no direct control over the sex of individual offspring (Avilés *et al.*, 1999). In contrast, the Neotropical spider *Anelosimus domingo* shows a precise sex ratio of at least one male per eggsac (Avilés *et al.*, 2000) indicating more control over the sex of individual offspring. A female-biased primary sex ratio with a proportion of males of 0.08 was reported in *A. eximius* (Avilés and Maddison, 1991) and in *D. socialis* with a male proportion of 0.28 (Rowell and Main, 1992). Under a heterogametic sex determination mechanism as in spiders ($X_1X_2 0$ with males as the heterogametic sex), an equal number of sons and daughters is expected (White, 1973). The primary sex ratio bias therefore suggests a mechanism that allows some degree of control over the two types of sperm (X_1X_2 and 0) in order to attain relative precision in the proportion of sons and daughters produced in each clutch (Avilés *et al.*, 2000; Hurst and Vollrath, 1992). The specific mechanism responsible for the sex ratio bias is not known.

Field data on the sex ratio among subadult and adult spiders in a colony reveal that the female bias is maintained throughout the colony life cycle. In *D. socialis*, Rowell and Main (1992) found a proportion of 0.19 males in adult and subadult colonies suggesting an increased bias compared with the primary sex ratio (0.28; Table I). In contrast to this pattern, six out of seven populations of *A. wau* examined in Papua New Guinea had less female-biased sex ratios in colonies with adults than in colonies of juveniles (Lubin, 1991). An explanation for either pattern could be differential mortality among the sexes or sex-biased emigration. The dispersal of females after mating to establish new nests may explain the increase in the proportion of males.

Henschel *et al.* (1995a) found strong female bias in the secondary sex ratio—12% adult males—in colonies of *S. dumicola*. But, when correcting for the number of sexually mature (reproducing) females in the colony, the operational sex ratio was almost even, with 42% males. This is because competition for resources creates asymmetric growth and many females do not mature or mature only after the males have died (Henschel *et al.*, 1995a; Ulbrich and Henschel, 1999). In the same species, colony adult sex ratios varying from extreme female biased to extreme male biased (T. B. and Y. L., personal observations) could indicate migration of one or both sexes. In field trials, we found that males left their natal nests to join nearby experimental colonies with unmated females in them (T. B. and Y. L., personal observations). Mass dispersal of females from large colonies (*S. mimosarum*: Crouch *et al.*, 1998; *S. dumicola*: Schneider *et al.*, 2001) may leave the nests with excess males. Hence, it is very difficult to make general conclusions about the causes of observed adult sex ratios in the social spiders.

E. MATING SYSTEM: INBREEDING AND ITS POPULATION-GENETIC CONSEQUENCES

Most cooperative group-living species go to great lengths to outbreed, with at least one sex undergoing premating dispersal and even strong behavioral taboos against mating with kin in some instances (Pusey and Wolf, 1996). By contrast, in social spiders, regular mating among nestmates of the same cohort, generation after generation, seems to be an almost general rule (Table I). In new colonies founded by a single female that mated with a male in the parental colony, mating among nestmates will be among full sibs (or partial sibs if the female mated with more than one male) already in the first generation within the colony. It would be interesting to know if females have a preference for mating with kin over nonkin; preliminary experiments in *S. dumicola* colonies with foreign and nestmate males suggest a lack of any preference (A. Maklakov and T. B., personal communication). Intense male–male competition over females has been observed in a few species (Table I). In the social theridiid, *A. wau*, males fight over access to molting females and engage in prolonged displays on the web, while females appear to be choosy; we do not know if this competition involves foreign as well as local males (Lubin, 1986).

The unusual trait of intracolony mating and resulting inbreeding yields a strongly subdivided population structure (Table III). The high level of intracolony mating results in large genetic differentiation among colonies and subdivision into colony lineages (high F_{ST} values, Table III; Riechert and Roeloffs, 1993; Smith and Engel, 1994; Smith and Hagen, 1996).

TABLE III

GENETIC DATA ON NESTMATE RELATEDNESS AND F-STATISTICS OF POPULATION STRUCTURE WITHIN AND BETWEEN COLONIES OF SOCIAL SPIDERS, AND A
COMPARISON WITH SOME SOLITARY AND SUBSOCIAL SPECIES[a]

Family	Species	Nestmate relatedness R	Structure within colonies relative to subpopulation F_{IS}, F_{IL}	Structure within colonies relative to total population F_{IT}	Structure among colonies within total population F_{ST}	Structure among colonies within regions F_{LR}, F_{SC}, F_{SR}	Structure among regions within total population F_{CT}, F_{RT}	Marker	Source
Agelenidae	*Agelena consociata* **social**	0.52	$F_{IS} = 0.13–0.16$	$F_{IT} = 0.458$	$F_{ST} = 0.517$			Allozymes	Roeloffs and Riechert, 1988; Riechert and Roeloffs, 1993
	Agelena aperta **solitary**	0.014	$F_{IS} = 0.075$					Allozymes	Riechert and Roeloffs, 1993
Eresidae	*Stegodyphus dumicola* **social**				$F_{ST} = 0.92–0.99$ $\Phi_{CT} = 0.495$[b]	$F_{SC} = 0.88–0.98$ $\Phi_{CR} = 0.44$[b]	$F_{CT} = 0.35–0.81$ $\Phi_{RT} = 0.098$[b]	mtDNA AFLP[b]	Johannesen *et al.*, 2002; Deborah D. Smith, personal communication[b]
	Stegodyphus sarasinorum **social**		$F_{IS} = 0.054$	$F_{IT} = 0.838$	$F_{ST} = 0.818$			Allozymes	Smith and Engel, 1994
	Stegodyphus lineatus **subsocial**	0.25	$F_{IS} = -0.07$	$F_{IT} = 0.15$	$F_{ST} = 0.21$ $\varphi_{ST} = 0.31$[b]			Allozymes AFLP[b]	Johannesen and Lubin, 2001 Bilde *et al.*, 2005[b]
Theridiidae	*Achaearanea wau* **social**		$F_{IS} = -0.088$	$F_{IT} = 0.786$	$F_{ST} = 0.804$			Allozymes	Smith and Engel, 1994

(*Continued*)

TABLE III (*Continued*)

Family	Species	Nestmate relatedness R	Structure within colonies relative to subpopulation F_{IS}, F_{IL}	Structure within colonies relative to total population F_{IT}	Structure among colonies within total population F_{ST}	Structure among colonies within regions F_{LR}, F_{SC}, F_{SR}	Structure among regions within total population F_{CT}, F_{RT}	Marker	Source
	Anelosimus eximius **social**	0.92 (Suriname) 0.176 (Panama)[d]	$F_{IS} = -0.075$ $F_{IS} = -0.083$	$F_{IT} = 0.886$	$F_{ST} = 0.885$	$F_{SR} = 0.9$	$F_{RT} = 0.365$	Allozymes	Smith and Engel, 1994; Smith and Hagen, 1996[d]
Thomisidae	*Diaea ergandros* **subsocial**	0.44	$F_{IL} = 0.15$	$F_{IT} = 0.35$		$F_{LR} = 0.23$	$F_{RT} = 0.081$	Allozymes	Evans and Goodisman, 2002[c]

[a]Hierarchical *F*-statistics measures the departure from panmixia—individuals relative to total population (F_{IT}), structure of colonies relative to total (F_{ST}), structure of colonies relative to region (F_{SR}) or (F_{SC}), structure of regions relative to total (F_{RT}) or localities relative to total (F_{CT}), and degree of nonrandom mating within colonies (F_{IS}).

[b]Deborah Smith (personal communication) uses an analogue to *F*-statistics to show structure of colonies relative to total population (Φ_{CT}), structure of colonies relative to region (Φ_{CR}), and structure of regions relative to total (Φ_{RT}).

[c]Evans and Goodisman (2002) use hierarchical *F*-statistics to measure the decrease in heterozygosity at different levels of the population due to true inbreeding within locales (F_{IL}), structure of locales within regions (F_{LR}), structure of regions within the total population (F_{RT}), or both inbreeding and population structure (F_{IT}).

[d]Disturbed roadside population might explain unusual low value (Smith and Hagen, 1996).

Within-colony relatedness can be higher than that of full-sibs ($r = 0.5$), for example, relatedness estimates in four populations of *A. eximius* showed values from 0.83 to 0.98 (Table III). This level of inbreeding among siblings and cousins would usually result in severe inbreeding depression and fitness loss, although regular inbreeding might purge deleterious alleles (Falconer, 1989; Roff, 1997).

