Patterns of reproductive success associated with social structure and microclimate in a spider system

THOMAS C. JONES*† **& SUSAN E. RIECHERT***

*Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville
†Department of Biological Sciences, East Tennessee State University, Johnson City

Species that vary in social structure within and among populations can provide unparalleled insight into the evolution of sociality. The theridiid spider *Anelosimus studiosus* varies widely in its social structure at the northern edge of its range. Colony sizes range from the solitary/territorial female with her offspring to cooperative colonies of tens to hundreds of adult females. In previous work, we developed an assured fitness returns 'brood-fostering model' that predicts that in cooler environments mothers in multiple-female colonies will have a selective advantage over solitary female nests. According to the model, at cool sites the rate of juvenile maturation is slowed, increasing the probability that the mother will die before the brood reaches independence. In her absence, other females would foster her brood. We tested this hypothesis by manipulating colony size and by monitoring the reproductive success of naturally occurring solitary and multifemale colonies in cold and warm temperature environments. Our results indicate that while multiple-female colonies have higher fitness at cool sites, the solitary female nests achieve higher fitness at warmer sites. The higher reproductive success of multifemale colonies at cold sites further reflects the total failure of solitary female nests at these sites. Solitary female nests that survived generally had higher reproductive success than multifemale colonies at all temperatures. In natural colonies, fitness was highest for smaller multifemale colonies in the colder environments and decreased in the larger colonies. We use these data to refine the brood-fostering model and discuss the results with regard to the observed polymorphism in social structure.

© 2008 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Keywords: adaptation; *Anelosimus studiosus*; environmental variation; parental care; social spider; sociality

Behaviourally interesting things occur along habitat gradients, particularly at the edges of species' ranges (Holt & Keitt 2005; Bahn et al. 2006). Edge populations often experience the greatest selective pressure, as locally adaptive genotypes are washed out by gene flow from the centre of the range (Kirkpatrick & Barton 1997). Similar evolutionary stress occurs when small 'habitat-pocket' populations experience maladaptive gene flow from larger surrounding populations (Riechert et al. 2001). Avilés (1999) developed a model predicting that sociality may allow species to

expand their ranges, or to persist in harsh conditions, by reducing the risk of complete colony failure. Social species often respond to habitat gradients by 'adjusting' their degree of sociality. For example, in the sweat bee family Halictidae, sociality appears to be reduced in cooler temperate regions, evidenced from comparisons among species (Wcislo 1997) and within species (Eickwort et al. 1996; Soucy & Danforth 2002). This follows the general prediction that sociality in arthropods should be more prevalent in the tropics, where seasons permit continuous colony function (Lin & Michener 1972). However, a few social arthropods show a reverse cline in sociality, including some ants (Kaspari & Vargo 1995; Blackburn et al. 1999), bees (Richards & Packer 1995; Cronin & Schwarz 2001) and a social spider (Jones et al. 2007). In these cases, colony size, or the frequency of social individuals, is

Correspondence and present address: T. C. Jones, Department of Biological Sciences, East Tennessee State University, Johnson City, TN 37614, U.S.A. (email: jonestc@mail.etsu.edu). S. E. Riechert is at the Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, TN 37996-1610, U.S.A.

higher in temperate regions or cooler microclimates (Cronin 2001; Jones et al. 2007). Such exceptions to the rule, which vary in social structure along environmental gradients, can provide unparalleled insight into the evolution of sociality.

In behaviorally polymorphic populations, costs and benefits to social groups relative to solitary individuals have been directly measured in cases of hover wasps (Field et al. 2000), allodapine bees (Schwarz et al. 1997), and particularly in depth in sweat bees (Smith et al. 2003, 2007). These cases found support for 'assured fitness returns' (AFR) models (Strassman & Queller 1989; Gadagkar 1990; Reeve 1991), in which helper individuals accrue indirect fitness by reducing the probability of complete brood failure. For example, Smith et al. (2003) found in a sweat bee that orphaned broods were destroyed by ants, favouring small eusocial groups that had a high probability of at least one adult surviving to repel the ants.

Another species that displays unusual variation in social structure, particularly at the northern edge of its range, is the scattered-line weaving spider *Anelosimus studiosus* (Hentz) (Araneae, Theridiidae). Until recently, this spider was considered solitary/territorial but also as subsocial (sensu Wilson 1975) because single mothers care for their developing young for an extended period of juvenile dependency (Brach 1977). Furey (1998) first identified populations at 36° latitude in the eastern U.S. (Tennessee) in which some nests contained multiple-breeding females (mean 3.7 females/colony, range 1−29). He further presented evidence of cooperative brood care (regurgitave feeding and guarding egg cases other than their own) and cooperative prey capture within these colonies. More recently, a latitudinal shift in the social structure has been quantified (Jones et al. 2007; Riechert & Jones 2008). A pure social structure of solitary female nests resides at lower latitudes (southern Florida, U.S.A., 26−28°), with the first appearance of mixed social structures occurs at 30° (Florida panhandle), and a subsequent increase in the frequency representation of multiple-female nests with increasing latitude to the limit of our studies at 36° (eastern Tennessee, U.S.A.). At 36°, solitary female colonies remain predominant in the social structure (86−88%; Riechert & Jones 2008), but within this latitude, the proportion of multiple-female colonies is higher in cooler sites than at warmer sites (Jones et al. 2007). We do not yet know whether multiple-female colonies form by nondispersal of juveniles or by coalescence of dispersing females.

Behavioural trials have identified social and solitary phenotype individuals in all populations, with the lowest proportion of social individuals at 26° and the highest at 36° (Riechert & Jones 2008). This social phenotype is associated with a suite of behaviours showing reduced aggression (Pruitt et al. 2008). Also, F1 rearing and colony transplant studies suggest a genetic underpinning between social and solitary behaviours (Riechert & Jones 2008).

