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Fostering model explains variation in levels of sociality in a spider system

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We developed an 'assured fitness returns' model for the evolution of sociality independent of high relatedness within colonies. We first developed this model based on parameters from the northern social spider *Anelosimus studiosus*, which shows a higher incidence of multiple-female colonies caring for a common brood at higher latitudes and colder conditions within latitudes. The mathematical model developed predicts that multiple females will cooperatively care for a brood in those environments in which a single female has a high probability of dying before her offspring are able to care for themselves. The frequency of multiple-female nests observed in variable temperature sites in eastern Tennessee, U.S.A., is consistent with that found in our latitudinal censuses: a higher frequency of multiple-female colonies was present at cold-water sites than at warm-water sites. A test of a critical model assumption found a positive correlation of temperature and juvenile development rate in both the field and the laboratory. Colony success in field studies was also consistent with model predictions.

The existence of multiple-female colonies at higher latitudes in the northern social spider *Anelosimus studiosus* (Hentz) (Araneae, Theridiidae) is the reverse of the general pattern identified for social spiders. *Anelosimus eximius* (Keyserling) and the other cooperatively social spiders are strictly tropical in distribution (Buskirk 1981; Riechert & Roeloffs 1993; Avilés 1997), fitting Wilson's (1975) hypothesis that sociality in arthropods first evolved in the tropics with secondary spread into temperate areas. His argument is that continuous colony function in the tropics permits the evolution of cooperative behaviour with the minimum number of adaptive modifications (see also Lin & Michener 1972). The haplodiploid social hymenopterans typically show this predicted clinal

pattern (e.g. *Polistes* wasps: Reeve 1991; European halictid bee, *Lasioglossum malachurum*: Richards 2000). Social behaviour in spiders, which have a diploid mechanism of inheritance, is less well developed than in insects. As in the insects, more social spider species are found in the tropics where there is reduced seasonality and a more constant associated prey supply (e.g. Buskirk 1981; Riechert et al. 1986; Avilés 1997).

However, it is difficult to make this type of generalization about the mechanisms underlying arthropod sociality, because the ecogeographical patterns observed for those social insects subjected to clinal studies are complex (Tschinkel 1991). Apparent reverse clines in the level of sociality have been reported for ants (Kaspari & Vargo 1995; Blackburn et al. 1999), for the North American bee, *Halictus ligatus* (Richards & Packer 1995) and among bees of the genus *Exoneura* (Cronin & Schwarz 2001). In these systems, higher levels of sociality are associated with harsher environmental conditions at higher latitudes (see also Cronin 2001).

Avilés (1997), Uetz & Hieber (1997) and Whitehouse & Lubin (2005) present recent reviews of our understanding of the evolution of sociality in spiders. Briefly, very few

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spiders are social (approximately 50 of the over 39 000 described species; Whitehouse & Lubin 2005). Most, but not all, social species are web builders, which belong to one of two classes: colonial and cooperative. In the colonial species, individuals share a supportive web structure but compete for web placement within this structure (Uetz & Hieber 1997). In the cooperative species ('cooperatively social': Riechert 1985), multiple adult females, males and juveniles maintain a common web and show cooperative prey capture and brood care. In the cooperative spider species there is often a distinct female bias: Avilés & Maddison (1991) found this female bias to be at the primary level in *Anelosimus eximius* and *Anelosimus domingo*. Cooperative social behaviour is believed to have evolved independently 12 or 13 times among seven spider families, and most species within genera containing social species are asocial (Avilés 1997).

Test System

Anelosimus studiosus has a broad distribution that ranges from Argentina in South America to New England in North America (Levi 1956). Although *A. studiosus* colonies that contain multiple, cooperating adult females have recently been discovered (Furey 1998), this species was initially described as one that simply showed maternal care (Brach 1977). Brach (1977) described an *A. studiosus* colony as being composed of one adult female, her juvenile offspring and possibly a few unrelated adult males that do not participate in web maintenance or communal prey capture. The mother guards her egg case and feeds newly emerged spiderlings through regurgitation. As the juveniles grow, they increasingly participate in web maintenance and prey capture. During this time, the mother accepts the entry of foreign juveniles and males into the nest but drives intruding adult females off. Brach (1977) considered *A. studiosus* colonies to be ephemeral because the brood disperses on reaching maturity and the mother often dies before this dispersal occurs. Males mature before females and abandon the home nest in search of mates. As the females of the brood mature, they are actively driven off by the mother, or a single dominant female offspring that subsequently uses this nest to rear her own brood.