Colonies are very often genetically monomorphic, containing females of identical haplotype, suggesting colony foundation either by a single female or by genetically highly related individuals. The latter could occur if multiple females originate from a monomorphic colony (Johannesen *et al.*, 2002) and establish a new nest by colony fission or by propagule dispersal (see Section III.C). A small proportion (13%) of *S. dumicola* colonies contained two to three haplotypes, which is the expected pattern if a ballooning female of a different haplotype joins an existing colony (Johannesen *et al.*, 2002). Similar long-range dispersal and introgression of different genotypes was also suggested as an explanation for colonies with multiple allozyme alleles in *A. wau* (Lubin and Crozier, 1985). Insufficient data are available for a range of social spider species to determine if they differ in the frequency of outbreeding, for example, depending on the predominant mode of dispersal. Another intriguing question is whether outbreeding depression occurs (as shown in bark beetles, Peer and Taborsky, 2005), though the ready acceptance of foreign spiders in social spider colonies (Table I) would argue against it.

The lack of a sex ratio bias in *Tapinillus* sp. 1 suggests that this species is outbreeding (Avilés, 1994; L. Avilés, unpublished data). This is likely obtained by males moving between different colonies. Thus, *Tapinillus* may represent a transitional stage, where the benefits of male mating dispersal are great enough to overcome the costs of movement; this species requires further study.

F. "BOOM AND BUST" COLONY DYNAMICS

The lack of juvenile dispersal and prevalence of inbreeding and female-biased sex ratios discussed above have marked consequences for population and metapopulation dynamics of social spiders. After initial establishment, colony growth may be rapid due to the female-biased sex ratio, increased reproductive potential due to cooperation, and the fact that many females reproduce (Avilés, 1997, 1999; Bilde *et al.*, 2007). As the colony grows, however, competition for food increases within the group and some females may not reproduce, slowing colony population growth. Dispersal by fission or by propagules could stabilize colony size at this point. Nevertheless, Aviles (1999) has shown by modeling that the initial rapid growth stages can cause

colonies to overshoot their carrying capacity, giving rise to a subsequent population crash. This intrinsic dynamical instability may explain the high colony extinction rate reported for some species (Avilés, 1997, 1999). The exact causes of this instability need further clarification. In social spiders, juveniles do not disperse individually; therefore, colony fission is the only possible immediate response to competition generated by rapid expansion. The daughter colonies from a fission event should then persist (although with the disadvantages mentioned in the previous section). An alternative explanation for colony extinction is an increase in susceptibility to parasites and pathogens with increasing colony size (see below).

Colony extinctions, often in conjunction with mass propagule dispersal (see above), have been described in a number of species. Three separate sets of data from South Africa show dramatic and synchronized extinctions of 80–100% of colonies over a period of 1–2 years in populations of *S. mimosarum* (Crouch and Lubin, 2001; Seibt and Wickler, 1988a). In one instance, the decline was accompanied by mass emigration of females and males (Crouch *et al.*, 1998). Vollrath (1986) recorded a 90% loss of colonies of *A. eximius* from a population in Panama, which was also accompanied by mass dispersal, and 90% of colonies died out in a population of *A. wau* over a few months, while other nearby populations suffered little mortality (Lubin, 1991; Lubin and Crozier, 1985). Sixty-three percent of colonies of *A. consociata* in a population in Gabon died out over a period of 3 years, possibly related to the inability of colonies to survive and reproduce during prolonged, unusually wet periods in these years (Riechert and Roeloffs, 1993). The direct causes of colony extinction are not known in most instances. Crouch and Lubin (2001) ruled out temperature, rainfall, treefalls, or other physical features of the environment as explanatory agents, but parasitoid wasps (Pompilidae, *Pseudopompilus funereus*) may have played a role in one *S. mimosarum* population, or a pathogen might spread rapidly through colonies with little genetic variation (Lubin, 1991; Roeloffs and Riechert, 1988; Vollrath, 1982). Alternatively, in a synchronized population, food may become limiting, leading to mass movement to new habitats. The latter explanation seems less likely, as both large and small colonies in a population went extinct (e.g., *A. wau*: Lubin and Crozier, 1985; *S. mimosarum*: Crouch and Lubin, 2001; Lubin and Crouch, 2003). The same factors that promote mass dispersal may be responsible also for colony extinction.

Not all species show the above pattern of ''boom and bust'' at the population level. Nevertheless, several species for which there are adequate data show rapid colony turnover (Avilés, 1997 and references therein, 2000; Avilés *et al.*, 2006). This is in marked contrast to colonies of some colonial (''territorial permanent-social,'' sensu Avilés, 1997) spiders. For example, large colonies of the araneid *Cyrtophora moluccensis* in Papua New Guinea are known

to have occupied the same sites continuously for at least 12 years (or ∼18 generations; Lubin, 1980), whereas colonies of most social spiders have a life span of only 2–7 generations (Avilés, 1997; Lubin and Crouch, 2003).

The distribution of social spider colonies in the environment reflects the processes of colony establishment, growth, dispersal, and extinction. Some social species are rare, and colonies can be found only sporadically and not clustered, for example *Achaearanea vervoorti* in New Guinea cloud forest (Levi *et al.*, 1982) and *A. domingo* in the understory of tropical rainforests of northern South America (Avilés, 1997). The dispersal modes of these species are not known.

In many species, colonies occur in clusters, with clusters of colonies separated by areas of apparently similar, but unpopulated habitat (*A. wau*: Lubin and Crozier, 1985; *A. consociata*: Riechert, 1985; *A. eximius*: Vollrath, 1982; Pasquet and Krafft, 1989; all three social *Stegodyphus* species, Lubin and Crouch, 2003; Seibt and Wickler, 1988a). Sometimes, colonies occupy nearly continuous stretches of vegetation along forest edge or roadsides, on fences or bridges, and along streams or rivers; in such instances, local prey abundance at ecotones or near water is a likely cause of this distribution. Colony clusters often have interconnected nests indicating that they are formed by fission; further evidence is the high relatedness among individuals within a colony cluster (Roeloffs and Riechert, 1988, for *A. consociata*). In a sparse population of *S. dumicola* at the edge of the hyperarid Namib Desert, we found a higher proportion of scattered propagule-disperser colonies than in a dense population in the higher-productivity savanna, where most small colonies were derived by fission and clustered around larger ''mother'' colonies (Bilde *et al.*, 2007). These observations suggest that fission occurs mainly when conditions are favorable, perhaps as a means of reducing within-colony competition while still remaining in a high-productivity habitat. These clusters, however, become susceptible to increasing parasite and disease loads, which can lead to mass extinction. As suggested by Hamilton (1987), such inbred colonies would have two means of escape—long-distance dispersal and outbreeding. The interplay between food resources, dispersal modes, and population genetic consequences is a fruitful avenue of future research.

IV. PHYLOGENETIC RELATIONSHIPS AMONG SOCIAL SPIDER SPECIES

Three striking features emerge from the distribution of social species across spider families (Table I): (1) a remarkably high number of independent origins of sociality that are distributed among unrelated taxonomic clades, (2) a concentration of origins of sociality within clades where maternal care is common (Avilés, 1997), (3) an apparent lack of diversification of the social clades (see below). These patterns prompt the questions: whether

there are certain conditions broadly applying to spiders of widely different taxonomic clades under which cooperation evolves, and whether there are certain common consequences of sociality for these spiders?

A. COMMON FEATURES OF SOCIAL EVOLUTION

The subsocial pathway to sociality proposed by Kullmann (1972) suggests that sociality should arise in clades with extended maternal care through the retention of young in the maternal nest. Based on the phylogeny by Coddington and Levi (1991), Avilés (1997) showed that indeed the majority of social events, with the exception of *Mallos* (Bond and Opell, 1997; Jackson, 1978, 1979), occurred in clades where subsocial behavior (maternal care) has been reported. Phylogenies of two genera, *Anelosimus* and *Stegodyphus*, confirm both the origin of sociality within clades with maternal care, supporting the hypothesized subsocial route to sociality, and that sociality is a derived condition, suggesting multiple transitions from subsocial to social behavior (Agnarsson, 2006; Agnarsson *et al*., 2006; Johannesen *et al*., 2007). We lack knowledge of the degree of maternal care in the closest relatives or sister species of social species in the remaining genera, and we lack phylogenies for these groups; therefore, a quantitative phylogenetic test of the hypothesis that permanent-sociality evolves through a transition from subsocial to social behavior is not yet feasible (Agnarsson *et al*., 2006).