Until the discovery of multifemale colonies of *A. studiosus* in Tennessee, the known cooperatively social spiders were restricted to tropical regions, where prey densities are thought to be high enough to support these colonies (Buskirk 1981; Whitehouse & Lubin 2005) and where favourable temperatures year-round permit continuous reproduction and overlapping generations (Riechert & Roeloffs 1993). Benefits to sociality in spiders include: reduced individual silk costs, the ability of groups to capture larger prey, and higher overall survivorship in tropical habitats (reviewed by Avilés 1997). The challenge to explaining the social behavioural variation in *A. studiosus* is to identify advantages of sociality to larger colonies in the northern part of its range that would not be similarly advantageous in the south, where only solitary nests are found. Jones et al. (2007) introduced a modification of an AFR model called the 'brood-fostering model' to explain this clinal trend. Briefly, in multiple-female colonies, mothers that die are hedged against complete brood failure by the presence of other adult females in the colony who would foster their brood. We know from previous work that in single-female colonies all offspring are lost if mothers disappear before their offspring are independent (Jones & Parker 2000, 2002). Although not yet directly observed in natural conditions, such fostering is likely to occur since these spiders do not discriminate kin from nonkin juveniles under experimental conditions (Brach 1977; Furey 1998). However, in the model, mothers do pay a cost in maximum possible reproductive success, which declines as colony size increases (as seen in a congener, Avilés & Tufiño 1998) because of intracolonial competition. The model predicts that in the cooler north, where juvenile development is slower (Jones et al. 2007), the risk of a mother dying before her brood is independent is higher than in the warmer south. Thus, the model predicts a greater benefit to being in a multiple-female colony in the cooler north. The brood-fostering model differs from previous AFR models in that all adult females are reproductive and the benefits are in 'direct fitness' (indirect fitness would be affected by relatedness among mothers in the colony, but is not considered; Hamilton 1964).

The brood-fostering model makes several predictions: (1) in areas where multiple-female colonies are most abundant (i.e. in cooler environments), females in multiple-female colonies should have higher average per capita reproductive success than solitary females, (2) complete failure of single-mother colonies should be higher in cooler environments, (3) complete colony extinction should decrease with the number of mothers and (4) mothers in 'surviving' single-mother colonies should have the highest reproductive success overall, because of intracolonial competition. We tested these predictions, comparing colony success in different temperature environments through manipulative field experiments as well as observations of natural colonies.

METHODS

All study areas used for nest collections, field manipulations and natural colony observations were in eastern Tennessee at 36° latitude. In this area, flood control by the Tennessee Valley Authority creates stable water temperature variation: warm water occurs above dams and cool water occurs below dams as water flows through from the bottom of the lakes above. Because *A. studiosus* has an

affinity for the shrubs overhanging water bodies (usually within 2 m of the water), local populations probably experience different microclimates. We have not quantified the effect of water temperature on the microclimate within webs, but cooler water sites are associated with slower juvenile development (Jones et al. 2007). The locations of all sites used in this study and their mean summer temperatures are shown in Fig. 1. In eastern Tennessee, spiders overwinter in their colonies as subadults, then mature and disperse (if they disperse) in April, producing egg cases in May.

Field Manipulations of Colony Size in Different Temperature Environments

Two sites that differed in the temperature environment offered to *A. studiosus* served as transplant sites in year 1 of the manipulative study, a colder-water (16 °C = mean summer temperature) site at Melton Hill Lake (MH) and a warmer-water (24 °C) site along Abrams Creek (AC) (Fig. 1). In late May of 2002, brooding females and their egg cases were obtained from naturally occurring solitary female and multifemale nests. We artificially created new nests in a geometric progression (i.e. 1, 2 and 4) of foundresses/colony. Females from solitary female nests were used in producing the single-female treatment to control for the possibility that females from larger colonies might be unable to function singly. We used females collected from multifemale colonies in creating the two- and four-female treatments to control for potential agonistic interactions among foundresses. Riechert & Jones (2008) found that individuals from solitary colonies typically show an asocial behavioral phenotype, but that females collected from multifemale nests show a social phenotype. Once each new colony had established a silk nest on a sprig of artificial foliage in the laboratory, we wove this foliage sprig and nest into natural foliage at one of the two field sites (MH and AC). This method of colony establishment was first applied in Jones & Parker (2002) and used in another field experiment conducted in eastern Tennessee (Riechert & Jones 2008). We successfully established 15−18 replicates of each foundress number treatment on preferred vegetation, virginia pine, *Pinus virginiana*, and ironwood, *Carpinus caroliniana*, at the two sites. Each transplanted nest was placed within 0.5−1.5 m from the water, and at least 1 m from neighbouring nests (natural or experimental) to eliminate interaction or mixing. This distance is well in excess of the dispersal distance of *A. studiosus* (Riechert & Jones 2008). Silk spread from the artificial foliage onto surrounding vegetation served as evidence of nest establishment. Each transplant location was demarcated with a permanent tag that denoted the nest's treatment and replicate.