The above description of *A. studiosus* colony structure is based on work with populations in southern Florida, U.S.A. (27°N) (Brach 1977), and southern Florida (26°N) and Louisiana, U.S.A. (30°N) (Jones & Parker 2000, 2002). However, Furey (1998) reported the existence of variable colony structure in *A. studiosus* in eastern Tennessee (36°N). Although the prominent nest type in the two populations he studied consisted of a single female and her offspring, multiple-female colonies were sufficiently abundant to result in an overall mean number of 3.7 females/colony. In Furey's (1998) study, he also provided evidence for cooperative foraging, group maintenance of the web, indiscriminate brood care and limited dispersal for nests containing multiple females and their broods. Such activities are characteristic of the cooperatively social/communal spider species studied to date (e.g. the

A. studiosus congener, *A. eximius*: Vollrath 1982; Pasquet & Krafft 1992; Avilés & Tufiño 1998).

The Problem: Clinal Variation

Brood-fostering models

We explored the variation in social strategies of *A. studiosus* and developed a model that explains the greater incidence of cooperative brooding under colder environments (i.e. with increasing latitude and colder water river systems within a given latitude). We also experimentally tested a critical assumption of the model: that temperature affects juvenile development rate. One potential advantage to social spiders is that offspring have multiple caregivers (Christenson 1984; Avilés 1993). Strassmann & Queller (1989) noted that if all adults die around the time of colony founding in social hymenoptera, then the colony will be lost, and there is less chance of all founders dying if there is a high number of initial founding females. Gadagkar (1990) developed a model that explored the conditions under which it would benefit an individual wasp to forgo founding a colony of her own to join and help another foundress. This model was based on the assumption that helpers have little or no direct reproductive success. It required high levels of relatedness among foundresses, as facilitated by haplodiploidy. Reeve (1991) developed a survivorship insurance model for *Polistes* wasps that incorporated the observation that the proportion of multiple-foundress colonies is directly related to the proportion of single-foundress nest failures. Using empirical demographic data, he was able to estimate how the time interval within a breeding season and the relatedness among foundresses affect an individual's decision to nest singly or to join an established nest as a helper. Field et al. (2000) tested and found support for this type of 'survivorship return' model in tropical hover wasps, *Liostenogaster flovolineata*.

We extended the models developed for wasps to explain variation in the number of females constituting colonies in a social spider system. Our model deviates from those developed for the social insects in that: (1) there is no division of labour among colony foundresses; (2) the spider system is diploid rather than haplodiploid; and (3) foundresses are assumed to be unrelated (although relatedness may affect the model's predictions).

Fostering hypothesis

The brood-fostering hypothesis is based on the fact that young *A. studiosus* are dependent on the mother for food and protection for an extended period (termed the 'altricial period' here for simplicity) (Jones & Parker 2000, 2002). We assume that if the mother in a single-female colony dies before her brood has passed the critical altricial period for a given environment, her fitness will be 0 because the brood will die as well. On the other hand, if a mother in a multiple-female colony dies, the surviving females will foster the deceased female's brood. We assume that the altricial period of young *A. studiosus* is longer at higher latitudes and in colder environments, explaining the fact that the incidence of multiple-female colonies is

higher under these conditions. Alternatively, it is possible that the probability of a mother dying before the altricial period has passed might change with latitude and environmental conditions, regardless of the length of the altricial period (e.g. there may be a higher predation risk at higher latitudes).

Fostering model

In quantifying the fostering hypothesis, an individual mother's expected reproductive success (RS) for a given colony size (N = number of adult females present), is divided into two parts: (1) the RS that a female can expect if she survives through her offspring's altricial period ($RS_{N,\text{surv}}$); and (2) the RS that a female can expect if she does not survive through her offspring's altricial period ($RS_{N,\text{die}}$). Each of these values is multiplied by its probability of occurrence, and the sum of these products represents a mother's total expected reproductive success for a given colony size ($RS_{N,\text{Total}}$). We based some of our parameters on those found for a related species (described in more detail below). A mother's probability of surviving her offspring's altricial period is related to the daily mortality risk (β) and the duration of the altricial period in days (d) by the equation:

$$\text{Probability of survival} = (1 - \beta)^d. \tag{1}$$

Thus, the equation for a mother's expected total reproductive success is:

$$RS_{N,\text{Total}} = (1 - \beta)^d \times (RS_{N,\text{surv}}) + \left(1 - (1 - \beta)^d\right) \times (RS_{N,\text{die}}) \tag{2}$$

where

$$RS_{N,\text{surv}} = 25N^{-0.6} \tag{3}$$

and

$$RS_{N,\text{die}} = (RS_{N,\text{surv}}) \times \left(1 - \left(1 - (1 - \beta)^d\right)^{(N-1)}\right). \tag{4}$$

We used the relation in equation (2) to explore quantitatively the reproductive success that individual females might experience in contexts that include variation in the number of breeding females present, the duration of juvenile dependency and the daily risk of mortality. We solved the equation recursively under a range of colony sizes (1–10 adult females), daily mortality risks (0.01–0.1) and altricial period lengths (10–30 days). These values were chosen to elucidate qualitative patterns and are not based on statistical distributions from observed data. For simplicity, β and d are assumed to be unaffected by colony size.