In addition to a transition from subsocial to social group living, permanent-sociality in spiders is usually accompanied by a transition from outbreeding to inbreeding mating systems (Avilés, 1997; Riechert and Roeloffs, 1993). Since each social clade contains only 1–2 species, there may have been 18 such transitions (Agnarsson *et al*., 2006). The causal relationships resulting in the costly transition to extreme inbreeding remain largely unknown and pose an important challenge to understanding social evolution in spiders (see Section VI). It is currently believed that factors promoting the loss of mating dispersal underlie the transition to permanent-sociality (Avilés and Bukowski, 2006; Agnarsson *et al*., 2006; Bilde *et al*., 2005), implying that inbreeding is a consequence of group living (with the exception of *Tapinillus*) (Avilés, 1997). A history of inbreeding in subsocial ancestors may have facilitated the transition to inbreeding mating systems through purging of the most deleterious alleles (Bilde *et al.*, 2005).

B. CASE STUDIES

1. Stegodyphus *(Eresidae)*

Within the family Eresidae, maternal care is widespread in all known genera and appears ancestral to three derived cases of permanent-sociality (Johannesen *et al*., 1998, 2007; Kraus and Kraus, 1988; Kullmann, 1972).

The three social species of *Stegodyphus* are found in three distinct species groups, possibly of paraphyletic origin, supporting three independent derivations of sociality (Fig. 1; Johannesen *et al.*, 2007; Kraus and Kraus, 1988). Interestingly, while the social species are found in tip clades, analyses of sequence divergence suggest that the social lineages are neither young nor transient. On the contrary, the large intraspecific divergence of these social lineages suggests that they are old and remarkably stable over evolutionary time. An alternative possibility is that they have undergone cryptic speciation and the three apparently old species are in fact a complex of cryptic species (Johannesen *et al.*, 2007). It is remarkable that despite their old age, the social *Stegodyphus* have not diversified and evolved cladogenetically. Indeed, Avilés (1997) suggested that social spiders are ''caught in sociality'' and that they are constrained evolutionarily by genetic or ecological factors perhaps due to the high level of inbreeding, and the combination of these factors hinders evolvability. Interestingly, low diversification applies also to clades of subsocial *Stegodyphus*: Johannesen *et al.* (2007) found no difference in the rate of lineage diversification between social and closely related subsocial lineages. However, we lack as yet a complete phylogeny for the genus, and hence, it remains unresolved whether lack of diversification is characteristic of all *Stegodyphus* or of social spiders in general (see discussion below). In addition, a lack of a priori expectations for speciation rates makes it difficult to assess whether diversification is constrained in the genus *Stegodyphus* or has to do with specific characteristics of subsocial and social clades.

2. Anelosimus *(Theridiidae)*

Agnarsson *et al.* (2006, 2007) have produced a detailed phylogeny of the social *Anelosimus*, which led to the following conclusions: (1) there are five or six independent origins of sociality in the genus, depending on the placement of *A. eximius* in the phylogeny; (2) several pairs of social–subsocial sister species can be recognized (Fig. 2); and (3) there seem to be no instances of diversification within the social clades, a pattern similar to the social *Stegodyphus*. Thus, analyses of *Anelosimus* and other social theridiids support the hypothesis that maternal care is a predisposition for the transition to permanent-sociality (Agnarsson, 2006; Agnarsson *et al.*, 2007).

Agnarsson (2006) divided the species of *Anelosimus* into three social categories: quasi-social (permanent-social), subsocial, and quasi-solitary. In the latter category, he included species that have maternal care, but the young leave the maternal nest at an earlier stage than in the subsocial species. Thus, for example, in *Anelosimus arizona* subadults or even adults have premating dispersal to establish individual nests (Table II; Bukowski and Avilés, 2002), whereas in *Anelosimus pacificus* and a number Madagascan species young disperse shortly after the end of maternal care,
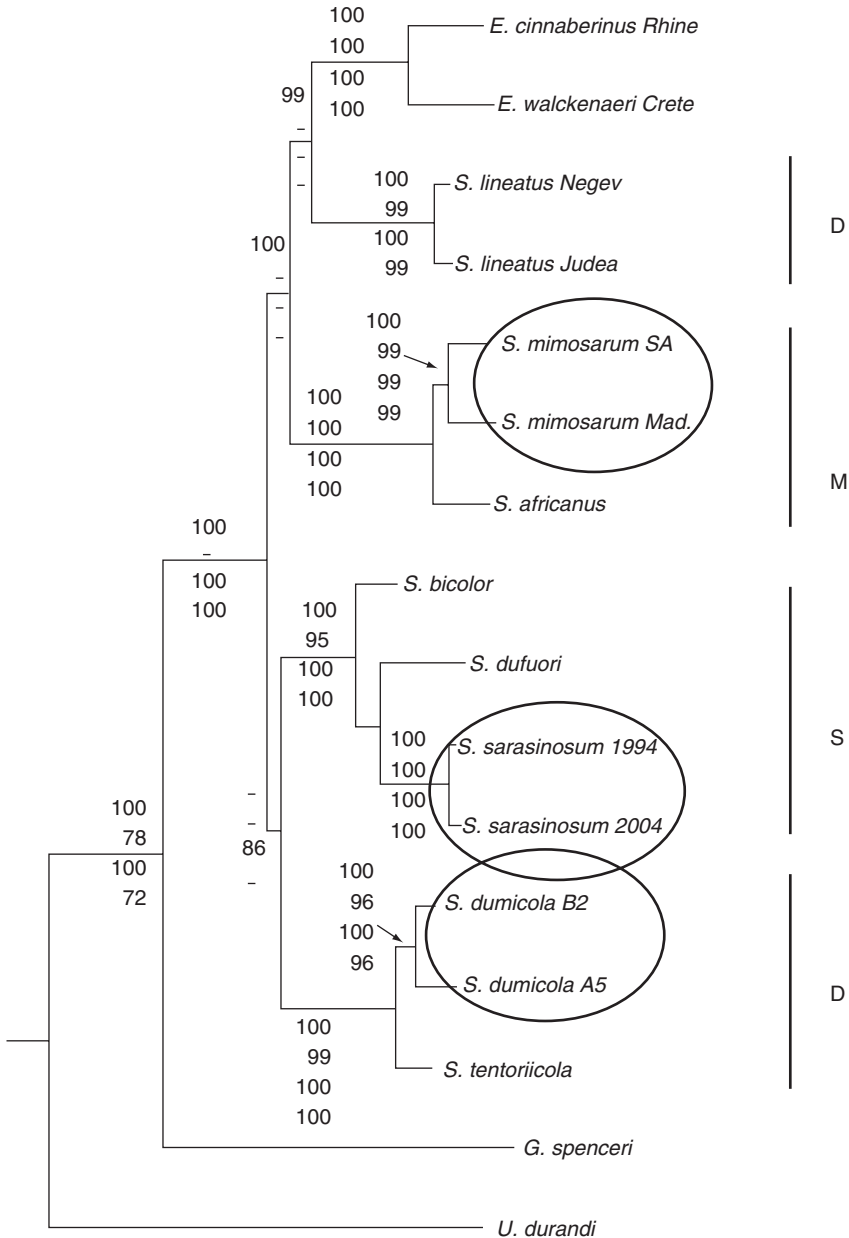
FIG. 1. A partial molecular phylogeny of *Stegodyphus* (Eresidae) [modified from Johannesen *et al.* (2007), with permission of the publisher]. Social species are circled. Probability levels of Bayesian inference and bootstrap scores for maximum likelihood (ML), neighbor joining (NJ), and maximum parsimony (MP) are shown in this order starting from above.

at a much younger instar (Agnarsson and Kuntner, 2005). Three such "quasi-solitary" species form a single clade that is nested within a clade of subsocial and social species, which led Agnarsson *et al*. (2007) to suggest a reversal from subsocial to quasi-solitary behavior. Within the genus *Anelosimus*, however, there is actually a continuum of levels of subsociality, from dispersal of young at the end of maternal care, through dispersal at later instars, to groups of sisters remaining together and sharing a nest, or joining to form a new nest as in some populations of *A. studiosus* in North America (Furey, 1998) and in *A.* cf. *studiosus* in Uruguay (Ghione *et al*., 2004). In all of these instances, outbreeding is maintained through male dispersal. As we discuss below (Section VI), there appears to be considerable flexibility in subsocial life histories both among and within *Anelosimus* species, and ecological factors are likely to play a dominant role in determining the length of the group-living stage. Thus, the proposed reversal more likely reflects different ecological conditions favoring early or late dispersal.