We visited the two sites every 2 weeks from colony establishment in June to October, coinciding with the end of the growing season of this species in eastern Tennessee (Jones et al. 2007). Each tag was located on the visits and the colony was checked for survivorship. On the occasion of the last check in October, we collected all surviving colonies at each site. These were dissected in the laboratory
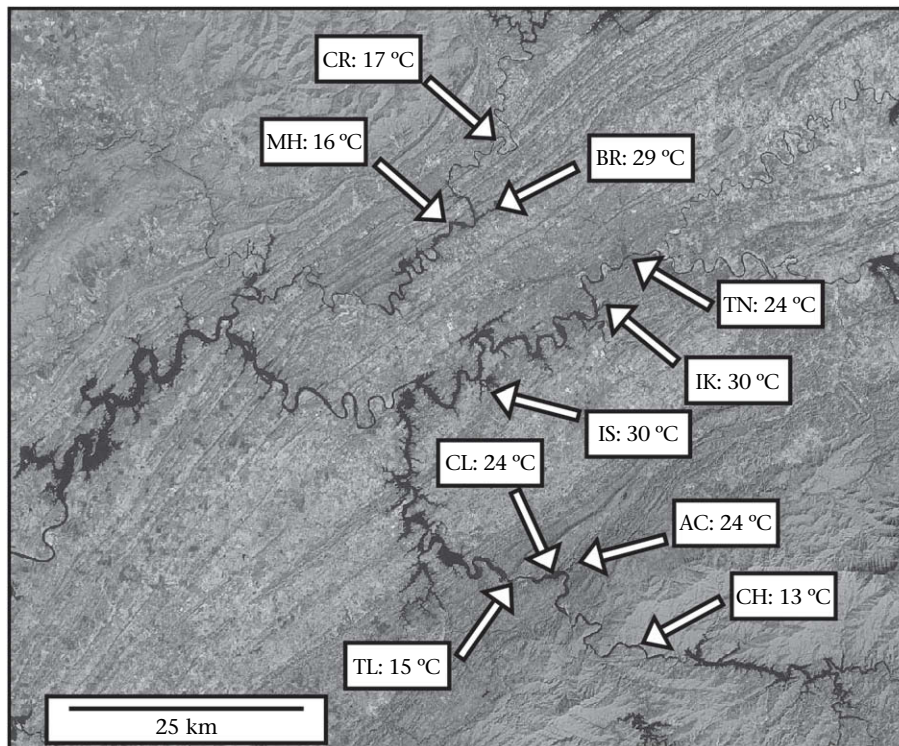

Figure 1. Map of the 10 eastern Tennessee sites used in this study and their corresponding mean summer water temperatures. CR = Clinch River; MH = Melton Hill; BR = Bull Run Creek; TN = Tennessee River; IK = IC King Park; IS = Ish Creek; TL = Tellico Lake; CL = Chilhowee Lake; AC = Abrams Creek; CH = Cheoah Lake.

and colony composition was recorded as the numbers of juveniles successfully reared. (Dispersal from the home nest in this species occurs the following spring at 36°.)

We repeated the experiment in 2003 using eight new sites across three river systems: two Clinch River sites, Clinch River (CR) and Bull Run Creek (BR); three Tennessee River sites, Tennessee River (TN), I C King Park (IK) and Ish Creek (IS); and three Little Tennessee River sites, Cheoah Lake (CH), Tellico Lake (TL) and Chilhowee Lake (CL). The range of temperature environments at these sites was wider than that offered in 2002 (Fig. 1). We successfully established 16−17 replicates of each treatment at each of the eight sites. The protocol was completed as described for year 1.

Measurement of Reproductive Success in Natural Colonies

In early June 2004, we identified two sites to be used in the colony manipulation studies that had cooler stable water temperatures and naturally occurring single-female and multifemale colonies: Melton Hill Lake (MH) and Chilhowee Lake (CL) (Fig. 1). Note, however, that our estimate of mean summer water at CL temperature probably missed cold pulses associated with evening water releases. We monitored 25 solitary female nests at each site for colony survival at 2-week intervals throughout the growing season from June to October. In addition, we tagged 10 multifemale colonies at MH (range 5−42 females, mean 21.6, median 17) and 20 multifemale colonies at CL (range 2−18 females, mean 3.95, median 2) for monitoring. We limited the census to colonies that were accessible for inspection with minimal damage to the web and nest structure. The instars of individuals present were estimated by visually comparing them to individuals of known stages that had been preserved in an acrylic block. Coincident with the completion of the last census in October, we collected the nests for dissection in the laboratory.

Testing the Brood-fostering Model

The brood-fostering model (Jones et al. 2007) predicts a mother's expected reproductive success by the equation:

$$RS_{N,Total} = (1 - \beta)^d \times (RS_{N,surv}) + \left(1 - [1 - \beta]^d\right) \times (RS_{N,die}).$$

Incorporated were the daily mortality risk to mothers (β), the duration of the period that juveniles were dependent on their mother (d), the relationship of individual reproductive success (RS) to colony size if a mother survives the dependency period ($RS_{N,surv}$), and the relationship of individual RS to colony size if a mother dies during dependency period ($RS_{N,die}$). Originally, data from a congener were used to estimate $RS_{N,surv}$ (Avilés & Tufiño 1998), and that curve was scaled by the probability that at least one other female would survive to foster the brood if the mother in question died, to get $RS_{N,die}$. No estimates of β or d were available, but certain combinations of values did predict that colonies with two to five females would have the highest individual RS (Jones et al. 2007).

We used data from the monitoring of natural colonies to provide more accurate estimates of three model parameters $RS_{N,surv}$, β and d. We used all of the natural colonies monitored at the two cold-water sites to obtain an estimate of $RS_{N,surv}$, the relationship of individual reproductive success (RS) to colony size if a mother survived the dependency period. Estimates of the daily mortality risk to females (β) and period of juvenile dependency (d) for cold sites were obtained from the solitary female nest data available from the two sites. Parameter values for β and d at warm sites were already available from previously published data (Jones et al. 2007).

RESULTS

Experimental Manipulations

Two-temperature site comparison

A chi-square test completed on nest survivorship in 2002 for the cold and warm sites identified a significant deviation from random expectations ($\chi_2^2 = 7.88$, $P < 0.02$). Inspection of individual cell contributions to the chi-square value identified survival of nests at the cold site (MH) as the major contributor. Nest survivorship increased with foundress number at the cold site, but no foundress number differences were detected for the warm site (AC) (Table 1). Regression of individual RS against foundress number for all colonies found no relationship at the cold site (MH: $R^2 = 0.006$, $P = 0.62$; Table 1), and a weakly significant decrease at the warm site (AC: $R^2 = 0.09$, $P = 0.04$; Table 1). However, mean individual RS for all colonies was highest for four foundresses at the cool site and for one foundress at the warm site. Mean individual RS for colonies that survived to collection and census significantly decreased with the number of foundresses (MH: $R^2 = 0.34$, $P = 0.006$; AC: $R^2 = 0.25$, $P = 0.006$; Table 1). Overall means of individual RS for all colonies were 5.6 at the warm site and 6.6 at the cold site, and were not significantly different (ANOVA with colony size nested within site: $F_{1,107} = 1.17$, $P = 0.35$). However, pairwise comparisons of individual RS identified significant differences between sites in the four-foundress treatment: mean RS was 8.0 at the cold site and 2.8 at the warm site ($F_{1,35} = 10.5$, $P < 0.004$).