The general relations between the two components of reproductive success and colony size are presented in Fig. 1. If the mother survives the altricial period of her young (solid line in Fig. 1, equation (3)), her reproductive success is depicted as an exponentially decreasing function of colony size similar to that observed for fecundity in *A. eximius* (Avilés & Tufiño 1998). RS decreases because of competition among females.
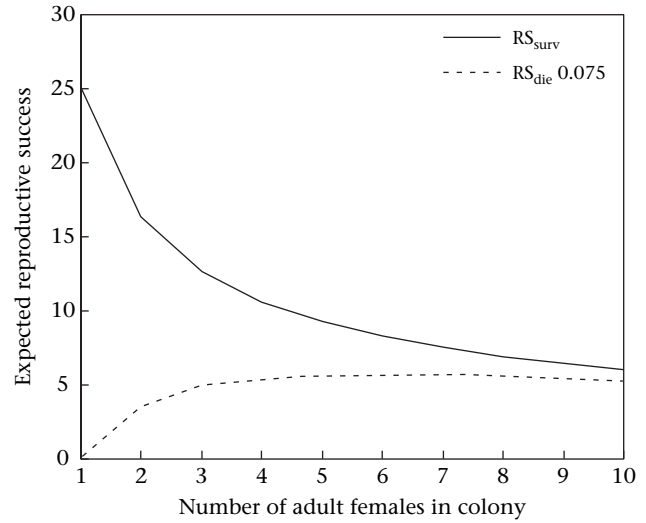

Figure 1. An example of the relation between the number of *A. studiosus* females in a colony and expected individual reproductive success for a female in the event that she survives or dies during the period of brood dependency (altricial period). The lower curve in this example was calculated at $\beta = 0.075$ and $d = 20$.

The lower curve shown in Fig. 1 (dashed line, equation (4)) describes the relation between the RS of a female that dies before her offspring reach independence and colony size. It was derived by multiplying the value of the upper curve (at each colony size) by the probability that at least one adult female survives the altricial period. Separate lower curves were calculated for each value of β and d (equation (4)). The curve begins at zero for an initial colony size of one because there are no other females to foster the brood and, thus, the entire brood fails. It approaches the upper curve depicting RS for a surviving female as the numbers of females present in a colony increases. This is because the model assumes that there is an increasing probability that at least one other female will survive to foster the brood through the altricial period.

METHODS

Field Observations of Colony Structure

We assessed latitudinal variation in *A. studiosus* colony structure by measuring and collecting webs from two sites at each of three latitudes, which encompassed the majority of this species' range in the eastern U.S.A. We completed the sampling in September 2000 at locations offering dense populations of *A. studiosus*. Northern sites in eastern Tennessee were Bull Run Creek (36°00′N, 84°08′W) and the French Broad River below Douglas Dam (35°56′N, 85°59′W). Mid-range sites in northern Florida were the Appalachicola River below Seminole Lake (30°40′N, 84°50′W) and the Ochlocknee River (30°15′N, 84°40′W). Southern sites in the Florida everglades were canals along State Road 41 (25°45′N, 80°50′W) and State Road 29 (26°05′N, 81°20′W). Perhaps because of the increased prey requirements

associated with cooperation, *A. studiosus* colonies are found most commonly near water. This association with bodies of water effectively linearizes populations along shorelines.

We measured each nest in situ by taking the three orthogonal dimensions to the nearest centimetre, with the first measurement being the maximum linear dimension of the colony. As sampling proceeded, we removed each fourth colony for later dissection. Web volumes were estimated as the product of the height, width and depth of the colonies (after Riechert et al. 1986). Furey (1998) previously demonstrated that web volume provides a good estimate of adult female number/colony size (N) in *A. studiosus*. We further obtained detailed information on nest composition (numbers and developmental stages) from the nest dissections.

In addition to the latitudinal censuses, we completed a more extensive survey of variation in colony structure within the northernmost latitude in Tennessee (36°). Flood control mechanisms along river systems in eastern Tennessee create stable variation in water temperature. The microhabitats directly below dams are, on average, cooler because of the cold water flowing through from the bottom of the lake above (mean summer water temperature difference above and below dams in this study was 10.8°C). We selected a 1-km-long transect of dense *A. studiosus* colonies at each of seven sites on the Little Tennessee River system and recorded water temperature at the beginning, middle and end of each transect. We completed colony size assessments at these sites (as described above) in June 2002, when females were producing egg cases.

Tests of Effects of Temperature on Development Rate

We used field measurements and laboratory and field experiments to test the critical model assumption that cooler temperatures lead to slower juvenile development. We collected brooding female *A. studiosus* from Collier-Seminole State Park Ochopee, Florida, U.S.A. (26°N latitude) in January 2005 for use in a controlled-temperature laboratory-rearing test. We isolated the females with their egg cases in 1-pint (0.51-litre) clear plastic containers with minimal substrate, and maintained them at ambient room temperatures until the juveniles emerged from the egg cases. We placed alternate hatched broods with moms in one of two temperature treatments: 27°C or 22°C. The temperatures used in the experiment reflected average cold water and warm water temperature differences for eastern Tennessee sites in the summer. Humidity and a 12:12 h light:dark cycle were standardized between the Conviron Environmental Chambers, and the spiders were watered and fed pinhead crickets, *Gryllus* sp. and termites, *Reticulitermes* sp., ad libitum twice weekly. We censused each colony weekly, recording the numbers and instars of juveniles and numbers of exuvia in the web. We then removed all exuvia, dead prey and dead spiders.