C. SOCIALITY IN SPIDERS: AN EVOLUTIONARY DEAD END?

A striking similarity between the *Stegodyphus* and *Anelosimus* phylogenies is the lack of diversification of the social clades, despite the old age at least of the *Stegodyphus* social lineages (Agnarsson *et al*., 2006; Johannesen *et al*., 2007). This characteristic has led to the suggestion that permanent-sociality accompanied by regular inbreeding is an evolutionary dead end (Agnarsson *et al*., 2006; Avilés, 1997; Whitehouse and Lubin, 2005). The argument is that short-term benefits of inbreeding, such as the elimination of dispersal costs and an increased rate of reproduction, are selected against in the long term because of reduced speciation rates or an increased risk of extinction (Agnarsson *et al*., 2006). In the case of the social spiders, continued mating among group members leads to very high inbreeding coefficients, which may result in a long-term loss of adaptive potential (Keller and Waller, 2002). Agnarsson *et al*. (2006) proposed that the social clades in the Theridiidae are phylogenetically isolated and subject to high rates of extinction. While the social *Stegodyphus* also lack diversification, these lineages are relatively old, suggesting that they were able to track environmental changes over evolutionary time or that their environment

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Bayesian probability scores and bootstrap scores less than 95% and 70%, respectively, are denoted with -. The three *Stegodyphus* species-groups based on Kraus and Kraus (1990) are denoted with respect to the social species: D (*dumicola*), M (*mimosarum*) and S (*sarasinorum*). The groups of Kraus and Kraus (1990) were confirmed with the exception of *S. lineatus*, which belongs to a fourth phylogenetic group. The relationship between *S. lineatus* and *Eresus* sp. suggests paraphyly of the genus *Stegodyphu*s. Two species used as out-groups are *Gandanameno spenceri* (Eresidae) and *Uroctea durandi* (Urocteidae).
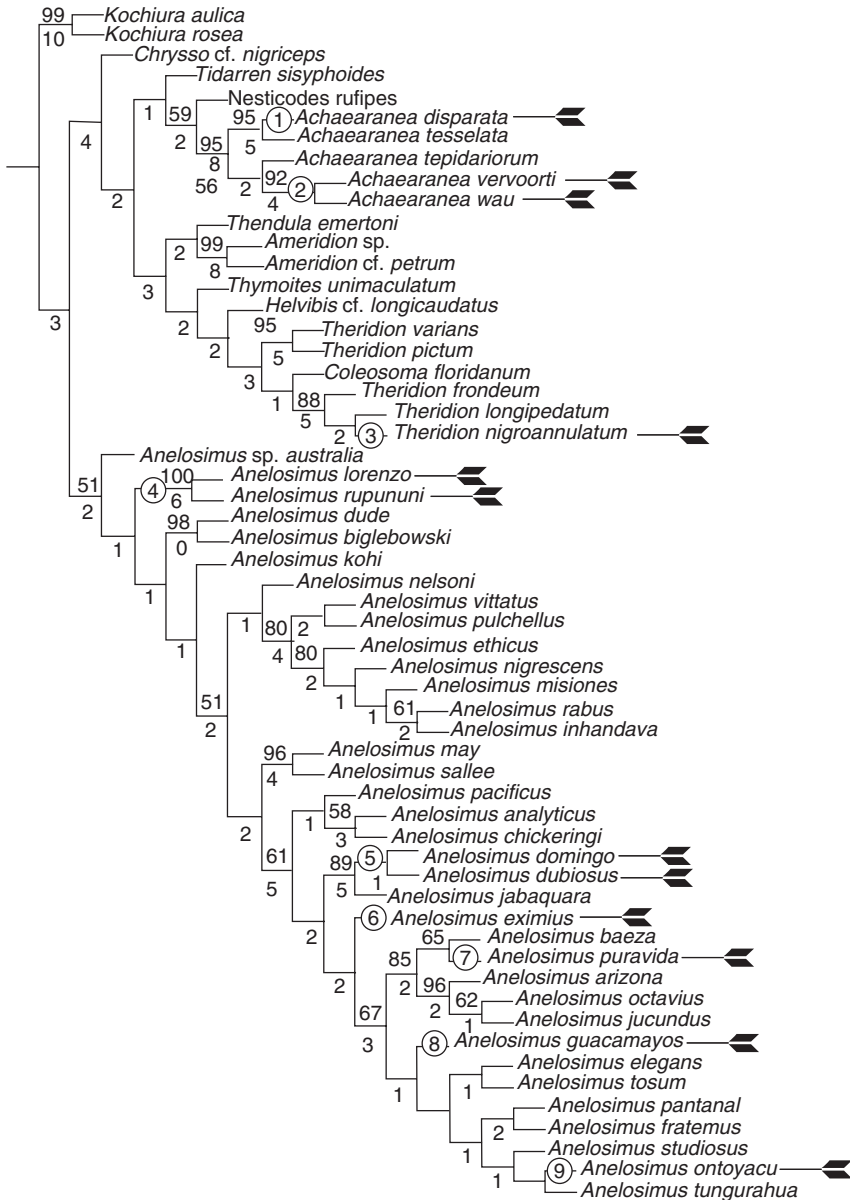
FIG. 2. Interrelationships of social and subsocial Theridiidae based on molecular phylogeny [modified from Agnarsson *et al.* (2006a), by permission from the publisher]. Numbered circles show counts of independent social origins; arrows indicate social species; numbers above branches are bootstrap support values; below branches, Bremer support values. All the species within the clade have either documented maternal care or their behavior is unknown (see Agnarsson, 2006, Appendix).

has remained rather stable over evolutionary time (Johannesen *et al*., 2007). Furthermore, the sister lineages of the social *Stegodyphus* species have not diversified either; hence, in *Stegodyphus*, we cannot draw the conclusion that speciation is reduced in the social lineages in comparison with their closest subsocial relatives. To determine if permanent-sociality is truly an evolutionary dead end, or the social lineages need more time to diversify, we require information about the phylogenetic relationships of other social and subsocial species, and we need to establish what rate of diversification should be expected in the social and subsocial sister lineages.

V. Evolution and Maintenance of Sociality in Spiders: Relevant Models

The subsocial route for evolution of group living points to maternal care, constraints limiting dispersal, and the transition to an inbred mating system, as common features characterizing the transition from periodic-social to permanent-social living. Once sociality has evolved, there may be additional selective forces promoting further development of the society. The objective of this section is to consider relevant models of social evolution which may play a role in the evolution of cooperation and the development of complex traits or social behaviors, and to review empirical evidence that support predictions from theory. The models included in this section are not mutually exclusive. It seems particularly relevant to discuss multilevel selection frameworks here since group level benefits are increasingly ascribed crucial selective forces in social evolution (Avilés, 1993a; Leigh, 1999; Okasha, 2004; Reeve and Keller, 1999; Wade, 1978). In discussing various models, we have included relevant empirical evidence from subsocial and transitional as well as social species.

A. Kin Selection

To date, kin selection has been the most successful and widely accepted explanation for the evolution of societies and cooperation (Frank, 1998; Griffin and West, 2002, 2003; Hamilton, 1964; Maynard Smith, 1964; West-Eberhard, 1975). Kin selection can be defined as ''the evolutionary process which occurs when individuals interact with one another in a non-random way with respect to kinship and these interactions affect fitness'' (from Wade and Breden, 1981). Individuals can increase fitness by their own reproduction (direct fitness) or through indirect fitness, by the reproduction of relatives with whom they share genes identical by descent (narrow

definition) or with whom they share the gene(s) of interest (broad definition) (West *et al.*, 2007). Together, direct and indirect reproduction constitute an individual's inclusive fitness. Genes coding for cooperation among individuals, which increase the reproduction of their relatives and hence their inclusive fitness, can spread in the population and lead to the evolution of more or less obligate helping behavior. The more genes identical by descent that individuals share, the higher the inclusive fitness benefits and, hence, the incentive to forego own reproduction and engage in helping behavior. This is the model known as Hamilton's rule (Hamilton, 1964).

Kin selection is most likely to occur when high relatedness within the group confers inclusive fitness benefits to individuals that cooperate, for example in nest defense, foraging, or alloparental brood care. Therefore, cooperative behavior is likely to be found in animals that live in family groups (Bourke and Franks, 1995; Emlen, 1991; Frank, 1998; Griffin and West, 2003; Koenig and Dickinson, 2004). Family structure arises through parental care, which results in overlapping generations or delayed dispersal of young, which remain in sibling groups.

Cooperation and permanent group living in spiders presumably originated in family groups consisting of a female and her offspring, where extended maternal care provided sufficient benefits for siblings to remain in the nest and postpone dispersal (Agnarsson *et al.*, 2006; Avilés, 1997; Buskirk, 1981; Johannesen *et al.*, 2007). This transition in life history resulted also in mating among siblings within the nest and consequently overall high relatedness among group members, thereby increasing the opportunities for kin selection to operate (Michod, 1982, 1993; but see Section VI).

