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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