To assess the effect of temperature on juvenile development rate in natural colonies we conducted weekly surveys of juvenile growth at two warm-water sites (Ish Creek and I.C. King Park) and two cool-water sites (Melton Hill and Chilhowee Lake) in eastern Tennessee (26°N latitude). Water temperature was recorded weekly at each site, and temperature sensors, positioned at each site, recorded daily high and low air temperatures in the vicinity of the *A. studiosus* nests. We marked 20 webs with single brooding females at each of these sites and surveyed juvenile growth in these webs each week for 8 weeks following the emergence of spiderlings. Each colony was then collected and dissected as described for the latitudinal surveys.

RESULTS

Model Predictions

Over the range of parameter values we used, the expected individual reproductive success (RS) decreases as the duration of the altricial period (d) increases (Fig. 2a–d). RS also decreases as the daily mortality risk increases within a particular altricial period (Fig. 2a–d). A single female achieves a high RS at lower risks of mortality (i.e. $\beta = 0.01$). When daily risk of mortality is high ($\beta = 0.05$ or above), a single female achieves a high RS only in the case of a very short altricial period (Fig. 2b–d). Multiple-female colonies are favoured for higher values of daily risk of mortality and longer altricial periods, and the predicted optimal group size increases as a function of these two parameters (Fig. 2c, d). The relatively low optimal group sizes reflect the parameters used, but have yet to be estimated empirically.

Field Observation of Colony Structure

There was a highly significant effect of latitude on colony volume ($R^2 = 0.15$, $P < 0.001$), with mean volume increasing with latitude (26°N: 135 cm^3, $N = 203$ nests; 31°N: 165 cm^3, $N = 234$ nests; 36°N: 202 cm^3, $N = 346$ nests). For all latitudes the majority of colonies were single-female colonies ranging in volume from 100 to 250 cm^3 (mode = 150–200 cm^3; Fig. 3). The frequency of multiple-female colonies differed between sites (26°N: 0.00; 31°N: 0.06; 36°N: 0.21). Colony volume was directly related to the number of adult females within each colony, and will be explored in depth elsewhere.

Colony size determinations made at seven sites along the Little Tennessee River system in eastern Tennessee demonstrate the influence of temperature environment on the incidence of multiple-female colonies at 36°N latitude. There was a significant negative correlation between mean water temperature and mean nest volume ($R^2 = 0.88$, $F_{1,5} = 43.8$, $P = 0.0012$; Fig. 4). While the single-female colony was the prominent social strategy at all sites, there was increased variation in nest volume as site water temperature decreased (regression of standard deviation in nest volume on water temperature: $R^2 = 0.94$, $F_{1,5} = 80.4$, $P = 0.0002$). This finding reflects the fact that larger nests containing multiple adult females
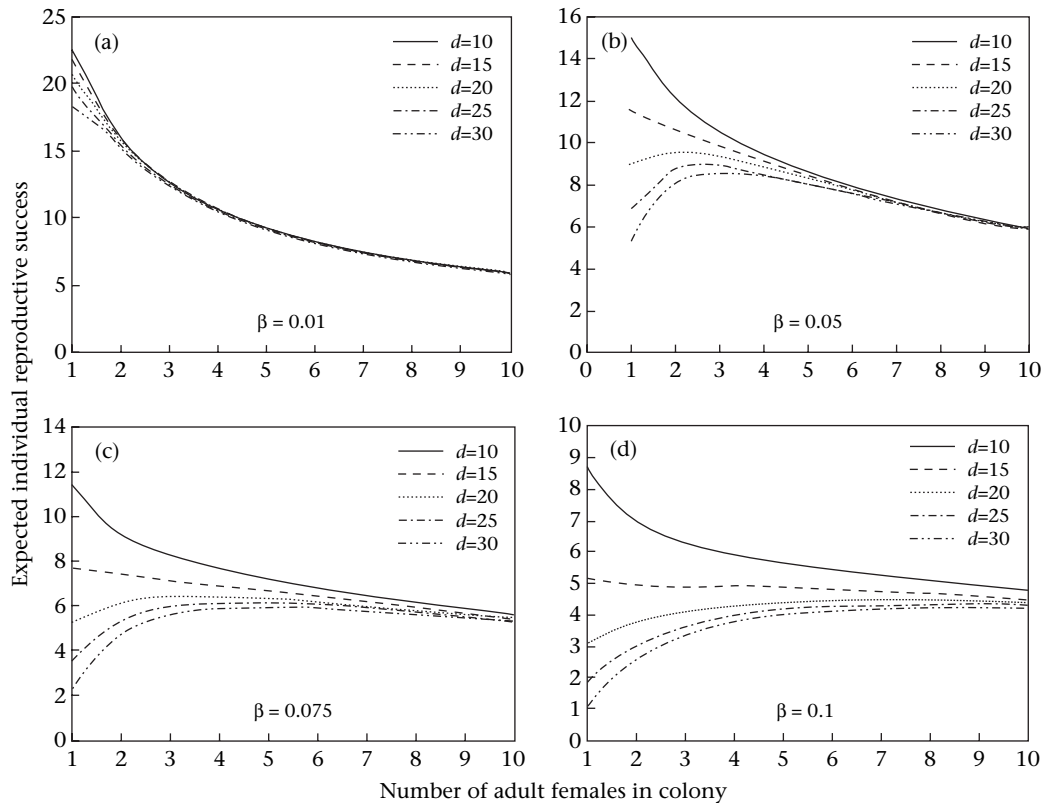
Figure 2. Expected individual reproductive success of female *A. studiosus* as a combined function of the number of females present and the length of the brood altricial period (d) for four daily mortality risks (β).

increased in frequency with decreasing water temperature (Fig. 5).

