

SOCIALITY IN THERIDIID SPIDERS: REPEATED ORIGINS OF AN EVOLUTIONARY DEAD END

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Abstract.—Evolutionary “dead ends” result from traits that are selectively advantageous in the short term but ultimately result in lowered diversification rates of lineages. In spiders, 23 species scattered across eight families share a social system in which individuals live in colonies and cooperate in nest maintenance, prey capture, and brood care. Most of these species are inbred and have highly female-biased sex ratios. Here we show that in Theridiidae this social system originated eight to nine times independently among 11 to 12 species for a remarkable 18 to 19 origins across spiders. In Theridiidae, the origins cluster significantly in one clade marked by a possible preadaptation: extended maternal care. In most derivations, sociality is limited to isolated species: social species are sister to social species only thrice. To examine whether sociality in spiders represents an evolutionary dead end, we develop a test that compares the observed phylogenetic isolation of social species to the simulated evolution of social and non-social clades under equal diversification rates, and find that sociality in Theridiidae is significantly isolated. Because social clades are not in general smaller than their nonsocial sister clades, the “spindly” phylogenetic pattern—many tiny replicate social clades—may be explained by extinction rapid enough that a nonsocial sister group does not have time to diversify while the social lineage remains extant. In this case, this repeated origin and extinction of sociality suggests a conflict between the short-term benefits and long-term costs of inbred sociality. Although benefits of group living may initially outweigh costs of inbreeding (hence the replicate origins), in the long run the subdivision of the populations in relatively small and highly inbred colony lineages may result in higher extinction, thus an evolutionary dead end.

Key words.—*Anelosimus*, evolution of sociality, inbreeding, levels of selection, mating system, preadaptations, sex ratio bias.

Received February 10, 2006. Accepted August 22, 2006.

Some traits may evolve by short-term selective advantage, but in the long term result in lowered speciation rates or elevated extinction rates (e.g., Normark et al. 2003). Such evolutionary dead ends are poorly understood phenomena, and can represent a conflict of levels of selection on traits that may be selectively advantageous within but disadvantageous between species. Traits suggested as evolutionary dead ends include parthenogenesis (e.g., Normark et al. 2003), self-fertilization (e.g., Takebayashi and Morrell 2001), and ecological specialization (e.g., Stireman 2005), although support for such hypotheses remains mostly ambiguous (e.g., Nosil and Mooers 2005). Sociality in spiders may be another example (Avilés 1997). In nonterritorial permanent-social or quasi-social spiders, here referred to simply as “social,” colony members cooperate to build and maintain their web or nest, capture prey cooperatively, and share brood care (reviews include Kullmann 1972; Buskirk 1981; D’Andrea 1987; Avilés 1997; for a list of social species that updates Avilés [1997], see Appendix available online only at: <http://dx.doi.org/10.1554/06-078.1.s1>). Almost all these species mature and breed within the natal nest generation after generation (Riechert and Roeloffs 1993; Avilés 1997; Bilde et al. 2005; Avilés and Bukowski 2006). As a result, social spider populations are strongly inbred and highly subdivided, as evidenced by allozyme and DNA studies (Lubin and Crozier 1985; Smith 1986; Roeloffs and Riechert 1988; Smith

and Hagen 1996; Johannesen et al. 2002). Sex ratios are also dramatically female biased, as much as 10:1 (Avilés and Maddison 1991; Rowell and Main 1992; Avilés et al. 1999, 2000), probably because colony-level selection overpowers fisherian selection for 1:1 sex ratios within the isolated colony lineages (Avilés 1993).

Social spiders are rare (23 of over 39,000 spider species) and phylogenetically scattered in 11 genera across eight widely separated families. In almost all cases, social species are phylogenetically adjacent to species with periodic-social or subsocial behavior (Figs. 1 and 2, online Appendix, see also Avilés 1997, fig. 23-3, table 23-1). Social species may have originated from subsocial ancestors through prolongation of tolerance and cooperation to adulthood (Kraus and Kraus 1988; Wickler and Seibt 1993; Agnarsson 2002, 2004, 2006a) and suppression of the premating dispersal phase (Kullmann 1972; Gundermann et al. 1993; Wickler and Seibt 1993; Schneider 1995; Avilés 1997), yielding an inbred mating system (Riechert and Roeloffs 1993; Avilés 1997).

