Relatedness and genetic structure in a socially polymorphic population of the spider \textit{Anelosimus studiosus}

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Abstract

The evolution of sociality remains a challenge in evolutionary biology and a central question is whether association between kin is a critical factor favouring the evolution of cooperation. This study examines genetic structure of \textit{Anelosimus studiosus}, a spider exhibiting polymorphic social behaviour. Two phenotypes have been identified: an ‘asocial’ phenotype with solitary female nests and a ‘social’ phenotype with multi-female/communal nests. To address the questions of whether these phenotypes are differentiated populations and whether cooperative individuals are closely related, we used microsatellites to analyse individuals from both communal and solitary nests. We found no evidence of differentiation between social and solitary samples, implying high rates of interbreeding. This is consistent with the hypothesis that these phenotypes coexist as a behavioural polymorphism within populations. Pairwise relatedness coefficients were used to test whether cooperating individuals are more closely related than expected by chance. Pairwise relatedness of females sharing communal webs averaged 0.25, the level expected for half-siblings and significantly more closely related than random pairs from the population. Solitary females collected at similar distances to the communal spider pairs were also more closely related than expected by chance (mean relatedness = 0.18), but less related than social pairs. These results imply that low dispersal contributes to increase likelihood of interaction between kin, but relatedness between social pairs is not explained by spatial structure alone. We propose that these phenotypes represent stages in the evolution of sociality, where viscous population structure creates opportunities for kin selection and cooperation is favoured under certain environmental conditions.

Keywords: \textit{Anelosimus studiosus}, genetic structure, microsatellites, kin selection, pairwise relatedness, spider sociality

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Introduction

The fitness of any organism depends on its ability to procure resources, defend itself and reproduce. Generally, for communal living to be favoured by natural selection, the social group should meet the above requirements for an individual on average more successfully than the individual could achieve on its own (Vucetich \textit{et al}. 2004; Whitehouse & Lubin 2005; Scantlebury \textit{et al}. 2006; Safi & Kerth 2007; Smith \textit{et al}. 2007). This can be achieved through cooperation, where each individual expects to benefit from the group or altruism, where some individuals make sacrifices that enhance the mean fitness of the group (Futuyma 2009, p. 417). Altruism is unlikely to evolve unless altruistic behaviours preferentially benefit individuals also possessing genes causing altruism, e.g. when interactions are between closely related individuals (Hamilton 1964; Baglione \textit{et al}. 2003; Ebensperger \textit{et al}. 2004). Considerable controversy persists as to whether kin selection is critical for the evolution of sociality (Wilson &
Hölldobler 2005; Foster et al. 2006; Wilson & Wilson 2007; Hughes et al. 2008; Shavit & Millstein 2008). In order to address the problem empirically, studies must focus on taxa in the early transitional stages of sociality because lineages with highly elaborated systems of cooperation might have lost the signatures of initially important processes (Schwarz et al. 2007; Hughes et al. 2008).

It has become apparent that the conditions for the evolution of sociality are more complex than previously thought with more flexibility of individual roles in social structures (Schwarz et al. 2007). Past studies have relied on direct observation of matings, births and dispersal to estimate relatedness within populations (Roeloffs & Riechert 1988), which are difficult to obtain in wild populations. Highly variable molecular markers provide researchers the ability to estimate genetic relatedness between individuals in wild populations with unknown pedigrees, which is extremely useful in the study of the mechanisms of kin selection (Blouin et al. 1996; Csilléry et al. 2006). The interplay between cooperation and conflict require knowledge of kin composition (Ross 2001) so in systems where sociality is polymorphic and rare (e.g. spiders), the use of molecular markers allows insight into how sociality has evolved and is being maintained.