A classical way to infer kin selection is to identify the level of within-group relatedness in relation to the degree of cooperation (Emlen, 1991; Griffin and West, 2002). Since most of the social spider species studied show extremely high levels of relatedness (Table III; Avilés, 1997; Riechert and Roeloffs, 1993; Smith and Engel, 1994; Smith and Hagen, 1996), cooperation in foraging and brood care is expected to provide inclusive fitness benefits. The identification of genetic relatedness within cooperating groups per se, however, is not necessarily sufficient to infer kin selection since cooperation may incur costs of group living such as kin competition and it is not obvious that there will be a net advantage to cooperation (Griffin and West, 2002, 2003; Hamilton and May, 1977; Queller, 1992). In cooperatively breeding birds and mammals, there is good evidence that helping behavior increases with the degree of relatedness (Crespi and Choe, 1997; Emlen, 1991; Griffin and West, 2002, 2003; Koenig and Dickinson, 2004).

Experimental tests of the effect of kinship on fitness in social spiders are largely lacking. Cooperation in brood care did not differ between small experimental groups of the social *S. dumicola* comprising either females

from two distant populations or from a single population in Namibia, as measured by the number and size of young raised by these females (M. Salomon, personal communication). In the subsocial *Stegodyphus lineatus*, growth and mass gained was higher in cooperatively feeding groups of siblings compared with nonsiblings indicating a role of kin selection in the evolution of communal feeding (Schneider, 1996b; J. Schneider and T. B., personal communication). Further experimental manipulations of relatedness and cooperation need to be performed in order to assess the role of kin selection in the evolution and maintenance of cooperation.

1. Kin Recognition

Recognition in the form of group closure as seen in the social Hymenoptera has not been shown; on the contrary, social spiders appear to accept unrelated and foreign individuals into the colony with no apparent discrimination (D'Andrea, 1987; Darchen and Delage-Darchen, 1986; Kullmann, 1968; Pasquet *et al.*, 1997; Seibt and Wickler, 1988a). In nature, mixed groups of the subsocial *D. ergandros* can be found, indicating that young disperse to join other nests (Evans, 1999). While population genetic data usually show very low genetic variation within social spider colonies, which suggests colony founding by one or a few related individuals, there is evidence for the sporadic occurrence of unrelated individuals within a colony, suggesting the inclusion of long-distance dispersers (Johannesen *et al.*, 2002; Lubin and Crozier, 1985; D. R. Smith, personal communication). However, based on the genetic data, it seems likely that this phenomenon is the exception rather than the rule, that is, there is very little migration between colonies. If social spiders rarely experience foreign spiders immigrating naturally into their colonies, selection for mechanisms for use in kin discrimination behaviors such as group closure may be low or absent.

In subsocial spider species, there are studies showing discrimination of genetic kin. In experimental groups of *D. ergandros*, sibs survived better than nonsibs and under conditions of starvation, cannibalism was directed at nonsibs (Evans, 1999). Similarly, groups of young siblings of the subsocial *S. lineatus* were less cannibalistic than groups of unrelated juveniles under experimental conditions of low food availability (Bilde and Lubin, 2001). In the latter species, there is also evidence to suggest that sib groups have a higher growth rate than groups of unrelated young (Schneider, 1996b). These studies indicate that kin recognition can occur and that kin selected benefits may accrue at least in certain situations. In the field, however, it is not known if discrimination of nonkin exists in colonies of social species. In contrast, no behavioral discrimination of sibs or nonsibs as mates was found in controlled breeding experiments of two subsocial species (*S. lineatus*: Bilde *et al.*, 2005; and *A. arizona*: Avilés and Bukowski, 2006).

2. *Inbreeding and Kin Selection*

In models of kin selection, alleles associated with cooperative behaviors increase in frequency because cooperative individuals increase the fitness of individuals with whom they are genetically related (Wade and Breden, 1981). Inbreeding increases the degree of genetic similarity among individuals; from Hamilton's rule, it therefore follows that kin selected traits should be favored in inbred populations. Through computer simulations, Wade and Breden (1981) showed that inbreeding favored the evolution of cooperation by changing the balance between opposing forces of individual and group level selection. Inbreeding reduces the genetic variance within the group and increases between-group variance, which results in weaker within-group and stronger between-group selection, as the intensity of selection depends on the amount of genetic variance on which selection can act (Falconer, 1989). The important point is that inbreeding creates strong population subdivision through isolated breeding units, which allows selection among the isolated lineages to overcome counteracting selection within them (Wade and Breden, 1981; Wilson and Colwell, 1981). It is becoming increasingly recognized that social evolution involves multilevel selection when group-level differences in productivity select for traits such as female-biased sex ratios that would not be maintained without strong population subdivision (Avilés, 1993a; Leigh, 1999; Okasha, 2004; Reeve and Keller, 1999; Wade, 1978).

B. Multilevel Selection (Group Selection)

In addition to selection pressures acting on individuals within groups, natural selection can also operate at the level of the group or society in a multilevel selection framework (Alexander and Borgia, 1978; Leigh, 1999; Okasha, 2004; Reeve and Keller, 1999; Wade, 1978; Williams, 1966). Within-group selection acting on individuals will usually select against cooperation when the cost paid varies with the degree cooperation among individuals. Within-group selection follows selfish-genes models, where selfish types are favored at the expense of cooperative individuals who pay the costs of helping. Group-level selection favors cooperation, when cooperation among individuals within a group yields higher overall group productivity than other groups, for example by increased survival or reproduction, or better colonization ability. Group-level selection requires differentiation among groups (Hamilton, 1967), but does not necessarily require high relatedness within the group (Rissing *et al.*, 1989). The conditions that must be met for selection to act on processes at the level of the group are (1) high variance and population substructure, which can be achieved if

groups are founded by one or a few individuals; (2) limited migration among groups; and (3) high turnover rate, where some groups reproduce while others go extinct (Avilés, 1993a; Leigh, 1999; Okasha, 2004; Reeve and Keller, 1999; Wade, 1978). Under these conditions, selection at the level of the group may override individual selection within the group.

The social spiders may provide the conditions necessary for group selection (see Section III; Avilés, 1986, 1993a; Avilés and Tufiño, 1998; Bilde *et al*., 2007; Smith and Hagen, 1996): colonies are founded by few females (Avilés, 1997; Jacson and Joseph, 1973; Lubin and Robinson, 1982; Main, 1988; Seibt and Wickler, 1988b; Vollrath, 1982), there is limited migration between groups (Avilés, 1997; Main, 1988; Roeloffs and Riechert, 1988; Seibt and Wickler, 1988b; Vollrath, 1982), and there are very high extinction rates, which means that only few groups proliferate (Avilés and Tufiño, 1998; Bilde *et al.*, 2007; Crouch and Lubin, 2001; Henschel, 1998; Vollrath, 1982). Propagule dispersal and initiation of new colonies occurs mainly by individuals from large colonies (Avilés, 1997; Lubin and Robinson, 1982; Schneider *et al.*, 2001; Vollrath, 1982). There is an extreme degree of population structure because of the low number of founders and repeated inbreeding within colonies (see previous section, Smith and Hagen, 1996; reviewed in Avilés, 1997). Studies of life-history traits in colonies of increasing size classes have revealed that group living in spiders is associated with high per capita reproductive costs (Avilés, 1997; Avilés and Tufiño, 1998; Bilde *et al*., 2007; Riechert, 1985; Seibt and Wickler, 1988b). The benefits of group living are enhanced colony (group) survival with increasing colony size, at least until the colony reaches an intermediate optimal size. Survival benefits at the level of the colony (the group) may outweigh the individual costs paid due to a decrease in fecundity with increasing colony size (Avilés and Tufiño, 1998; Bilde *et al.*, 2007).

Another interesting aspect of group selection models is the evolution of female-biased sex ratios, which can evolve by higher-level (between-group) selection (Avilés, 1986, 1993a; Wilson and Colwell, 1981). This is because higher-level selection favors larger colonies that have a greater probability to survive and reproduce. A female-biased sex ratio would allow the group to grow at a higher rate and reach the threshold beyond which survival benefits and group productivity are maximized. Avilés (1993a) used a simulation model to show that a female-biased sex ratio evolves in populations where isolated lineages grow for a number of generations, proliferate after reaching a certain threshold size, and eventually become extinct. Smaller populations, lower migration rates, and higher turnover rates resulted in an increasingly female-biased sex ratio, while a proliferation threshold was essential, that is only colonies above a certain population size give rise to successful new colonies. These conditions appear to describe the dynamics of some social

spiders, for example, *A. eximius* and *S. dumicola*. Thus, while ecological benefits may give advantages to large colony size, higher-level selection will promote a sex ratio bias that enables colonies to grow rapidly and reach the threshold for proliferation (Avilés, 1986, 1993a).