As summarized by Avilés (1997), inbred spider sociality poses a number of significant questions (see also Riechert and Roeloffs 1993; Johannesen et al. 2002; Bilde et al. 2005; Avilés and Bukowski 2006). Does it originate only rarely, as the costs of inbreeding depression in the transition from outbred to inbred breeding systems would predict (Charlesworth and Charlesworth 1987; Waser 1993; Keller and Waller



FIG. 1. Interrelationships of social and nonsocial Theridiidae (one of 19 most parsimonious trees shown) and *Stegodyphus*. Numbered circles show counts of independent social origins; arrows indicate social species; numbers above branches are bootstrap support values; below branches, Bremer support values. The optimization of maternal care within Theridiidae is based on Agnarsson (2004, 2006a). All the species within the maternal care clade have either documented maternal care, or their behavior is unknown (see online Appendix). *Stegodyphus* relationships are shown as a tree for clarity (box) based on a nonquantitative hypothesis of Kraus and Kraus (1988). The theridiid phylogeny is based on a quantitative analysis including all social theridiids.

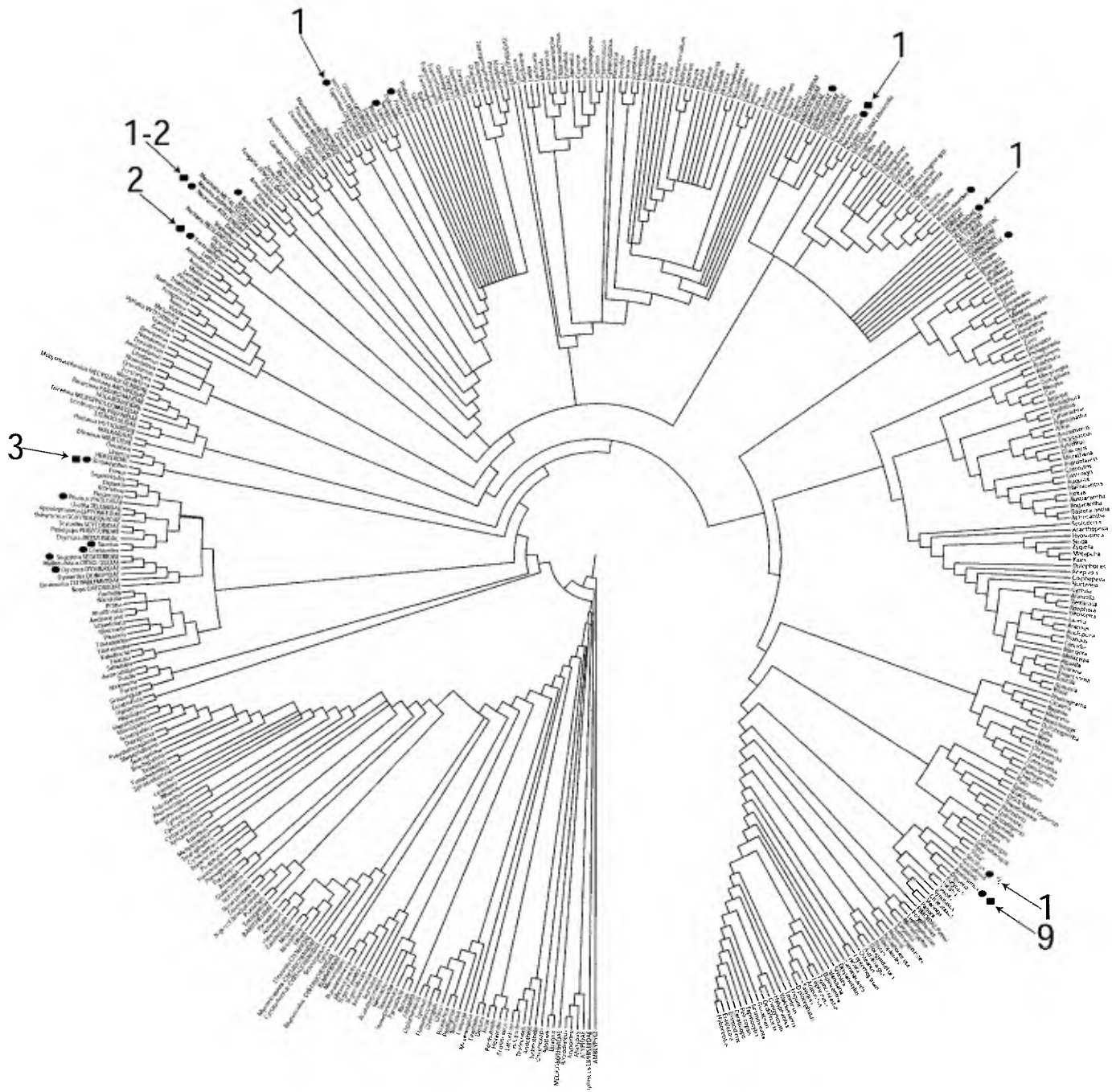


FIG. 2. A sketch of spider phylogeny compiled from 67 quantitative phylogenetic analyses of higher-level spider systematics, presented as a visual aid only. Filled circles show the estimated distribution of maternal care; squares, the distribution of inbreeding (identical to that of biased sex-ratios; unknown for Nesticidae). Filled circles indicate that at least one species of the family shows maternal care, but in most families the situation for most species is unknown. Numbers indicate estimated number of social origins within a particular family/genus (arrows, to the nearest genus if the social taxon is omitted). Although maternal care and sociality coincide at this coarse level, statistical tests of the correlation would require better data on the distribution maternal care and social status and a truly quantitative phylogenetic hypothesis.

2002; Roff 2002)? What factors facilitate its origin? Does it promote speciation, as the strongly subdivided populations would predict? Does it promote extinction, as inbreeding and fast turnover of isolated and dynamically unstable colony lineages would predict? If spider sociality is distributed as few relatively large clades, few origins and high speciation

rates are supported. If the pattern is phylogenetically scattered and ‘‘spindly,’’ multiple origins and low diversification rates are supported.

We address these questions by exploring the phylogenetic distribution of sociality in the spider family Theridiidae, which contains an amazing 11–12 social species (Avilés