Eight-temperature site comparison

A two-way ANOVA of colony survival found a highly significant effect of foundress number ($F_{2,256} = 34.12$, $P < 0.001$) and a significant effect of mean summer temperature ($F_{7,256} = 3.62$, $P < 0.03$). The proportion of surviving colonies was highest for four-foundress colonies at all sites and lowest for single-foundress colonies (Fig. 2). Higher colony survival was also associated with warmer temperatures at all colony sizes, but the influence of temperature on colony survival was most pronounced in the case of the single-female nests: correlation between site temperature and surviving number of foundresses was 0.88 for single-foundress nests, 0.71 for two-foundress nests and 0 .74 for four-foundress nests (Fig. 2).

Table 1. Summary data for *A. studiosus* colonies established with different numbers of foundresses (1, 2 or 4) at two field sites in eastern Tennessee (36° latitude) affording different temperature environments*

Site	Proportion of colonies surviving			Mean individual RS (all colonies)			Mean individual RS (surviving colonies)		
	1	2	4	1	2	4	1	2	4
Melton Hill, 15.6 °C	0.27	0.47	0.79	6.8	5.1	8.0	24.0	11.9	9.9
Abrams Creek, 24.1 °C	0.53	0.73	0.6	9.4	4.7	2.8	17.6	6.0	5.1

*Mean summer water temperature is given for each site.

There was no significant effect of foundress number (ANOVA: $F_{2,256} = 1.76$, $P < 0.15$) or temperature ($F_{7,256} = 1.69$, $P < 0.12$) on individual RS (including colony failures) and a negative but nonsignificant interaction between colony size and temperature ($F_{2,7} = 1.68$, $P < 0.06$) on individual RS. This interaction reflects the much higher reproductive success of single-foundress nests in high summer temperature environments (linear regression: $F_{7,84} = 12.85$, $P = 0.002$), a trend that was not observed in two- and four-foundress nests (Fig. 3).

The individual RS data available for surviving nests are presented in Fig. 4. Clearly, if a single-female nest survives, it is the strategy that provides the greatest fitness reward across all environmental temperatures. An ANOVA of individual RS of surviving colonies identified a significant effect of foundress number ($F_{2,187} = 53.8$, $P < 0.001$), a trend towards an effect of temperature ($F_{7,187} = 1.84$, $P < 0.1$), and a highly significant interaction between colony size and temperature ($F_{3,7} = 3.22$, $P < 0.001$). Again, the interaction effect was driven by the increase of RS with temperature in single-female colonies (Fig. 4).

Comparing Model Predictions to Natural Observations

At the initial census, multiple-female colonies at the two cold sites had 2–18 (CL) and 5–42 (MH) females. The relationship of estimated web volume to colony size (number of adult females) was highly significant ($R^2 = 0.88$, $P < 0.001$) and described by the relationship: web volume $(cm^3) = 2947x$, where x is the number of adult females. Solitary female nests at these cold sites had a survivorship of 52% (CL) and 44% (MH) compared to 80% and 100%, respectively, for nests in multifemale colonies. Of the eight multifemale nests lost at site CL, seven were two-female nests and the eighth was a three-female nest: all of the larger nests survived at CL, as was the case for MH, which had no two- and three-female nests included in the census.

The data from both sites were pooled to estimate the relationship of mean individual RS and colony size (Fig. 5). Overall mean RS per female increased from 7.1 for single females to 8.7 for two females and 13.7 for three females (filled circles, Fig. 5). Although the number of nests containing more than five females was small compared to the number of nests containing five of fewer adult females, the reproductive success of individuals in colonies containing fewer than 10 females was greater than that observed on average for solitary females (Fig. 5). However, the RS achieved by a female in colonies of 10 or more females was lower than that achieved by a solitary female (Fig. 5).

An exponential equation provided the best description of the relationship of individual RS (of surviving colonies) to colony size (Fig. 6). Essentially, RS was highest for single-female colonies and decreased in a curvilinear fashion with colony size. We calculated estimates of daily mortality risk (β) from the rate of single-female colony loss over the altricial period (because we were more certain of these rates than those for multiple-female colonies). Estimates of daily mortality were 0.0056 at cold sites and 0.0036 at warm sites. Estimates of durations of juvenile dependency (d) (calculated as the time from emergence to the presence of fourth-instar juveniles; Jones & Parker 2002) were 72.8 days at cold sites and 57 days at warm sites. The mean RS of single-female colonies was 11.1 at warm sites. The model predictions of individual RS in relation to colony size were higher for warm sites than for cold sites at a given colony size (Fig. 7). The model predicted the highest individual RS for colonies of three females. The predicted individual RS was lower for single-female nests than for multifemale nests containing 2–14 females at cold sites and 2–8 females at warm sites.

DISCUSSION

A survey of *A. studiosus* populations across 10° of latitude found a significant increase in the proportion of multiple-female colonies with latitude, with the highest proportion occurring at 36° in eastern Tennessee (Jones et al. 2007). The brood-fostering model described in that study hypothesized that multiple-female colonies in the north have a selective advantage by increasing the probability that at least one mother will survive in the colony to nurture the brood to independence. In our 2002 manipulation of colony size, four-foundress colonies had the highest individual RS at a cold-water site, and single-foundress colonies had the highest RS at the warmer Abram's Creek (Table 1). These results suggested that local environmental temperature variation associated with river impoundments in eastern Tennessee significantly affected the social structure of *A. studiosus*.