Avilés (1993a) argued that Hamilton's (1967) local mate competition (LMC) model for the evolution of female-biased sex ratios in structured populations and the group selection model presented for social spiders are "two extremes of a continuum in which the same selective forces are involved." Hamilton's (1967) argument was that when mating occurs among the progeny of one or a few founders of a group, the best strategy is to produce exactly enough sons to fertilize all the daughters, which results in a departure from the sex ratio equilibrium proposed by Fisher (1930). Inseminated females then disperse to colonize new resources. Hamilton originally considered one generation of inbreeding in his model, while there was much controversy whether the LMC model can explain the maintained female-biased sex ratio during subsequent generations of inbreeding (as is the case of social spiders) (Avilés, 1993a; Bulmer and Taylor, 1980; Charnov, 1982; Nagelkerke and Sabelis, 1996; Nunney, 1985; Werren, 1983; Wrensch and Ebbert, 1993). Frank (1987) pointed out that in structured populations, the interaction between cooperative effects that result in higher group productivity and genetic relatedness will favor a skewed sex ratio. Avilés (1993a) considered multigenerational groups and argued that natural selection selects acts against the female-biasing allele within groups, so female-biased sex ratios are maintained in the metapopulation only because they increase productivity and thus proliferation of the groups in which they occur. The social spider model becomes a LMC model if the number of generations of local mating is reduced to one before the groups disperse (Avilés, 1993a). The main point is that female-biasing alleles can only be maintained if groups that contain a higher proportion of females are most successful in producing dispersers (Wilson and Colwell, 1981; see also Charnov, 1982). In Avilés model, three conditions must be met: (1) a group-level selective advantage of biased sex ratios, (2) enough population subdivision to create between-group variance, and (3) a nonzero rate of group turnover (Avilés, 1993a).

The underlying process of sex ratio evolution may be adaptive parental control of the sex ratio (Nunney, 1985). Yet, in the social spiders, there is no evidence for adaptive changes in the sex ratio with increasing colony size (Henschel *et al*., 1995a; Lubin, 1991). It may be that the social spiders are unable to alter the sex ratios of their offspring in response to environmental or genetic changes if they lack adaptive control over sex ratio determination (Hurst and Vollrath, 1992). The heterogametic sex determination system in

spiders suggests that social spiders cannot adjust sex ratios as easily as seen in some haplo-diploid insect systems (see Section V.D; Avilés *et al.*, 1999, 2000; White, 1973).

The unique traits of the social spiders including constraints on dispersal, selection for rapid colony growth, and continued inbreeding over multiple generations resulting in very high intracolony relatedness suggest that the conditions for colony-level benefits to maintain the female-biased sex ratios are present. Hence, the female-biased sex ratio of the social spiders prompts some very interesting questions for further studies: What is the sex ratio determination mechanism in social spiders? How is the seemingly fixed female-biased sex ratio maintained? Is there potential for adaptive adjustments of the sex ratio with colony size and age?

C. ECOLOGICAL BENEFITS

Social groups can form when individuals aggregate because of inherent advantages of group living. These benefits are usually associated with defense against predators or detection and harvest of food resources (Alexander, 1974). This route to group living predicts an increase in aver-age individual fitness as a function of group size, where costs and benefits of group living result in an optimum group size at some intermediate level (Avilés, 1999; Emlen, 1991; Rannala and Brown, 1994). Group living in spiders may be advantageous as a defense against predators (Henschel, 1998), but there is no evidence that aggregation in response to predation pressure was the route to group living (as is proposed for the social gall thrips and aphids, coined ''fortress defenders''; Costa, 2006). Similarly, there is no evidence that social spider groups form in response to foraging benefits, on the contrary, resource competition as revealed by a reduction in body size and individual reproductive success with increasing colony size suggests a growing competition over food with group size (Avilés and Tufiño, 1998; Bilde *et al.*, 2007; Seibt and Wickler, 1988b). Nevertheless, both protection and foraging could provide net benefits to living in groups within a range of group sizes and may be factors that act to maintain sociality.

The presence of multiple females in a nest may ensure that at least some of the brood will survive to maturity. This is the basis of the ''fostering model'' proposed by Jones *et al*. (2007). In this model, a female's reproductive success depends on the probability that she will survive until the young become independent and is a function of the number of females in the colony, as well as the length of the period of dependence of the young on maternal care (altricial period) and the risk of mortality. The assumption is that if the mother dies during the altricial period, another female will foster

her young. In the case of relatively long altricial periods, this model predicts an advantage to group living. The model was developed to explain the occurrence of colonies of *A. studiosus* containing multiple reproducing females in cool temperate habitats, where development time is long relative to warmer, subtropical habitats (Furey, 1998). Such a scenario might provide an initial advantage to reproducing in a group independent of relatedness among its members.

D. ECOLOGICAL CONSTRAINTS

Constraints models assume the formation of groups by delayed dispersal of offspring, which remain in their natal group because of factors that restrict their individual dispersal and breeding attempts (Emlen, 1991; Koenig and Dickinson, 2004). Individuals that remain in the group may pay a net per capita fitness cost compared with solitary breeding. However, a low probability of breeding successfully, for example because of limited breeding sites, may shift the balance in favor of group living. Differences between years and geographical areas are likely to cause variation in the magnitude of the constraint, leading to predictable patterns in the size of groups and the benefits of helping behavior.

Delayed dispersal of offspring in the natal nest leads to the formation of genetic family groups. This route to sociality is predominant in cooperatively breeding birds and mammals (Emlen, 1991; Koenig and Dickinson, 2004) and is carried to the extreme in the social spiders where the elimination of pre-mating dispersal and formation of sibling groups further lead to mating among group members and hence inbreeding (reviewed in Avilés, 1997). The expected benefits of delayed dispersal are reduced costs of mobility, including predation, desiccation, search costs for suitable habitat or mates, avoiding competition with nonrelatives (Andersson, 1994; Hamilton and May, 1977), and foraging benefits (saving silk, capture of larger prey, reduced variance in prey capture; see Avilés, 1997). Some major costs are expected from group living: increased homozygosity or loss of heterozygote advantage as a consequence of inbreeding (Charlesworth and Charlesworth, 1987; Roff, 2002) and competition among kin over food and reproduction (Griffin and West, 2002; Hamilton and May, 1977).

Constraints on dispersal appear to be a strong factor favoring group living in social spiders, overriding the negative effect of declining fecundity with increasing group size (Avilés and Tufiño, 1998; Bilde *et al.*, 2007).

E. GAME THEORY MODELS

Cooperation based on reciprocity can be an evolutionarily stable strategy (ESS) even among unrelated individuals (Axelrod and Hamilton, 1981; Trivers, 1971). Two conditions must be met: (1) an individual is not able

to cheat without the other individual being able to retaliate, that is defectors are recognized; and (2) the probability of the same two individuals meeting must be high. Hence, game theory models usually imply individual recognition, but perhaps group recognition and repeated interactions among members of a group are sufficient for it to play a role in the maintenance of sociality. Cooperation may evolve initially either through kin selection mediated by recognition cues or clustering, or by reciprocation of cooperative actions (Axelrod and Hamilton, 1981).

In the social spiders, group members usually remain in the colony throughout their life span (review in Avilés, 1997) and therefore have repeated interactions. Thus, the second condition for cooperation based on reciprocity is met. It is unknown, however, whether specific individuals recognize and remember previous specific interactions and whether kin discrimination is under positive selection (see Section V.A.1).

Packer and Ruttan (1988) suggested that there will be a temptation to cheat, in this case to join in feeding without participating in the actual capture, if the prey is large, but not if it is small enough to be monopolized by a single individual. Cooperation can be maintained in spite of cheating if a single individual is unlikely to succeed in capturing prey on its own. As group size increases, the degree of cooperation should decrease because the advantage of group capture will be outweighed by the losses to cheaters. Thus, it is not necessary to invoke reciprocity. The data on group foraging in spiders described earlier (Section III.A) are consistent with these ideas: not all individuals feeding on a prey item were involved in capturing it, the first spiders to feed tried to prevent others from joining, and joiners reduced the value of prey for the hunter (Ward and Enders, 1985; Willey and Jackson, 1993).

F. By-Product Mutualism

Cooperation via by-product mutualism occurs when an individual pays an immediate cost of not cooperating (Brown, 1983; Connor, 1995). The immediate benefits outweigh the costs of cooperating, and the benefits for the group are shared so that either all individuals cooperate or none cooperate. By-product mutualism differs from reciprocity in two fundamental ways: (1) there is no temptation to cheat and (2) no scorekeeping is required, where reciprocity requires some form of keeping track of your partner's behaviors.

