



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

(Received 3 April 2007; initial acceptance 26 July 2007;
final acceptance 31 July 2008; published online 23 October 2008; MS. number: A10735R)

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.

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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 (regurgitative 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 intracolony 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 intracolony 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

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