We, thus, expanded the experimental manipulation of colony size in the next year to eight sites along three river systems. These sites offered a greater range of temperature variation. Again individual RS varied with colony size in the same pattern as that observed in the two-locality test. Several of the brood-fostering model's predictions were
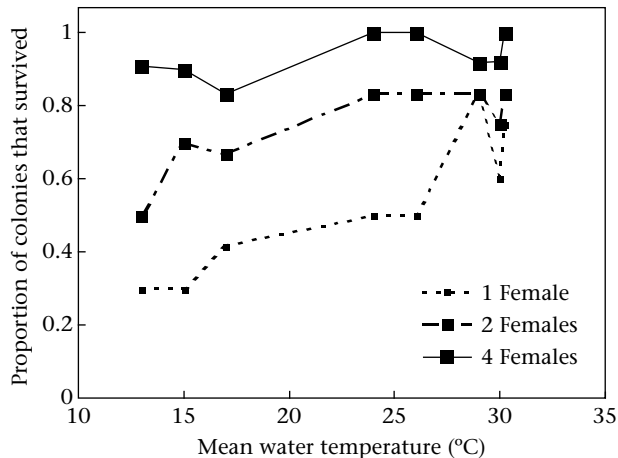
Figure 2. The proportion of surviving colonies by mean summer water temperature in the colony size manipulation experiment. Plotted are colonies of one, two and four founding mothers.

Figure 4. Means and SEs of individual reproductive success (RS) for surviving reconstituted colonies of one, two and four foundresses transplanted to the temperature environments.

confirmed by these results. Specifically, our finding that survivorship of colonies increased with foundress number at all sites (Fig. 2) suggests that the presence of multiple adults decreases the probability of complete brood failure. This is akin to Gadagkar's (1990) model of 'assured fitness returns' (see also Queller 1989), in which helper individuals reduce the likelihood of complete brood failure, assuring some RS through inclusive fitness (Hamilton 1964). In our model, however, a direct fitness benefit is expected: each mother is assured of some direct RS if she dies, because surviving mothers will foster her brood. This occurs because female *A. studiosus* do not discriminate egg clutch and juvenile kin from nonkin (Brach 1977; Furey 1998). Overall, these results support Avilés' (1999) hypothesis that sociality allows a species to expand its range or to survive in harsher environments.

Our brood-fostering model also predicts that individual RS will be higher for mothers in multiple-female colonies when a female has a high probability of dying before her brood has reached independence. This would be the case
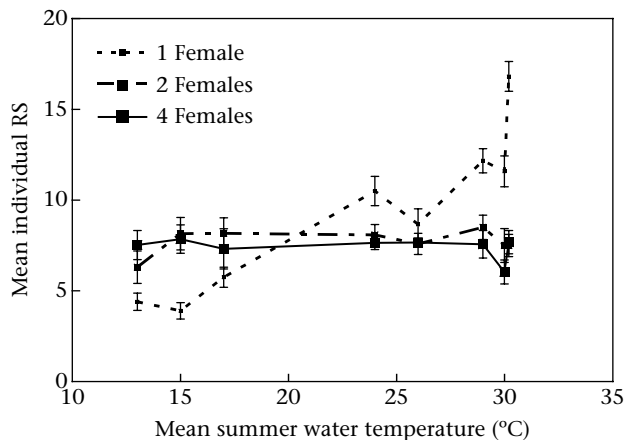
where colder local environments and latitudes slow brood development, an effect confirmed by laboratory experiments and by monitoring of brood development in the field (Jones et al. 2007). The results of our manipulative study did not discriminate a difference in mean RS between multifemale colonies of two versus four foundresses at warm or cold sites. It was clear, however that both classes of multifoundress nests produced a higher mean individual RS at cold sites than did the single-foundress nests, while the single-foundress nests produced significantly higher individual RS at warm sites (Fig. 3).

The brood-fostering model separates expected RS into two components based on whether the mother (1) survives the period of brood dependence or (2) dies before her brood is independent. The model is a type of bet-hedging strategy in a general sense, because a solitary female that survives the period of her brood's dependence

Figure 3. Means and SEs of individual reproductive success (RS) for reconstituted colonies of one, two and four foundresses transplanted to temperature environments.
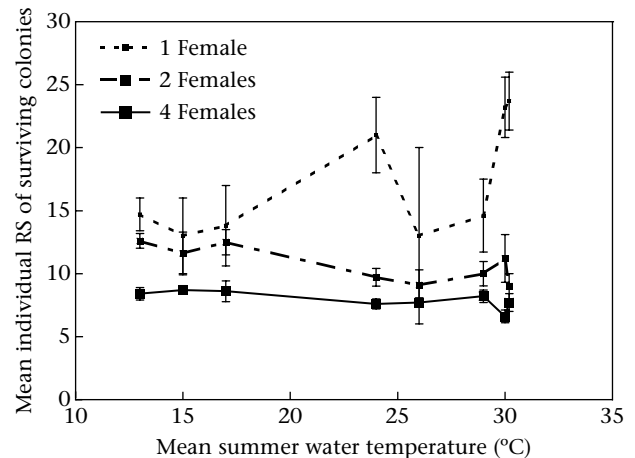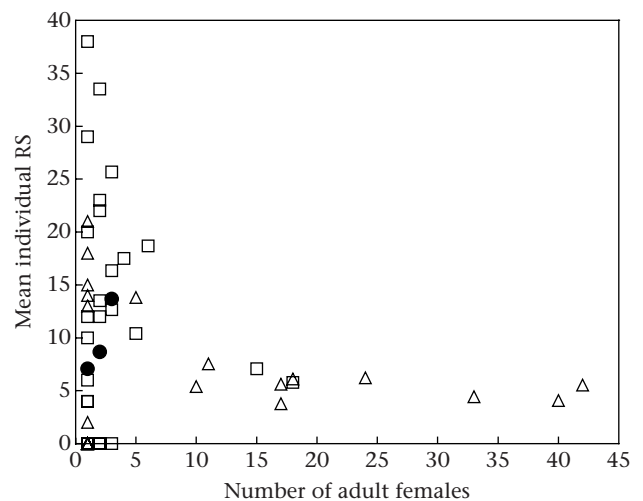