The African social spider *S. dumicola* suffers from ant attacks, and during ant raids, the spiders take turns in spinning cribellate silk below the entries to their nests, thereby physically preventing casualties (Henschel, 1998). Comparing survival between solitary individuals and groups, all solitary females died during ant attacks, whereas some individuals survived in 85% of the larger colonies (Henschel, 1998). Presumably, the more spiders that

can contribute in preventive silk spinning, the greater the chance of colony survival. This may be an example where immediate survival benefits outweigh the cost of cooperation. In the context of by-product mutualism, the net benefit of cooperation, in this case increased survival, should be greater than the benefit of not contributing in nest defense and saving silk. Another example comes from the African *A. consociata* where the energetic costs of maintaining individual nests during the rainy season are alleviated by cooperative building of capture webs (Riechert *et al.*, 1986).

VI. TRANSITIONS IN THE EVOLUTION OF SOCIALITY: PROCESSES AND PATTERNS

The evolution of sociality in spiders was accompanied by changes in the dispersal pattern and breeding structure and in the degree of cooperation in reproduction among individuals within the group. How did these changes come about and what were the preconditions for the transition to sociality? Selection favoring the transition to sociality could differ from the mechanisms that maintain sociality. The phylogenetic evidence points to a subsocial-to-social transition route (though *Mallos gregalis* may be an exception to this, as maternal care is not known to occur in this genus), and therefore, our discussion focuses on traits found in subsocial species that may have facilitated the transition to sociality. Subsocial species provide a window onto the ways these changes might have come about.

A. FROM PREMATING TO POSTMATING DISPERSAL

The shift from premating dispersal of offspring in the solitary and subsocial species to postmating dispersal, or no dispersal in some generations, in social species is a seemingly unlikely and puzzling transition given the generality of the (largely) theoretical benefits to dispersal (Hamilton and May, 1977; Lambin *et al.*, 2001). Understanding the factors that promoted a loss of premating dispersal is the key to understanding the evolution of sociality in spiders (Waser *et al.*, 1986, 1994). Thus, the clues to the evolution of philopatry of both sexes should be sought in the behavior, life history, and demography of the subsocial species (Avilés and Gelsey, 1998).

Premating dispersal of both sexes is seen in all subsocial species (Table II), although the timing or distance of dispersal may differ between the sexes. In the subsocial *A. arizona* (Theridiidae) (formerly cf. *jucundus*), females disperse as subadults or mature in the maternal nest, but males mature and disperse before their female siblings reach adulthood (Aviles and Gelsey, 1998; Powers and Aviles, 2003). In some other subsocial species, dispersal is more flexible. In *D. ergandros* (Thomisidae), mated females disperse to establish individual nests, but males apparently can disperse either before or after reaching adult stage (Evans, 1995). This species is subsocial in the

sense that the colonies last only a single generation. Yet, by having female postmating dispersal, it conforms to the typical constellation of social traits described above. Males seemingly have a mixed dispersal strategy, but unlike its social congener, *D. socialis, D. ergandros* has an unbiased sex ratio, suggesting that inbreeding is not common (Evans, 1995). Relatedness among young within the nest decreased with age of the young, an indication that also the young move between nests (Evans, 1999); this may be the way outbreeding is maintained. In other facultatively group-living species such as some *A. studiosus* populations and *A.* cf. *studiosus* in Uruguay, males apparently retain the behavior of dispersing out of the parent nest. It is unknown, however, whether a mixed breeding strategy occurs with some inbreeding as well as outbreeding. Further study of these species that appear to be at the transition between subsocial and social is needed.

There is a considerable variation in the duration of maternal care and timing of dispersal. In a subsocial agelenid (*Coelotes terrestris*) and amaurobiid (*Amaurobius ferox*), as well as in subsocial eresids (for example, *S. lineatus*), young disperse from the maternal nest as small juveniles, while in subsocial *Anelosimus* (e.g., *A. jucundus, A. arizona*, or *A. studiosus*), dispersal occurs at a later (often penultimate) instar and there is a long period during which juveniles remain together in the nest after the female dies (Table II). Agnarsson *et al.* (2007) distinguished between ''quasi-solitary'' species, in which young disperse at a small body size and after a short period of maternal care, and typical subsocial, in which dispersal occurs at a later (often penultimate) instar and there is a long period during which juveniles remain together in the nest after the female dies. Rayor and Taylor (2006) refer to these two categories as ''transient'' and ''prolonged'' subsocial, respectively, and acknowledge that these reflect a continuum of subsocial behavior. The common denominator of all of these species is that juvenile dispersal follows a period of obligatory maternal care, while the stage at which dispersal occurs may be dictated by food conditions and intranest competition (Aviram, 2000) or other environmental conditions. When abundant prey were provided, *S. lineatus* young could remain together until they were adults (Schneider, 1995) and the addition of prey lengthened the duration that the young remain in the maternal nest in a range of species tested (*Theridion pictum*: Ruttan, 1990; *C. terrestris*: Gundermann and Krafft, 1993; *A. ferox*: Kim, 2000; *Tegenaria atrica*: Pourié and Trabalon, 2001). The delay of juvenile dispersal appears to be a gradual phenomenon and shows considerable plasticity both among and within species, while the loss of premating dispersal accompanying regular inbreeding may have been a more abrupt transition.

Breeding site philopatry in its extreme form of remaining in the maternal nest could have benefits for both young and adult stages (Jones and Parker, 2002). For juveniles and maturing females, the nest is a costly resource, with

its large investment in silk and protective structure (Kim, 2005; Myles, 1988; Seibt and Wickler, 1990). In stable habitats, with low year-to-year spatial variation in resources, it may be advantageous for females to remain in the previously successful maternal nest. Remaining in the nest could have benefits associated with group living as well (see Section V.C). But, even if females benefit from philopatry by inheriting the nesting site and obtaining more food, they will face competition from close relatives (Griffin and West, 2002; Hamilton and May, 1977). Indeed, in subsocial *A. studiosus*, long-lived mothers chase maturing female offspring from the nest (Brach, 1977; Furey, 1998; Jones and Parker, 2002).

For males, the presence of females on the nest assures that they will find a mate, but why should males not disperse to find additional, and in particular unrelated females? Data on the conditions that reduce the value of mating dispersal for males are critical to understand the evolution of this inbred social system (Waser *et al.*, 1994). Restricted opportunities for finding unrelated females can limit male dispersal. When females are clustered in kin groups, the distance to an unrelated female may be quite large. Kin clusters, risk of predator attacks, and extreme environmental conditions may all favor a reduction of mate-searching behavior (Andersson, 1994). In the subsocial *S. lineatus*, males mated with one or two females on average (Maklakov *et al.*, 2005; Schneider and Lubin, 1998) and the distribution of distances that males traveled was bimodal, such that males first visited a nearby female and later moved to a distant female (Bilde *et al.*, 2005). As neighboring spiders are often siblings, these philopatric matings enhance population substructuring into kin groups (Bilde *et al.*, 2005; Johannesen and Lubin, 1999, 2001). This type of male mating dispersal could represent a first step toward inbred sociality.

B. FROM OUTBREEDING TO INBREEDING

The systems of dispersal and breeding are linked. Social species lacking premating dispersal of either sex have regular and continuous inbreeding (Avilés, 1997; Riechert and Roeloffs, 1993; Smith and Hagen, 1996), while subsocial species with premating dispersal of both sexes outbreed (Avilés and Bukowski, 2006; Bilde *et al.*, 2005). In subsocial species with multiple breeding females, there is a potential for inbreeding. In the Australian huntsman spider *D. cancerides*, young mature in the nest and may remain as adults (L. Rayor, personal communication) and potentially inbreed. Allozyme data suggest, however, that the young in a nest are derived from different fathers (Rowell and Avilés, 1995). Foreign males are accepted into the colony (L. Rayor, personal communication), suggesting male movement between nests. This is supported also by the lack of female-biased sex ratios (Rowell and Avilés, 1995).