1997; Agnarsson 2006a; Avilés et al. 2006). We map sociality on a novel phylogeny (based on Agnarsson 2004, 2006a,b) and, using a newly developed method, test whether the distribution is unexpectedly spindly. We then evaluate the results in the context of other social spiders as well as inbred social systems in general.

At issue is the balance between forces driving the evolution of a trait and those determining the fate of lineages bearing it. If sociality arises frequently, but thereafter dooms its lineages to early extinction or no speciation, then these processes at different scales of time and levels of selection conflict. Social spiders have already been a focus of attention in the study of multilevel selection (Avilés 1986, 1993, 2000; Smith and Hagen 1996), and their biased sex ratios are thought to reflect trade-offs between individual- and colony-level selection (Avilés 1993, 2000). In this study we explore whether layered over these processes is a third level of selection, differential speciation, and extinction of species lineages.

MATERIALS AND METHODS

Categorization of Social and Breeding System

For the purposes of this study, we categorize species as “solitary” if progeny receive little or no maternal care and disperse soon after eclosing from the egg sac. In some species, newly eclosed progeny passively receive maternal care before they disperse; we consider these species as solitary with extended maternal care. Species are “subsocial” if the progeny, typically of one female, remain together long enough to contribute to communal activities, but disperse prior to mating. We consider species such as *Anelosimus studiosus* subsocial even if some populations occasionally form colonies with more than one female (see Furey 1998, Jones et al. 2007). Species are “social” if colony members remain in the natal nest past reproductive maturity, so that the nests typically contain multiple adult females and their progeny. Inbreeding and/or female-biased sex ratios have been documented in all but two social species: *Delena*, in which equal sex ratios and outbreeding are known, and *Tapinillus*, in which they are suspected (Avilés 1994; Rowell and Avilés 1995). Given their dispersal patterns, solitary and subsocial species, here broadly referred to as “nonsocial,” are assumed to be primarily outbred. Absence of biased sex ratios and/or of strong inbreeding have been demonstrated in a few cases by molecular studies (e.g., Smith and Engel 1994; Johannesen and Lubin 1999) and sex ratio estimates (Avilés and Maddison 1991; Lubin 1991; Bilde et al. 2005). Because mothers look after their progeny in both subsocial and social species, extended maternal care characterizes both social systems. Although these categories overlap in some cases, and some species do not fit neatly into one or the other, for our purposes the critical distinction is whether populations are so strongly subdivided (i.e., inbred) that the sex ratio bias is at least two females per male.