The density of spider colonies (colonies/km) was significantly related to water temperature as well ($R^2 = 0.90$, $F_{1,5} = 57.9$, $P < 0.0006$; Fig. 4): nest densities were lower at colder sites than at warmer sites (overall range of densities was 7.9–47.1 colonies/km). We used Furey's (1998) regression relationship between web volume and number of adult spiders to estimate the number of adult females/km at each site. The total number of spiders/km increased significantly with water temperature ($R^2 = 0.86$, $F_{1,5} = 39.3$, $P = 0.0015$). Thus, the cold-water sites had both fewer colonies and lower population sizes despite the greater frequency of colonies with multiple females at these sites.

Effect of Temperature on Development

In the laboratory-rearing experiment we estimated the length of the altricial period (in days) from emergence from the egg sac to the day that the majority of individuals within a colony reached the fourth instar. This is a biologically relevant measure because it is the stage at which juveniles are independent and capable of surviving on their own (Jones & Parker 2000, 2002). Mean times for juveniles to reach independence at 22°C (45.4 days) and at 27°C (28.7 days) were significantly different ($F_{1,21} = 22.3$, $P < 0.001$). A similar pattern was observed in the natural colonies. In this case, the colonies were dissected 8 weeks after young emerged from the egg sac, and

instar stages were recorded and averaged for each colony. Average instar stage was significantly higher for colonies at the warmer water sites ($F_{1,43} = 8.8$, $P = 0.005$; Fig. 6). There was also a significant increase in the average number of surviving juveniles at 8 weeks within colonies at the warmer sites ($F_{1,57} = 6.8$, $P = 0.011$; Fig. 7). This effect was driven by the fact that more broods/colonies failed at cooler sites. The effect disappeared when we included in the analysis only those colonies that survived until collection ($F_{1,43} = 1.2$, $P = 0.28$; Fig. 7). In the chamber experiments, there was no significant effect of temperature on juvenile survivorship ($F_{1,43} = 0.41$, $P = 0.52$).

DISCUSSION

Field censuses of *A. studiosus* populations confirm Furey's (1998) observation of the presence of multiple-female colonies in Tennessee, although the prominent social strategy at all three latitudes was the single-female nest. Census results further demonstrated that mean web volume increased with latitude when all nests were included, but not when the analysis was limited to nests occupied by single females. Thus, the increase in mean web volume with increasing latitude reflects the low frequency of multiple-female colonies in northern Florida (30°N) and the higher frequency of multiple-female colonies at Tennessee sites (36°N); no multiple-female colonies were found at sites in south Florida (26°N).
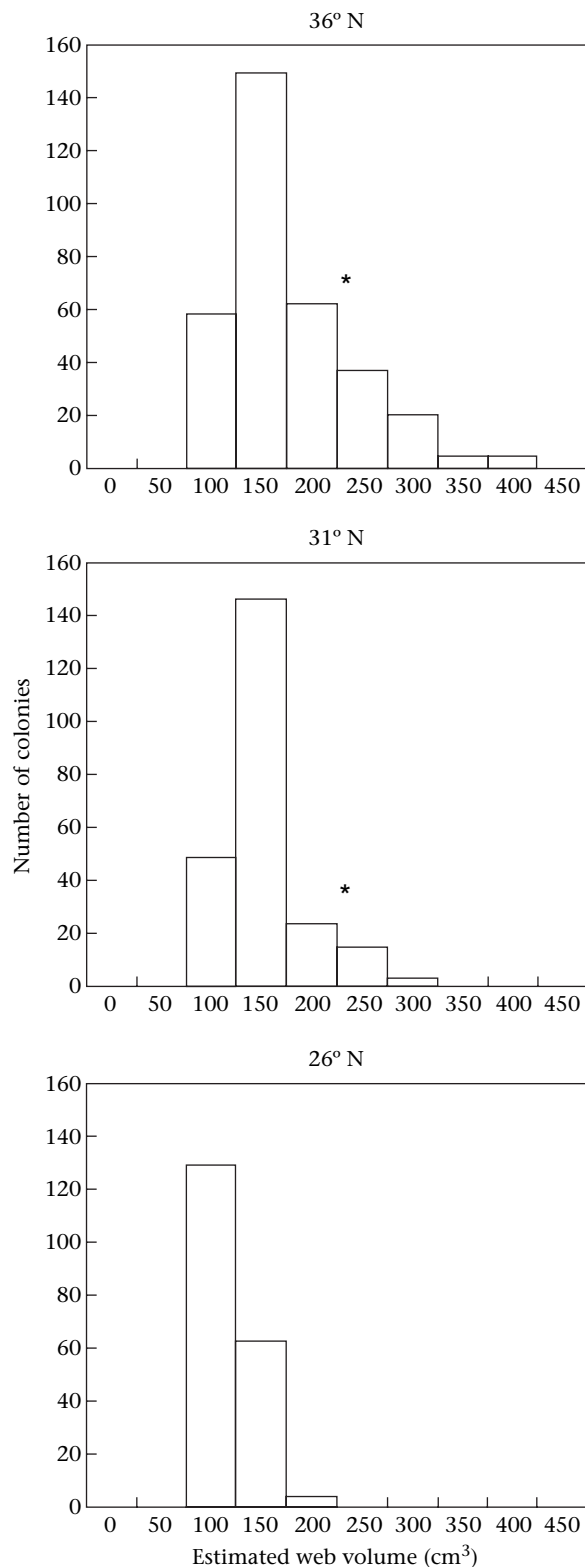
Figure 3. Numbers of *A. studiosus* colonies plotted by colony volume for three latitudes ranging from southern Florida to eastern Tennessee, U.S.A. The asterisks indicate the colony volume above which the colonies contain multiple females.