Figure 5. Mean individual reproductive success (RS) per nest for all colonies monitored at two cold-water sites: □: = Chilhowee Lake (CL); △: = Melton Hill (MH). ●: overall mean individual RS values for colonies with one, two and three adult females.
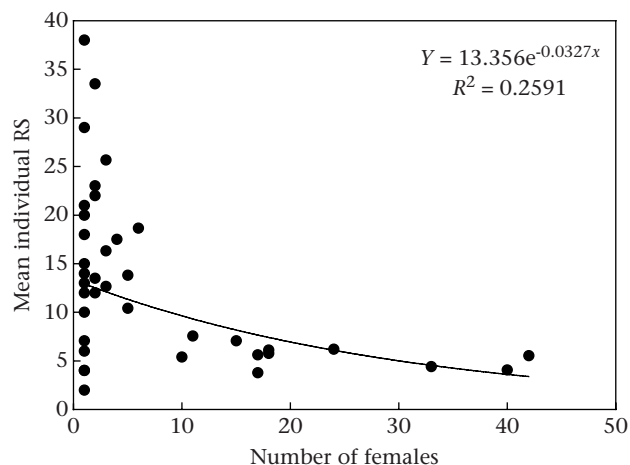
Figure 6. The observed mean individual reproductive success (RS) of mothers by colony size, in natural colonies that survived to collection. The best-fit exponential curve with its corresponding R^2 value is included.

would have the highest RS, but brooding females in multifemale colonies trade the possibility for maximum RS for a greater mean RS. We tested this prediction on the subset of nests from the experimental manipulations of colony size that survived to collection. We assumed that in these surviving colonies a mother must have lived long enough for her brood to become independent because previous work showed that all colonies whose mothers died (or disappeared) before juveniles reached the fourth instar were lost (Jones & Parker 2002). In this study, surviving single-foundress colonies had the highest RS at all sites, followed by two-, and then by four-foundress colonies (Fig. 4). The importance of factoring in complete colony failures to understanding the costs and benefits of social groups and solitaries is shown here. Similarly, in the sweat bee *Megalopta genalis*, Smith et al. (2007) found that surviving colonies showed a per capita decrease in RS with colony size that did not exist when nest failures were accounted for.

The reproductive success of individuals in natural *A. studiosus* colonies showed a pattern similar to that predicted by the brood-fostering model (Fig. 5). Average individual RS for colonies of two to six foundresses was higher than the average for single-foundress colonies. However, the individual RS achieved in the multifemale colonies above 10 foundresses fell off to below that of solitary females. The relationship of individual RS to colony size, for surviving colonies (Fig. 6), was generally similar to the pattern observed in the permanently social congener *A. eximius* (Avilés & Tufiño 1998).

When we refined the brood-fostering model presented in Jones et al. (2007) by replacing the parameter values borrowed from *A. eximius*, the predicted relationship of RS to colony size (Fig. 7) was similar to that of naturally occurring colonies (Fig. 6) and to that predicted in the original model (Jones et al. 2007). The experimental manipulations and natural observations confirm that there is a selective advantage to being in multiple-female colonies at cold sites in eastern Tennessee. There is a discrepancy, however, between the manipulative experiments

and the model predictions for warm sites. The model predicts that small multiple-female colonies at warm sites should have the selective advantage, but our experiments showed that single females had the highest RS (Fig. 7). This discrepancy probably reflects the fact that we did not know the actual (natural) relationship of individual RS to the number of foundresses for warm sites, where multiple-female colonies are rare, so we had to use estimated $RS_{N,surv}$ from the data collected at cold sites. Another difference between the model predictions for cold sites and the observed data was that the model predicted a higher RS for single-female colonies (8.6) than was actually observed (7.3). Conversely, the model predicted lower RS for single-female colonies at warm sites (10.5) than was actually observed (11.1). Again, these differences may be because we used the relation of RS to the number of foundresses curve generated from cool sites. However, as predicted by the model, the generated curves of RS for surviving colonies at warm versus cold sites showed that when RS in a multifemale colony dropped below that for a solitary female nest, the tipping point of the curve occurred at a lower colony size (7 females) at the warm-water sites than at the cold-water sites (13 females) (Fig. 7).

Social spiders and hymenopteran insects are two groups that seem particularly able to adapt, or facultatively adjust, their level of sociality to the environment. Although sociality is rare among spiders, the non-orb-web-building families are 'pre-adapted' for sociality in that social individuals mainly need to evolve conspecific tolerance, not novel behaviours (Krafft 1979). *Anelosimus eximius*, from tropical Central and South America, forms colonies of over 100 000 individuals. Purcell & Avilés (2007) found a pattern of decreasing colony size and increasing proportion of solitary individuals with increasing elevation. A similar pattern among other social *Anelosimus* species was also found in the region (Avilés et al. 2007). Costs and benefits of this behavioural shift remain to be quantified, but the shift does not appear to be a range-limit response, as overall density is not reduced at higher elevations (Purcell & Avilés 2007). Such a pattern of decreased sociality with cooler climate is theoretically predicted (Lin & Michener 1972) and it is most common among socially variable species (Schwarz et al. 1997; Wcislo 1997). In a phylogenetic analysis of ant species, Kaspari & Vargo (1995) found that colonies are an order of magnitude larger in temperate regions than in the tropics. They suggested that these colonies are superorganisms following Bergmann's rule, with larger organisms being found at higher latitudes. Cronin & Schwarz (2001) suggested that the increased proportion of multiple-reproductive (quasisocial) colonies in the allodapine bee *Exoneura robusta* in cooler climates is related to slower brood development, resulting in a single brooding opportunity. In warmer climates, this species can produce second broods and is typically eusocial. This case is the most similar to the pattern that we observed in *A. studiosus*.