Theridiid Phylogeny

We fused two morphological data matrices, theridiid genera (Agnarsson 2004, 2006b; Avilés et al. 2006) and *Ane-*

losimus species (Agnarsson 2005, 2006a) as described in Agnarsson (2003). We also added the social *Achaearanea disparata*, and the subsocial *A. tessellata* to form a new matrix containing 93 taxa and 288 morphological and behavioral characters as well as one new character unique to *A. disparata* and *A. tessellata*. This matrix contains all known social theridiids (available at <http://theridiidae.com/cladograms.html> and at treebase.org).

Phylogenies were inferred from the matrix using heuristic parsimony methods in NONA version 2.0 (Goloboff 1993) and PAUP* version 4.0 (Swofford 2002), using 1000 random stepwise additions, and the subtree-pruning and regrafting branch swapping algorithm. For further information on separate analyses of the source data matrices see Agnarsson (2004, 2005, 2006a,b).

Two of the 288 characters code for social traits for which all social species shared the same character state. Although inclusion of study characters during tree inference can be problematic (Coddington 1988; Brooks and McLennan 1991; Swofford and Maddison 1992), in this case inclusion biases the tree toward fewer origins, and therefore yields a more conservative test of independent origins.

Evolution of Sociality and Diversification

Because the characterization of the social system in two species was uncertain due to limited information (see online Appendix), all analyses were repeated with those species removed (“pruned” versus “unpruned” trees). Except as noted, our analyses of social evolution were separately conducted on each of the most parsimonious trees, while the figures depict an arbitrarily chosen tree (tree 1) among those.

Origins of sociality

We reconstructed the number of independent evolutionary origins of sociality within theridiids under parsimony and maximum-likelihood reconstructions of ancestral states in the program Mesquite (W. P. Maddison and D. R. Maddison 2005). The symmetric, one-parameter Mk1 model (Lewis 2001) was used in likelihood reconstructions. Parsimony reconstructions are expected to have error (Cunningham et al. 1998; Stireman 2005), but we use them primarily for a narrative discussion and to portray minimum numbers of origins, for which parsimony is conservative. Our statistical tests do not depend on the reconstructions, because reconstruction methods are incorporated in the derivation of null expectations.

Concentration of social origins

We used the concentrated-changes test as implemented in MacClade (Maddison 1990; D. R. Maddison and W. P. Maddison 2005) to evaluate whether social origins in the theridiids are concentrated in clades with maternal care, because this trait has been proposed as a preadaptation for spider sociality (e.g., Kullmann 1972; Krafft 1979; Avilés 1997). Because an exact enumeration of all theoretically possible distributions of nine social origins is not feasible for datasets of this size, we ran a simulated sample size of 10,000 of these for the test using the MINSTATE reconstruction option

and constraining state 0 to be ancestral. The use of parsimony reconstructions within the simulation of null expectations reduces concern over our use of reconstructed ancestral states as if they were observations (Maddison 1990).

Differential diversification: isolation of social lineages

To ask whether inbred social lineages have diversified as much as outbred nonsocial lineages, we developed a simple parametric bootstrapping test that used a test statistic reflecting the isolation of social lineages—the scattering of tiny clades across the phylogeny. We simulated the evolution of a binary character representing sociality (absent/present) under the null hypothesis that the character had no effect on speciation or extinction rates. The simulation used a single parameter (symmetrical) Mk1 model (Lewis 2001; D. R. Maddison and W. P. Maddison 2005) with state 0 (nonsocial) forced to be ancestral (as outgroups suggest), using a modified version of Mesquite 1.06 (W. P. Maddison and D. R. Maddison 2005). The rate of change used was that estimated by likelihood under the Mk1 model from the observed distribution of sociality on most parsimonious trees.