The challenge to our fostering model is to explain this apparent 'reverse cline' in sociality, by defining conditions that could promote a multiple-female social structure at more northern latitudes, but not at southern latitudes in the eastern U.S.A. Temperature clearly decreases with the 10° increase in latitude along this transect (mean annual temperatures: southern Florida = 23.5°C, northern Florida = 19.5°C, Tennessee = 14.5°C; Southern Regional Climate Center). The hypothesis that temperature plays a role in the observed variation in spider social structure is strongly supported by the incidence of higher frequencies of multiple-female colonies at cold-water sites in eastern Tennessee compared to warm-water sites in the same region. The fostering model assumes that there is a positive correlation between temperature and juvenile development rate, a correlation that was confirmed by our field measures and laboratory experiments. Because of this correlation, the altricial period should be longer in Tennessee than in northern Florida and much longer than in southern Florida. Thus, the overall probability that the mother will die during the altricial period will be increasingly higher with increasing latitude, purely as a consequence of the length of altricial period. The occurrence of multiple-female colonies also may be influenced by other factors besides temperature, which has been shown here to affect altricial period length. For instance, predation risk or prey availability could affect the daily risk of dying parameter in the model. We have emphasized temperature here since it offered the most obvious explanation of the observed frequency representation of multiple-female colonies within and among latitudes.

From our fostering model, as the conditions of daily mortality risk and duration of the juvenile altricial period vary, both single- and multiple-female colonies are predicted to occur. Multiple-female colonies are predicted to be the dominant strategy when a mother's probability of surviving the altricial period of her young is low, because under these conditions, reproductive success of females in multiple-female colonies will be higher than that of females in single-female colonies. The results of the fostering model also indicate that, under some risk conditions, RS remains higher for groups that are beyond optimal size predicted for single-female nests. This result affects expectations for colony sizes observed in nature as predicted by Giraldeau & Livoreil (1998). Females should remain in or join groups rather than establish isolated nests even though the group size may be larger than optimal. We presume that *A. studiosus* are not able to coordinate the establishment of optimally sized colonies and that members of optimally sized colonies cannot accurately assess colony size. Thus, successful colonies should continue to grow until they reach the point at which the average RS falls below that of single-female colonies. Note, however, that the predictions of this model are based on the relations between RS and colony size, which have not, but are currently being, determined for this species.

Our model suggests that the multiple-female colony strategy may be risk sensitive (Real & Caraco 1986) because it reduces the risk of complete nest failure. Multiple-female colonies may represent a 'conservative
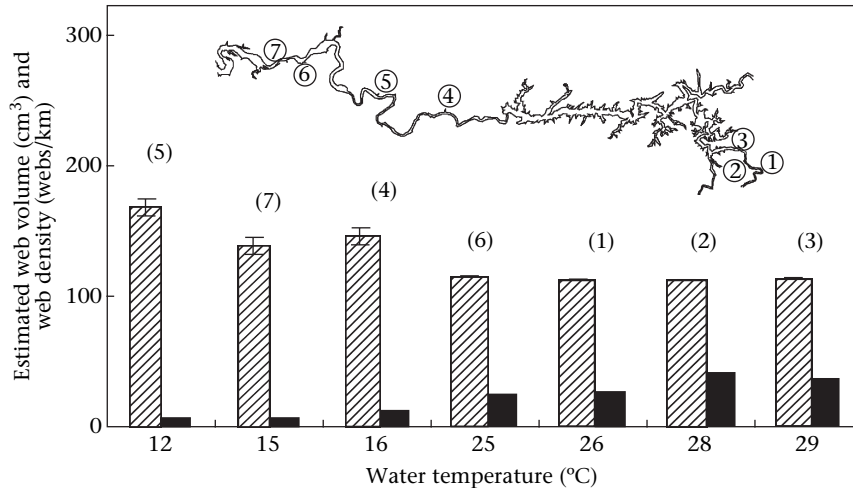
Figure 4. Web volumes (▨) and colony densities (■) recorded along the Little Tennessee River system, which shows stable variation in summer water temperatures due to flow control.

bet-hedging strategy' (Seger & Brockman 1987) whereby moms forgo the maximum potential RS (surviving as a single mom) for a less-than-maximal but less variable RS. Results of our field study of the effect of temperature on juvenile development supports this notion in that there was a greater risk of complete (single-female) colony failure at the cooler sites (where multiple-female colonies were more prevalent). There is evidence from other studies that spiders show risk-sensitive strategies. Reduced variance in prey capture was identified as one of the benefits to *A. studiosus* juveniles remaining in their natal webs (Jones & Parker 2002). Risk sensitivity in foraging success also affects the tendency of several species of orb-weaving spiders to aggregate (Caraco & Gillespie 1986; Caraco et al. 1995; Uetz 1998a, b).