The transition stage is expected to entail a loss of fitness caused by inbreeding depression (Roff, 1997, 2002); hence, many animals, including most social species (ants, social wasps, cooperatively breeding mammals, and birds) have various mechanisms to avoid or prevent inbreeding (Cook and Crozier, 1995; Greenwood, 1980; Johnson and Gaines, 1990; Pusey and Wolf, 1996). The fitness costs associated with inbreeding could act as a constraint on the evolution of sociality (Avilés, 1997; Avilés and Bukowski, 2006; Bilde *et al.*, 2005). If, however, the costs of inbreeding are not large and inbreeding avoidance is lacking or weak, the loss of outbreeding may not be a severe constraint (Chesser and Ryman, 1986; Waser *et al.*, 1986). Bilde *et al.* (2005) tested this hypothesis by subjecting the subsocial eresid *S. lineatus* to two levels of inbreeding: sib mating and within-cluster mating. The latter test simulated the level of inbreeding found in kin-structured populations in nature (Johannesen and Lubin, 1999, 2001). Behavioral inbreeding avoidance was lacking altogether and mild inbreeding depression was expressed only in the growth rate and adult body size. A similar sib-mating study was conducted on the subsocial theridiid *A. arizona* (formerly *A.* cf. *jucundus*) by Avilés and Bukowski (2006). In this species, inbreeding depression was evident only in postdispersal (penultimate-instar) young; there were no obvious inbreeding effects during the stages in the maternal nest, both when the mother was present and during the sibling cohabitation stage. Avilés and Bukowski (2006) suggested that the benefits of extended maternal care and of group living compensate for inbreeding costs, but that these benefits do not extend beyond the social stage. The impression from these two studies is that the fitness losses from inbreeding depression may have been overcome in a gradual process starting from philopatric dispersal of young, leading to kin-structured populations with occasional inbreeding, and ending with continuous inbreeding in nests of nondispersing offspring. A history of inbreeding could allow for purging of deleterious recessive alleles thus reducing the (short-term) cost of inbreeding (Charlesworth and Charlesworth, 1987).

C. From Maternal Care to Cooperative Breeding

Extended maternal care in the subsocial species takes the form of tending the eggsacs, for example moving them within the nest to obtain a better microclimate and protecting them from predators or parasites, and feeding of young by capturing prey for them, regurgitation of predigested prey, production of trophic oocytes, or by matriphagy (Evans *et al.*, 1995; Gundermann *et al.*, 1988; Jones and Parker, 2000; Kim and Horel, 1998; Kim and Roland, 2000; Kullmann *et al.*, 1971; Marques *et al.*, 1998; Rowell and Avilés, 1995). The young obtain direct benefits from extended maternal care in the form of improved survival and faster growth (Salomon *et al.*, 2005; Schneider, 2002). Maternal effects play a large role in the success of

the young in subsocial species: large females have both larger clutches and provide more resources during the maternal-care stages, resulting in larger young at the stage of independence (Aviram, 2000; Gundermann, 1997; Kim and Roland, 2000; Kim *et al.*, 2000; Salomon *et al.*, 2005). Young that disperse at a larger body size will have an advantage in survival and growth over smaller dispersers (Aviram, 2000; Jones and Parker, 2002). Extended maternal care comes at the expense of clutch size and, indeed, clutch sizes of species with maternal care tend to be small relative to those of similar-size females lacking maternal care (Schneider, 1996a), reflecting an evolutionary trade-off between number and size of progeny (Fox and Czesak, 2000; Stearns, 1992).

Cooperative breeding in the social spider species provides both the general benefits of group living that accrue to offspring (see Section V.C) as well as benefits derived specifically from allomaternal care. Allomaternal care involves guarding of eggsacs of several females placed together in a cluster or brood chamber or feeding of young by multiple females, some of which may be nonbreeders. Even without the presence of helpers, the benefits of group living alone may be sufficient to select for breeding together. For example, *A. jabaquara* females breed in the same nest but are intolerant of one another and defend their individual eggsacs and early instar brood from one another (Marques *et al.*, 1998). Several subsocial or transition species can be found in breeding groups, where females raise their young together (Table II; *D. cancerides, A. jabaquara, A. studiosus, A.* cf. *studiosus*). Once the young leave the vicinity of the guarded eggsac or brood, they will mix with young of other females and thus will benefit from a certain degree of allomaternal care. Jones and Parker (2002) showed direct benefits to the young and both indirect and direct fitness benefits to the reproducing females in breeding groups of *A. studiosus*. Thus, group living in these transition species has at least some of the components of cooperative breeding typical of inbred social species. The question is: do some females in these groups forego reproduction altogether and remain in the group as helpers, or do they disperse to breed solitarily when unable to breed in the communal nest? By extension, we need to ask: is helping a reproductive strategy in the social spiders, namely, an alternative to reproducing on one's own, or is it only a consequence of ecological constraints on reproduction?

Schneider (2002) investigated the physiological preconditions to helping behavior by cross-fostering young of the subsocial *S. lineatus* to females in different reproductive stages. Unmated females and females with an eggsac provided little or no care for foster young, while females with young of their own fed the foster young both by regurgitation and matriphagy (see Bessekon *et al.*, 1992 for a similar result with the subsocial agelenid spider

C. terrestris). Salomon and Lubin (2007) showed, however, that in the social *S. dumicola* nonbreeding adult and subadult females feed young both by regurgitation and ''allomatriphagy.'' Thus, a switch in reproductive physiology and behavior must have occurred at the transition to sociality that enabled subadult or unmated females to exhibit maternal behaviors. These directed allomaternal behaviors are not present in the outbred transition species. Thus, we propose that helping in the outbred transition species mentioned above is not an alternative reproductive strategy, but rather a by-product of maternal care where the young of different females mix in the nest and are treated equally by all reproducing females (but see Evans, 1998).

Under a kin-selection scenario, helping as a distinct reproductive strategy should develop in species where average relatedness among nest members is higher than among individuals within the breeding population at large (Michod, 1993). This could occur if sisters remain together in the maternal nest and breed together, as appears to be the case in *A. studiosus* and *D. cancerides* (Rowell and Avilés, 1995). If helping in these transition species is favored by kin selection, it is interesting that it has not developed further. Two further considerations add to the mystery. First, helping by nonbreeders is common in the social insects as well as in birds and mammals and is widely believed to have arisen by kin selection without inbreeding. The second and perhaps more basic problem is that when inbreeding is continuous and colonies, and even local populations, are genetically homogeneous, the strength of kin selection should decline and helping may no longer be favored (Michod, 1993). This paradox may be resolved, however, if colony-level benefits of helping are taken into account. As with the evolution of the female-biased sex ratios, a trait that increases group productivity would enable colonies to grow more rapidly to a size at which dispersing propagules can be produced (Avilés, 1986, 1993a; see also Section V.B). Additionally, helping behavior may have had a direct benefit during the transition to inbreeding by reducing the effects of inbreeding depression on individual reproduction, as suggested by Avilés and Bukowski (2006). Finally, once inbred sociality was established, helping would come under positive selection as a means of lowering the costs of competition in large colonies.

VII.   Summary: From Subsocial to Inbred Social, an Overview

A possible scenario for the evolution of sociality is the following: in a subsocial species with extended maternal care, some of the young inherit the maternal nest and breed together. Male dispersal at this stage will

maintain outbreeding. Care of the young is limited to one's own offspring, at least in the early development stages. This social structure may be seen in some *A. studiosus* populations, *A.* cf. *studiosus* in Uruguay, *A. jabaquara, S. tentoriicola*, and no doubt other species whose biology is less well known. Remaining in the maternal nest and breeding together is favored by kin selection combined with constraints on dispersal and independent nesting and/or large benefits from sharing resources.

Kin-structured populations and philopatric male mating dispersal will lower the barrier to full inbreeding by purging deleterious alleles and thus reducing the negative fitness consequences of inbreeding. At the same time, selection will act on reproductive traits such as the sex ratio and helping behavior in ways that favor rapid colony growth. This stage of the transition should occur only when local populations are already significantly inbred and male dispersal away from the local population is strongly disfavored. The conditions favoring this transition remain poorly understood. It is evident, though, that this is a one-way street: a reversal to subsocial from inbred social seems unlikely based on phylogenetic evidence, and further evolution of social clades likewise does not seem to occur. This evolutionary pathway has been portrayed as an "evolutionary dead end" (Agnarsson *et al.*, 2006; Avilés, 1997; Johannesen *et al.*, 2007). Nevertheless, many of the inbred social species are highly successful, are widely distributed geographically, and show considerable differentiation on a geographic scale. Furthermore, some species have a long evolutionary history. This pattern could come about only by means of continued small-scale evolutionary adjustments to the genome, namely, by microevolution at the geographic scale.

Numerous puzzles remain to be solved. What is the role of long-distance dispersal of mated females in these inbred social species? The fact that it occurs in most of the species studied so far, but by different and likely independently evolved methods, suggests that it is an essential element of this social system. The role of disease and parasitism in selecting for propagule dispersal (Hamilton, 1987) should be investigated further, both empirically and theoretically. How do the homozygous and variation-poor genomes adapt to a wide range of ecological conditions? Is cooperative breeding a risk-sensitive strategy that enables colonies to cope with a wider range of ecological conditions by reducing the variance in food intake within the colony? And, when do reproductive skew and helping by non-breeders become a group-selected strategy favoring rapid colony growth? Finally, what are the life-history consequences of inbred sociality—for example, body size, growth rates, fecundity, and mortality schedules—and how do they affect the potential for evolutionary change? The inbred social spiders provide a rich and fertile field for understanding evolutionary processes.

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