To measure diversification of inbred social lineages under the null hypothesis, we counted the number of nodes reconstructed by parsimony as having sociality (social nodes); nodes with equivocal (social or nonsocial) reconstructions were conservatively included in the count. The same reconstruction method was used in the simulation as in the analysis with observed data, thus making the use of parsimony reconstructions less problematic. Some nodes are terminal (sociality observed) and some internal (sociality inferred). We measured diversification as the proportion of social nodes that are internal, because internal nodes represent speciation events. If social lineages fail to diversify, then the observed would be expected to differ from the null by having most of its social nodes as terminals, that is, fewer social nodes would be internal. The distribution of proportions of internal versus terminal nodes for 10,000 simulated characters was compared to our observed data in each of the 19 most parsimonious trees.

We conservatively restricted the test of the isolation of social lineages to the clade *Kochiura* plus *Anelosimus* (where maternal care is optimized) because the concentrated-changes test suggested that social evolution throughout the tree was not homogenous; social origins occur only in that clade. The observed proportion of internal social nodes was calculated on all of the most parsimonious trees, and simulations and tests were done both on the unpruned and pruned trees.

We also measured the average depth of social clades by averaging over all social clades the number of branches on the longest path from an internal social node to a terminal. This statistic gave results similar to the above, and is not discussed further.

Differential diversification: sister clade comparisons

The above test is more powerful than comparing sizes of sister clades (e.g., Slowinski and Guyer 1993; Paradis 2005; see also Vamosi and Vamosi 2004) in cases where clades are young and neither sister has had time to diversify, but we also ran a Slowinski-Guyer test for comparison. This test was

restricted to *Anelosimus* because sister groups in *Theridion* and *Achaearanea* are poorly known. Conservatively, each social clade was compared to its entire, ancestrally nonsocial sister clade (of which three cases included social species).

A Look across Spiders

Figure 2 is a manually constructed summary cladogram spanning the order. We use it as a visual aid to demonstrate the phylogenetic scattering of social species, and the apparent overlap between the distribution of maternal care and sociality.

RESULTS

Sociality

Twenty-three spider species qualify as social under our definition (online Appendix; see also Figs. 1 and 2, Materials and Methods), but for two species data on social system are weak (*A. puravida* and the unidentified nesticid). Whitehouse and Lubin (2005) characterized *Phryganoporus candidus* (Desidae) as social, but we treat it as subsocial following the detailed study of Downes (1994).

Theridiid Phylogeny

The phylogenetic analysis of the combined theridiid matrix found 19 most parsimonious trees, one of which is shown in Figure 1. These trees are congruent with the analyses of Agnarsson (2004, 2005, 2006a,b) and Avilés et al. (2006). The only relevant variation among these trees with regard to our study is that the size of the sister clade of *A. guacamayos* ranges from two to five species, although this has no impact on our findings. As expected, the social *A. disparata* and subsocial *A. tessellata* are sister species. Although bootstrap support for some nodes in the phylogeny is low, the phylogenetic isolation of social species is generally supported by bootstrap values greater than 70. The separation of *A. guacamayos* and *A. oritoyacu* is not well supported (see Agnarsson 2006a), but for these species preliminary molecular data corroborate their separation (Agnarsson et al. 2007).

Multiple Origins of Sociality

Parsimony optimization requires nine (or eight, discounting *A. puravida*) origins of sociality within theridiids (Fig. 1). Four social *Anelosimus*, one *Achaearanea*, and the *Theridion* species have solitary or subsocial sister species or multispecies sister clades; only three pairs of social sister species occur (*Anelosimus rupununi* plus *lorenzo*, *A. domingo* plus *dubiosus*, and *Achaearanea wau* plus *vervoorti*). Likelihood ancestral states estimation (Mk1 model, state equivocal if the likelihood ratio is less than 2; see Pagel 2000) gives the same number of evolutionary origins. Avilés (1997) inferred at least 12 derivations of sociality in spiders, counting at least three times in theridiids (*Anelosimus*, *Theridion*, *Achaearanea*); three times in *Stegodyphus* (Eresidae); and at least once each in *Agelena* (Agelenidae), *Aebutina* (family placement uncertain, currently in Dictynidae), *Mallos* (Dictynidae), *Tapinillus* (Oxyopidae), *Delena* (Sparassidae), and *Diaea* (Thomisidae). With the addition of newly confirmed (*A. dubiosus*)