Risk-sensitive, bet-hedging strategies are common evolutionary responses to temporally variable environments because reducing variance in RS can yield higher fitness over time (for review see Philippi & Seger 1989). Recent studies have found evidence for bet hedging in such diverse taxa as fish (Einum & Fleming 2004), crustaceans

(Hakalahti et al. 2004), bees (Shafir et al. 2005) and plants (Tielbörger & Valleriani 2005). Hassall et al. (2006) found that grasshoppers may be bet hedging at extremes of their range where conditions are more likely to be unfavourable, but not in areas where conditions are consistently favourable. This is similar to what we observed in *A. studiosus*, with the frequencies of multiple-female colonies occurring at the highest frequencies at the northern edge of the species' range.

There is evidence from other social systems that foundresses may show bet hedging similar to that indicated for *A. studiosus*. A classic example comes from West-Eberhard's (1969) work with northern populations of the wasp *Polistes fuscatus* (Fabricius). In Michigan a single female starts a colony, but then accepts auxiliary queens into the colony. The foundress queen limits the reproductive success of additional potential foundresses by eating some of their eggs. Presumably, one of these
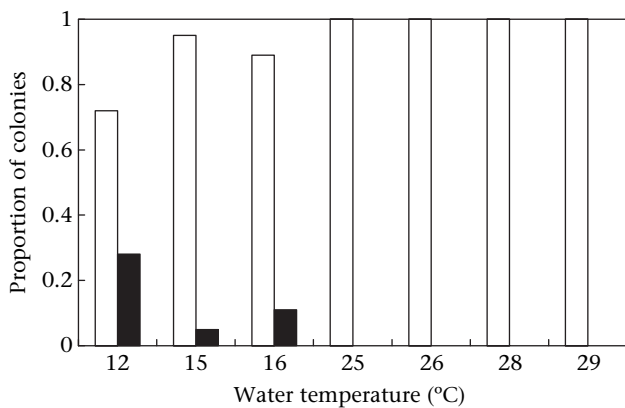

Figure 5. Relative proportions of single-female (□) and multiple-female (■) colonies at sites along the Little Tennessee River with respect to the water temperature of the site.
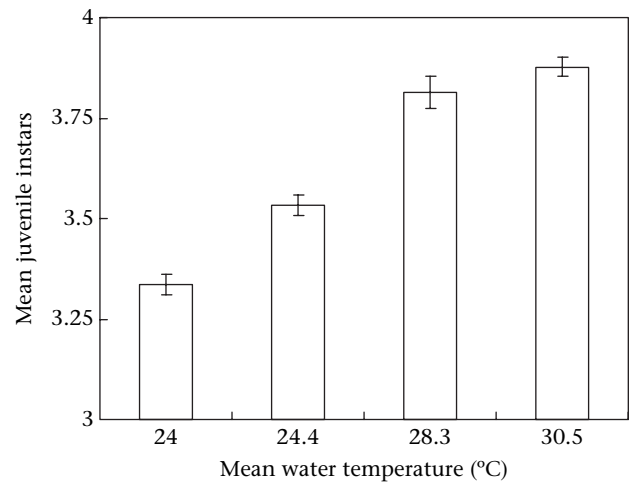

Figure 6. Mean ± SE number of juvenile instars collected 8 weeks after emergence from the egg sac, plotted by the mean water temperature at the site.
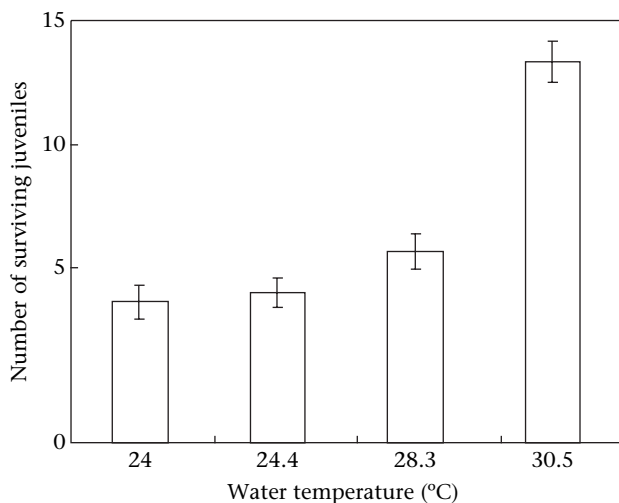
Figure 7. Mean ± SE number of surviving juveniles per colony, collected 8 weeks after emergence from the egg sac, plotted by the mean water temperature at the site.

females would take over the central reproductive role in the event of the loss of the controlling foundress.