Genetic relatedness studies of the tropical social (i.e. cooperative) spider species studied to date by allozyme electrophoresis provide within colony relatedness estimated from $F_{ST}$ and $F_{IT}$ on the order of 0.5 to over 0.9 (Riechert & Roeloffs 1993; Smith & Hagen 1996) with higher estimates found with AFLP fingerprinting for example, 0.58 averaged over sites of Stegodyphus dumicola (Smith et al. 2009), and estimates ranging up to 0.99 (reviewed in Aviles 1997; Lubin & Bilde 2007) based on $F_{ST}$ and $F_{IT}$ values. Although estimates are difficult to compare across different types of data and estimation procedures, the relatedness estimates are consistent with the expected proportion of genes shared by full sibs or parents and offspring. Relatedness estimates greater than 0.5 are caused by several generations of inbreeding within colonies. Subsocial spider species (species that have extended maternal care but live solitary as adults) examined to date with allozyme electrophoresis have a relatedness of about 0.25 within local groups (Johannesen et al. 1998; Johannesen & Lubin 2001), which is the proportion of genes half-siblings share in common. Thus, there might be a relationship between the degree of sociality and the level of kinship within groups. However, molecular studies have shown relatedness values in some eusocial species of ants, wasps, mole rats and sweat bees to be much lower than expected (e.g. Strassman et al. 1994; Burland et al. 2002; Kümmerli & Keller 2007; Soro et al. 2009).

Anelosimus studiosus

The genus Anelosimus Simon 1891 belongs to the comb-footed spider family, Theridiidae, that also includes the medically important widow genus, Lactroductus and the cosmopolitan Achaearanea. There are 53 described species of Anelosimus (Agnarsson et al. 2006), including several social species; most are tropical or subtropical in distribution (Aviles 1997; Agnarsson et al. 2006).

*Anelosimus studiosus* has a subtropical to temperate distribution in North and South America. From studies completed on a population in south Florida, Brach (1977) concluded that this species is subsocial in that it exhibits extended maternal care, but defends its nest against intrusion by other females. Furey (1998) first identified multiple female colonies in this species in East Tennessee. Since Furey’s (1998) initial study, the social polymorphism has been observed between latitudes and between cold and warm water environments within latitudes (Jones et al. 2007; Riechert & Jones 2008). While both solitary and social behavioural phenotypes are exhibited at all latitudes ranging from south Florida (26° latitude) to Tennessee (36° latitude), the social phenotype is rare at lower latitudes. The *A. studiosus* system, thus, differs from the other social spider species that are restricted to tropical and subtropical areas: *A. studiosus* exhibits a reverse latitudinal trend with more social nests at higher latitudes than in lower latitudes (Riechert & Jones 2008). The number of females per nest also increases with latitude ranging from a maximum of four to 40 females per nest at higher latitudes (see Riechert & Jones 2008).

Jones et al. (2007) present a model illustrating how multi-female nests might exist as a bet hedge against a mother’s dying before her brood reaches independence in colder environments where juvenile development is delayed. Further study has produced evidence consistent with the brood fostering hypothesis (Jones & Riechert 2008; Riechert & Jones 2008). The model is one of cooperation, rather than altruism and does not require that cooperating females be related. However, it assumes no cost of fostering (only a fixed cost of sharing a web with a number of other females), such that cheaters or brood parasites have no detrimental effects on colony success so long as one social female survives. If such costs exist, surviving females might increase the inclusive fitness of cooperative alleles if they preferentially foster related over unrelated offspring. Even in the absence of costs, an allele that causes females to favour related over unrelated offspring would tend to spread in a population where fostering is indiscriminate.

In this study, the genetic relatedness among individuals of a mixed phenotype population of *A. studiosus* is
examined at (36° N latitude), where multi-female nests approach a frequency of 15% in a predominantly solitary-female nest system. We applied five microsatellite markers to test for genetic differentiation between phenotypes, to test the hypothesis that multi-female colony members are more closely related than are solitary individuals living at similar spatial distances from one another and whether in both situations, pairs of females are more closely related than expected from random pairings of individuals.

**Materials and methods**

**Data collection**

We established two transects (100 m each) through an *A. studiosus* population that contained mixed single female and multi-female nests at a 36° latitude site in east Tennessee (Hardin Valley Park at the junction of Hickory Creek with Melton Hill Lake, Knox County, TN, USA). We marked every 5-m interval with flagging to permit us to collect pairs of spiders from meter intervals dictated by random numbers generated in Microsoft Excel. We searched an interval for a multi-female nest system. We applied five microsatellite loci has provided evaluation of relatedness within and between social groups such as ants (Parker et al. 1998; Chapuisat & Crozier 2001; Goropashnaya et al. 2001), social crab spiders (Evans & Goodisman 2002), rodent species (Ebensperger et al. 2004), eiders (McKinnon et al. 2006) and bees (Paxton et al. 1996).