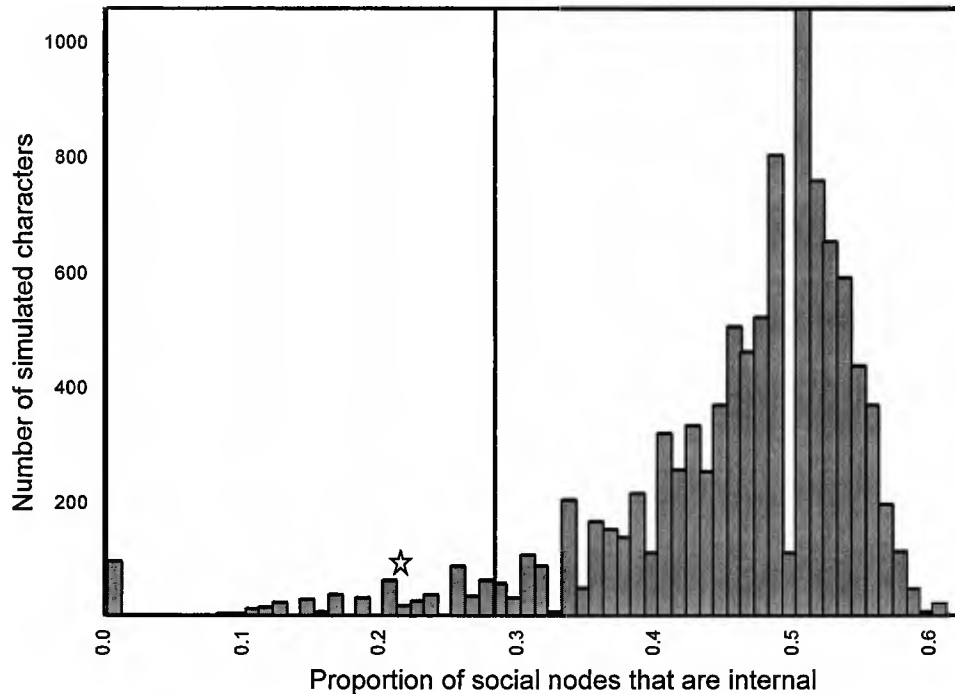


FIG. 3. A histogram of the proportion of simulated internal to total social nodes for 10,000 characters on the tree shown in Figure 1. The vertical bar shows the 0.05 cutoff point; the star indicates the observed data ($P = 0.034$).

or discovered (*A. guacamayos*, *A. oritoyacu*, and *A. puravida*) social taxa in the Theridiidae (Marques et al. 1998; L. Avilés unpubl. data) and recently described sociality in the Nesticiidae (Quintero and Amat 1996), we can now conclude that there have been at least 18 independent derivations of sociality in spiders (Fig. 2).

Concentration of Social Origins

The concentrated changes test shows that independent derivations of sociality are concentrated in the maternal care clade (Fig. 1). The concentration is significant both on the unpruned (nine origins, $P = 0.0051$ – 0.0079) and pruned (eight origins, $P = 0.0051$ – 0.0068) trees. This test is conservative: if the many hundreds of (nonsocial) theridiids not included for lack of phylogenetic data were added, or the tree were expanded to include the thousands of other (nonsocial) orbicularian spiders, statistical significance would increase.

Effect of Sociality on Diversification Rates

Differential diversification: isolation of social lineages

Spider sociality is significantly spindly (Fig. 3). On all 19 equally most parsimonious trees, three internal nodes and 11 terminals are reconstructed as social, giving a proportion of total social nodes that are internal of 0.2143. Estimated rates of change of the character over the 19 trees ranged from 0.1221 to 0.1254. Null ratios of internal to total social nodes ranged from 0 to about 0.61, with a $P = 0.05$ cutoff point at about 0.28. For unpruned trees $P = 0.033$ – 0.040 , and for pruned trees $P = 0.017$ – 0.022 .

Differential diversification: sister clade size comparisons

The sizes of social and nonsocial sister clades do not differ significantly by the Slowinski-Guyer test (Fisher combined probability, $\chi^2 = 17.46$, $df = 12$, $P > 0.05$), even if clades comprising one social and one nonsocial species are removed because neither may have had time to speciate ($\chi^2 = 14.69$, $df = 8$, $P > 0.05$). This is unsurprising since only the social *Anelosimus eximius* and the species pair *A. rupununi* and *A. lorento* have considerably larger sister clades (13 and 33 species, respectively).