In our study, we have emphasized bet hedging as it relates to the length of the altricial period. Other predictions of the fostering hypothesis do not involve the length of the altricial period per se, but nevertheless involve bet hedging. For example, the probability that a mother dies during the altricial period should be higher in Tennessee than in Florida (or at cooler versus warmer sites within Tennessee). This bet hedge predicts that the average individual RS for multiple-female groups will be lower than the average RS for single females that do survive. If, in some way, we were to create multiple-female colonies in southern Florida at 26°N latitude, the model predicts that the overall average RS for single females will be higher than that for individuals in multiple-female colonies. We are currently exploring the model's prediction at sites within Tennessee.

Brood-fostering Model in Relation to Other Models

The model we have developed is a type of assured fitness return (AFR) model (Strassmann & Queller 1989; Gadagkar 1990; Queller 1996) because the primary selective pressures are offspring dependence and adult mortality. In AFR models, if a mother dies before her brood reaches maturity, the surviving adults will rear the brood. This type of model was developed to explore the evolution of eusociality in bees and wasps in which individuals forgo dispersing and remain in their natal nest to help rear the brood. In the AFR models there is high reproductive skew, with helpers gaining little or no direct reproductive success. Helpers benefit indirectly through the increased production of nondescendant kin and the relatively low investment of resources compared to founding a new nest. There is considerable empirical support for AFR models among the bees and wasps (Strassmann & Queller 1989; Gadagkar 1990; Field et al. 2000) in which brood

survival depends on adult provisioning and defence. The halictid bee *Megalopta genalis* appears to have a social system most similar to that of *A. studiosus* (Smith et al. 2003). Wcislo (1997) identified this species as being facultatively eusocial: it shows wide within-population variation similar to that of *A. studiosus* at higher latitudes.

Because helpers sacrifice reproductive success in hymenopteran colonies, the AFR models developed for application to the social insects assume that there is high relatedness among colony members. However, even in the social insects, relatedness is context dependent and may under particular circumstances be quite low (Gadagkar 1990). Reproductive success within spider colonies is not skewed to the extent seen in the social insects because all individuals are, or at least have the potential to be, reproductive (but see Vollrath 1986). Our model differs from the AFR models developed to date because we assume that all individuals are breeders and that they merely sacrifice some RS by cooperating with others. On the other hand, they also will benefit from having their broods fostered if they die early. In our model, the costs and benefits of communal nesting to adult females are independent of degree of relatedness.

We did not know the extent to which our communal females were related, so we did not incorporate inclusive fitness effects in our model. If the females in a colony are related, as would be the case if *A. studiosus* colonies form by nondispersing broods, the loss of direct RS would be mitigated through a gain in indirect RS by rearing nondescendant kin. We are currently developing microsatellite markers to determine levels of relatedness within *A. studiosus* colonies.

An interesting parallel to the *A. studiosus* system is the case of multiple-foundress associations (pleometrosis) in ants (for review see Bourke & Franks 1995). In this case, multiple (usually unrelated) queens cooperate in founding a new colony. Like *A. studiosus*, all of the foundresses are totipotent and lay eggs. Unlike *A. studiosus*, however, when the workers begin to hatch, the foundresses typically become mutually aggressive and fight until only one remains, although in some cases workers kill all the queens except one (Bourke & Franks 1995). Rates of pleometrosis vary within and among ant species and they are positively associated with harsh conditions that greatly reduce the success of single-foundress colonies (Bourke & Franks 1995). Although usually only one queen survives to reproduce, all foundresses have the potential to be the survivor, and, thus, pleometrosis is considered to be a bet-hedging strategy. An even more intriguing parallel to *A. studiosus* is that rates of pleometrosis within and among species of leptothoracine ants increase with latitude and altitude (Heinze & Buschinger 1987). Altitude, in this case, is associated with cooler habitats just as water temperature is in our system.

Avilés (1999) developed a dynamic model that explains the evolution of cooperation in spiders. Her general model assumes that there is a synergistic effect of cooperation, which equates to the assured fitness component of brood fostering in our model. Other assumptions of her dynamic model that fit the life history of *A. studiosus* include: a cost to cooperation (decline in RS with colony size); scramble

competition within the group; and long-lived groups relative to individual life span. Our model relates to a prediction of Avilés' (1999) model that cooperation can allow populations to expand into or persist under harsh conditions by mitigating the risk of complete brood failure. This prediction fits the pattern of occurrence of multiple-female *A. studiosus* colonies, with cooler temperatures representing harsh conditions.

Our brood-fostering model presents a possible explanation for the reverse cline in levels of sociality in *A. studiosus*. The model predicts conditions under which multiple-female colonies would be favoured. However, even in *A. studiosus* populations where multiple-female colonies are present, single-female colonies are predominant. This may reflect the operation of a conditional strategy set, a mixed strategy set or a nonequilibrium system that is in a state of evolutionary flux as would be the case if there were annual variation in environmental conditions. We are currently exploring the nature and inheritance of attraction and tolerance, as well as expanding the brood-fostering model to incorporate the effects of intracolony relatedness, and annual and local environmental variation. Field experiments are underway that will test the RS predictions of this model as well.

Acknowledgments

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