Although our results suggest that there is an advantage to multiple-female colonies of *A. studiosus* at cold sites, one major discrepancy remains: even at these cold sites, solitary female nests are numerically prominent (Jones et al. 2007). Assuming that social structure is heritable
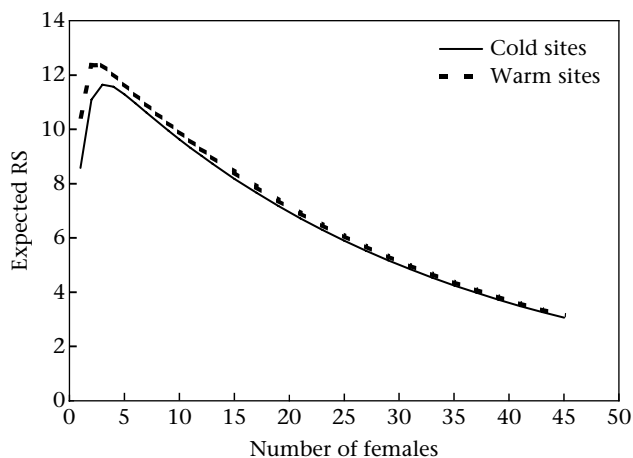
Figure 7. Brood-fostering model predictions of reproductive success (RS) by colony size, refined by parameter values obtained from monitoring natural colonies: relation between individual RS and colony size when the mother survives the period of brood dependency, $RS_{N,surv}$ (for colonies of all sizes) and the daily mortality risk to females, β (for solitary females). Curves for cold- and warm-water sites are plotted separately. Field and laboratory data for the period of juvenile dependency (d) in cold versus warm sites are from Jones et al. (2007).

(and evidence suggests that it is: Riechert & Jones 2008), why are multiple-female colonies not dominant at cold sites? We have several nonexclusive hypotheses that could explain the polyphenism. One possibility is that these populations are currently in flux and evolving towards higher levels of sociality. A tantalizing bit of circumstantial evidence supporting this is that the dams that create most of the habitat for *A. studiosus* at our study sites (large lakes, and consistently cool tail waters) were built during 1918–1979, a very brief period in an evolutionary framework. Another possibility is that significant gene flow occurs from warm-adapted populations to cold-adapted populations, preventing complete local adaptation. However, some evidence suggests that gene flow may not largely contribute to social structure because dispersal distances in *A. studiosus* (Riechert & Jones 2008) and in a related subsocial spider, *A. jucundus* (Powers & Avilés 2003), range only from centimetres to a few metres. We are currently using microsatellites to analyse gene flow in populations of *A. studiosus*. Yet another possibility is that the mix of multiple- and single-female colonies at cold sites is a response to annual variation in climate. It could be that, in colder years, multiple-female colonies have the selective advantage, but in warmer years, the balance tips towards single-female colonies, leaving the population to chase the optimal phenotype. Long-term studies of colony fitness and climate are warranted to examine this hypothesis. A final hypothesis is that there may be a balanced polyphenism. The fostering model predicts that small colonies can have higher fitness than single females, but that fitness of multifemale colonies will drop below that of solitary females at larger colony sizes (Fig. 7). Riechert & Jones (2008) present data that suggest that the level of tolerance/attraction among adult females is a quantitative trait. It can be imagined that the advantage to small

colonies would lead to an increase in the frequencies of tolerant alleles and a corresponding increase in colony size. As the frequencies of tolerant alleles increases, however, colonies could grow to the point where their fitness drops below that of solitary females, and the tolerant allele frequencies would decrease. The effect would be to balance tolerant and intolerant alleles, but recombination could lead to a stable polymorphism of colony sizes (including maladapted colony sizes). To explore this hypothesis we need to better understand the heritability of social behaviour, as well as to further refine the relationship of colony size to fitness.

Anelosimus studiosus is unusual in its level of variation in social structure. The experimental and observational data presented here support the brood-fostering hypothesis, but have led to many unanswered questions. This system is highly tractable, and future research should be able to work out the details and mechanisms underlying the social structure.

References

Avilés, L. 1997. Causes and consequences of cooperation and permanent-sociality in spiders. In: *Evolution of Social Behaviour in Insects and Arachnids* (Ed. by J. Choe & B. Crespi), pp. 476–498. Cambridge, Massachusetts: Cambridge University Press.

Avilés, L. 1999. Cooperation and non-linear dynamics: an ecological perspective on the evolution of sociality. *Evolutionary Ecology Research*, **1**, 459–477.

Avilés, L. & Tufiño, P. 1998. Colony size and individual fitness in the social spider *Anelosimus eximius*. *American Naturalist*, **152**, 403–418.

Avilés, L., Agnarsson, I., Salazar, P. A., Purcell, J., Iturralde, G., Yip, E. C., Powers, K. S. & Bukowski, T. C. 2007. Altitudinal patterns of sociality and the biology of a new midelevation social *Anelosimus* species in Ecuador. *American Naturalist*, **170**, 783–792.

Bahn, V., O'Connor, R. J. & Krohn, W. B. 2006. Effect of dispersal at range edges on the structure of species ranges. *Oikos*, **115**, 89–96.

Blackburn, T. M., Gaston, K. J. & Loder, N. 1999. Geographic gradients in body size: a clarification of Bergmann's rule. *Diversity and Distributions*, **5**, 165–174.

Brach, V. 1977. *Anelosimus studiosus* (Araneae: Theridiidae) and the evolution of quasisociality in theridiid spiders. *Evolution*, **31**, 154–161.

Buskirk, R. E. 1981. Sociality in the Arachnida. In: *Social Insects. Vol. 2* (Ed. by H. R. Hermann), pp. 281–367. New York: Academic Press.

Cronin, A. L. 2001. Social flexibility in a primitively social allodapine bee (Hymenoptera Apidae): results of translocation experiment. *Oikos*, **94**, 337–343.

Cronin, A. L. & Schwarz, M. P. 2001. Latitudinal variation in the sociality of allodapine bees (Hymenoptera: Apidae): sex ratios, relatedness and reproductive differentiation. *Australian Journal of Zoology*, **49**, 1–16.

Eickwort, G. C., Eickwort, J. M., Gordon, J. & Eickwort, M. A. 1996. Solitary behavior in a high-altitude population of the social sweat bee *Halictus rubicundus* (Hymenoptera: Halictidae). *Behavioral Ecology and Sociobiology*, **38**, 227–233.