DISCUSSION

Phylogenetics and the Multiple Origins of Spider Sociality

Eighteen to 19 independent origins of sociality among only 23 spider species is striking (Figs. 1, 2). Figure 2 shows that, in general, sociality evolves in the context of maternal care and is associated with inbreeding and female-biased sex ratios, except in *Tapinillus* and *Delena* (Avilés 1994; Rowell and Avilés 1995).

Transitions to an inbred mating system should be hindered by inbreeding depression (Charlesworth and Charlesworth 1987; Roff 2002). In nonsocial systems it is rare (psocids, naked mole rats, and bark beetles; Mockford 1957; New 1985; Sherman et al. 1991; Kirkendall 1993; O’Riain et al. 1996; Andreev et al. 1998; Burland et al. 2002), but in spiders the transition occurred at least 15 times (Fig. 2).

Frequent repeats of the sociality experiment in spiders may reflect particularly strong selection to remain in the natal nest versus dispersing for both males and females. Documented benefits of group living include saving on per capita invest-

ment in silk structures (Riechert 1985; Tietjen 1986), access to larger prey (Rypstra 1993; Jones and Parker 2000; Pekár et al. 2005), predator defense (Henschel 1998), and ready access to mates (Hölldobler and Wilson 1990; Yoder et al. 2004). Dispersal is both costly and risky and may, in some environments, be costlier than inbreeding. The inbred naked mole rats, for example, inhabit an environment where dispersal costs are high (Jarvis et al. 1994). Dispersal costs appear high for subsocial spiders (Avilés and Gelsey 1998; Johannesen and Lubin 2001; Jones and Parker 2002; Powers and Avilés 2003) and are likely to be even higher in environments where social species occur (Avilés and Gelsey 1998).

Recent experimental work also suggests that in spiders the cost of switching to inbreeding may be lower than anticipated. Studies in subsocial *Anelosimus* and *Stegodyphus* species (Johannesen and Lubin 1999, 2001; Bukowski and Avilés 2002; Bilde et al. 2005; Avilés and Bukowski 2006) suggest that in these systems: (1) behavioral mechanisms of discrimination against kin as mates may be absent, (2) some degree of inbreeding may already be present (Bilde et al. 2005), and (3) the presence of the mother and siblings in the group may help buffer against inbreeding depression (Avilés and Bukowski 2006). With the most deleterious recessive alleles purged by a history of mild inbreeding (Crnokrak and Barrett 2002), strong ecological incentives to remain in the social groups, and facilitating effects of group living, the transition to more complete inbreeding may thus not have been as difficult as previously believed (Avilés and Gelsey 1998; Avilés and Bukowski 2006; see also Waser et al. 1986; Day et al. 2003).

The concentration of origins of sociality in the maternal care clade supports the long-held view that extended maternal care and subsociality preadapt spiders for sociality (e.g., Kullmann 1972; Krafft 1979; Avilés 1997; Schneider 2002; Agnarsson 2004; Kim et al. 2005). Sociality in other taxa, for example in the Aculeate Hymenoptera, is also presumed to have evolved via maternal care and subsociality (e.g., Wilson 1975; Linksvayer and Wade 2005). However, in the Theridiidae the maternal care clade represents a single origin of this trait, which makes it difficult to exclude other unknown causal factors for the origin of sociality (see Maddison 1990, p. 555; Read and Nee 1995). Once spider phylogeny is better known and natural history data of more genera are available, this test can be extended to span the entire phylogenetic tree of spiders, across multiple origins of extended maternal care.

Dead End Hypothesis

Our results demonstrate that sociality in spiders has a spindly phylogenetic distribution: sociality occurs more often in phylogenetically isolated terminals than expected under the null model. Although analyzed here only in spiders, inbred sociality may be an example of a general evolutionary dead end. A similar spindly phylogenetic distribution has long been noted in asexual organisms (Stebbins 1950; Judson and Normark 1996; see also Haag and Ebert 2004). Normark et al. (2003, p. 74) succinctly commented: “[a] brief glance at the taxonomic distribution of asexuals gives the immediate impression that although asexuality often arises, it rarely per-

sists for long.” Why parthenogenesis may be a dead end is debated. Asexual species may tend to lose evolutionary arms races (Red Queen hypothesis; Van Valen 1973; Hamilton 1980), fail to diversify in environments where new genotypes are advantageous (tangled bank hypothesis; Ghiselin 1974; Bell 1982), compete poorly with sexuals when combinations of different genotypes confer positive group effects (Peck 2004), or accumulate deleterious mutations (mutation load reduction theory [Kondrashov 1993; Crow 1994] and Muller’s ratchet [Muller 1964]).

Any of these hypotheses might apply to all permanently inbred social systems such as spiders, psocids, naked mole rats, and some bark beetles (e.g. Mockford 1957; New 1985; Sherman et al. 1991; Kirkendall 1993; O’Riain et al. 1996; Andreev et al. 1998; Burland et al. 2002). Susceptibility to pathogens and inability to respond to changing environments (e.g., Slate and Pemberton 2002; Day et al. 2003; Schön et al. 2003; Pujolar et al. 2005) seem particularly relevant for social spiders due to their strong population subdivision, inbreeding, and high rates of colony turnover (Avilés 1993, 1997), all of which might erode genetic variability (Smith and Hagen 1996; Johannesen et al. 2002). Inbred social colonies, in spiders at least, also appear dynamically unstable. They are susceptible to extinction at small sizes due to Allee effects (Avilés and Tufiño 1998; Avilés 1999; Courchamp et al. 1999) and, in at least some species, to boom and bust patterns of growth at larger sizes (Avilés 1997, 1999; Avilés et al. 2006; Crouch and Lubin 2001). Thus, although perhaps initially successful within species, inbred sociality may be unusually vulnerable over the long term.

Low speciation and/or high extinction rates as causes of spindly phylogenetic distributions may be difficult to tease apart (Barraclough and Nee 2001). Sociality negatively affects diversification of social versus nonsocial lineages in spiders (dead end test), but social and nonsocial clades do not differ markedly in size (Slowinski-Guyer test). Higher extinction rates are thus sufficient to explain the data, but we cannot exclude the possibility that social spider clades also speciate less frequently.

The spindly distribution of sociality could also be due to asymmetric character change (Maddison 2006), so that sociality was lost so frequently that only a few scattered lineages would retain it at any given time. If we assume no differential diversification, Mesquite (Maddison and Maddison 2005) estimates sociality in the theridiid clade we studied must have been lost about three times more frequently than it is gained in order to explain our data (AsymmMk model: estimated forward rate 0.1517, backward rate 0.4686; ancestral state fixed at 0 to avoid the pathological behavior described by Schluter et al. 1997). Using these parameters to simulate character evolution yields values comparable to our observed test statistic and could thus alternatively explain the deviation from the null model ($P \gg 0.05$). Although asymmetrical change is thus a possibility, we favor species-level effects, such as extinction, rather than secondary loss because no evidence or hypothesis suggests that loss of sociality in spiders is more likely than gains. On the contrary, solitary social individuals and smaller colonies are less successful than groups in their environments (e.g., Avilés and Tufiño 1998), thus making reversals without emigration to

new environments unlikely. Regardless of whether sociality goes extinct or is quickly lost to reversal, our results show that it is unstable in the long term.

Social spiders represent a remarkable natural experiment in which the “same” evolutionary trial has rerun multiple times. These repetitions present an unusually clear example of potential conflict between levels of selection (within vs. among species) and of the repeated evolution of an evolutionary dead end. Our findings suggest general predictions about the long-term consequences of strong population subdivision and inbreeding. The methodology we developed can test evolutionary dead end hypotheses in a variety of circumstances other than inbred spider sociality, such as parthenogenesis in animals (e.g., Normark et al. 2003), self-fertilization in plants (e.g., Takebayashi and Morrell 2001), and specialization in phytophagous insects (e.g., Stireman 2005) and other organisms (Nosil and Mooers 2005).

ACKNOWLEDGMENTS

We are grateful to T. Barraclough for discussion on tests of evolutionary dead ends. J. Fletcher, J. Purchell, P. Salazar, A. Ingólfsson, L. May-Collado, D. Funk, and four anonymous reviewers provided helpful comments on the manuscript. Support for this research came from the National Sciences and Engineering Research Council of Canada grants (LA, grant 22R81375; WPM, grant 22R81325), the Smithsonian Scholarly Studies Program (JAC), and a Killam Postdoctoral Fellowship (IA).

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Corresponding Editor: D. Funk