Field, J., Shreeves, G., Sumner, S. & Casiraghi, M. 2000. Insurance-based advantage to helpers in a tropical hover wasp. *Nature*, **404**, 869–871.

Furey, R. E. 1998. Two cooperatively social populations of the theridiid spider *Anelosimus studiosus* in a temperate region. *Animal Behaviour*, **55**, 727–735.

Gadagkar, R. 1990. Evolution of eusociality: the advantage of assured fitness returns. *Philosophical Transactions of the Royal Society of London, Series B*, **329**, 17–25.

Hamilton, W. D. 1964. The genetical evolution of social behavior I and II. *Journal of Theoretical Biology*, **7**, 1–52.

Holt, R. D. & Keitt, T. H. 2005. Species' border: a unifying theme in ecology. *Oikos*, **108**, 3–6.

Jones, T. C. & Parker, P. G. 2000. Costs and benefits of foraging associated with delayed dispersal in the spider *Anelosimus studiosus* (Araneae: Theridiidae). *Journal of Arachnology*, **28**, 61–69.

Jones, T. C. & Parker, P. G. 2002. Delayed juvenile dispersal benefits both mother an offspring in the cooperative spider *Anelosimus studiosus* (Araneae: Theridiidae). *Behavioral Ecology*, **13**, 142–148.

Jones, T. C., Riechert, S. E., Dalrymple, S. E. & Parker, P. G. 2007. Fostering model explains environmental variation in levels of sociality in a spider system. *Animal Behaviour*, **73**, 195–204.

Kaspari, M. & Vargo, E. L. 1995. Colony size as a buffer against seasonality: Bergmann's rule in social insects. *American Naturalist*, **145**, 610–632.

Kirkpatrick, M. & Barton, N. H. 1997. Evolution of a species' range. *American Naturalist*, **150**, 1–13.

Krafft, B. 1979. Organisation et e'volution des sociétiés d'araignées. *Psychology*, **1**, 23–51.

Lin, N. & Michener, C. D. 1972. Evolution of sociality in insects. *Quarterly Review of Biology*, **47**, 131–159.

Powers, K. S. & Avilés, L. 2003. Natal dispersal patterns of a subsocial spider *Anelosimus* c.f. *jucundus* (Theridiidae). *Ethology*, **109**, 725–737.

Pruitt, J. N., Riechert, S. E. & Jones, T. C. 2008. Behavioural syndromes and their fitness consequences in a socially polymorphic spider, *Anelosimus studiosus*. *Animal Behaviour*, **76**, 871–879.

Purcell, J. & Avilés, L. 2007. Smaller colonies and more solitary living mark higher elevation populations of a social spider. *Journal of Animal Ecology*, **76**, 590–597.

Queller, D. C. 1989. The evolution of eusociality: reproductive head starts of workers. *Proceedings of the National Academy of Sciences, U.S.A.* **86**, 3224–3226.

Reeve, H. K. 1991. Polistes. In: *The Social Biology of Wasps* (Ed. by K. G. Ross & R. W. Mathews), pp. 99–148. Ithaca, New York: Cornell University Press.

Richards, M. H. & Packer, L. 1995. Annual variation in survival and reproduction of the primitively eusocial sweat bee *Halictus ligatus* (Hymenoptera-Halictidae). *Canadian Journal of Zoology*, **7**, 933–941.

Riechert, S. E. & Jones, T. C. 2008. Phenotypic variation in the social behaviour of the spider *Anelosimus studiosus* along a latitudinal gradient. *Animal Behaviour*, **75**, 1893–1902.

Riechert, S. E. & Roeloffs, R. M. 1993. Inbreeding and its consequences in the social spiders. In: *The Natural History of Inbreeding and Outbreeding* (Ed. by N. Thornhill), pp. 283–303. Chicago: University of Chicago Press.

Riechert, S. E., Singer, F. D. & Jones, T. C. 2001. High gene flow levels lead to gamete wastage in a desert spider system. *Genetica*, **112–113**, 297–313.

Schwarz, M. P., Silberbauer, L. X. & Hurst, P. S. 1997. Intrinsic and extrinsic factors associated with social evolution in allodapine bees. In: *Evolution of Social Behaviour in Insects and Arachnids* (Ed. by J. Choe & B. Crespi), pp. 333–346. Cambridge, Massachusetts: Cambridge University Press.

Smith, A. R., Wcislo, W. T. & O'Donnell, S. 2003. Assured fitness returns favor sociality in a mass-provisioning sweat bee, *Megalopta genalis* (Hymenoptera: Halictidae). *Behavioral Ecology and Sociobiology*, **54**, 14–21.

Smith, A. R., Wcislo, W. T. & O'Donnell, S. 2007. Survival and productivity benefits to social nesting in the sweat bee, *Megalopta genalis* (Hymenoptera: Halictidae). *Behavioral Ecology and Sociobiology*, **61**, 1111–1120.

Soucy, S. L. & Danforth, B. N. 2002. Phylogeography of the socially polymorphic sweat bee *Halictus rubicundus* (Hymenoptera: Halictidae). *Evolution*, **56**, 330–341.

Strassman, J. E. & Queller, D. C. 1989. Ecological determinants of social evolution. In: *The Genetics of Social Evolution* (Ed. by M. D. Breed & R. E. Page Jr), pp. 81–101. Boulder, Colorado: Westview Press.

Wcislo, W. T. 1997. Behavioral environments of sweat bees (Halictinae) in relation to variability in social organization. In: *Evolution of Social Behaviour in Insects and Arachnids* (Ed. by J. Choe & B. Crespi), pp. 316–332. Cambridge, Massachusetts: Cambridge University Press.

Whitehouse, E. A. & Lubin, Y. 2005. The functions of societies and the evolution of group living: spider societies as a test case. *Biological Reviews of the Cambridge Philosophical Society*, **80**, 347–361.

Wilson, E. O. 1975. *Sociobiology*. Cambridge, Massachusetts: Belknap/Harvard University Press.