In order to analyse the length of the PCR products in the ABI 3100 laser detection system, a fluorescent tag was added using a modified method for fluorescent labelling of PCR fragments developed by Schuelke (2000). A nested PCR reaction mixture contained a 1:4 ratio of an extended locus-specific forward primer with an added universal tag [the sequence UEACT for universal EcoRI ACT: (5' GAC TGC GTA CCC AAT TCA CT 3')], and a 1:1 ratio of the reverse primer, and a labelled universal primer (G5 series dye) that was complimentary to the extension added to the locus-specific forward primer. The reaction mixture (total of 25 µL) contained 1.5 µL of DNA, 12.06 µL of H2O, 5.0 µL of 5X PCR reaction Buffer (Promega), 2.0 µL of 10 mM dNTPs, 2.5 µL of MgCl, 0.125 µL GoTaq® (Promega), 0.3125 µL of modified forward primer and 1.25 µL of reverse and universal primers, which were run under modified cycling conditions described by Schuelke (2000). PCR conditions for each primer are as follows: C106, D126, B225 (94 °C for 5 min, 30 cycles of: 94 °C for 30 s, 56 °C for 45 s, 72 °C for 45 s and eight cycles of: 94 °C for 30 s, 53 °C for 45 s and 72 °C for 45 s and a 72 °C extension for 30 min). Primers D110 and D112 followed the above cycling conditions except the
annealing temperatures were changed from 56 °C to 57.3 °C. 1.0 μL of PCR product for each marker was added to a 0.75 μL LIZ standard and formamide mix bringing the total volume to 15 μL, which was then multiplexed on an ABI 3100 Prizm Genetic Analyser in the Molecular Biology Research Facilities lab at the University of Tennessee.

Data analysis

To interpret the fragment analysis from the ABI 3100, microsatellite data peaks were scored by Peakscan, a software package available at the Applied Biosystems website (http://marketing.appliedbiosystems.com/mk/get/PSI_login). Each individual was scored for the number of base pair variations at the five loci examined. Out of the 200 individuals collected, 160 individuals had complete allelic data and were used in this analysis with the goal of evaluating the relatedness of these individuals partitioned into 40 pairs each of solitary individuals and multi-female nest individuals. The software package CERVUS (Kalinowski et al. 2007) provided summary statistics for the data set including heterozygosity, number of alleles per locus and tests for deviation from Hardy-Weinberg Equilibrium (HWE).

An AMOVA was performed in Arlequin (Excoffier et al. 2005) to address the question of whether social and solitary phenotypes represent demographically separated populations. This program partitions the variance among different hierarchical levels: we used partitions between social and solitary phenotypes, among pairs within social and solitary groupings and among individuals within pairs. Significance is assessed by randomization at each hierarchical level (Fitzpatrick 2009). If significant variation occurs between social and solitary groups, then we would infer that the two phenotypes represent distinct evolutionary units. If little difference between the two groups can be found, then we would support the view that the phenotypes represent within-population polymorphism.

Genetic relatedness between individuals in this study is mathematically represented as the probability that individuals share respectively, zero, one or two alleles of each marker tested that are identical by descent (IBD) (Blouin 2003; Kalinowski et al. 2006). Several relatedness estimators are used to perform statistical analysis for the IBD probabilities. These use either linear regression (Queller & Goodnight 1989; Lynch & Ritland 1999; Wang 2002) or maximum-likelihood (Kalinowski et al. 2006) based methods. We initially applied the two most common regression methods (Queller & Goodnight 1989; Lynch & Ritland 1999) along with the maximum-likelihood based estimator (Kalinowski et al. 2006). All three were significantly correlated (Spearman coefficients between 0.61–0.79 for the social data set and 0.82–0.92 for the solitary data set; all P values < 0.0001). We present only the likelihood results. The likelihood estimator has the desirable property of being bounded at 0 and 1 (facilitating its interpretation as a probability). In addition, it is possible to include an assumption that null alleles are present in some or all loci when using the program ML-RELATE (Kalinowski et al. 2006). Due to the high likelihood of null alleles in microsatellites, the data was analysed both with and without null alleles, however no significant differences were detected in the output so to be conservative null alleles were assumed present.

We applied a simple randomization test using R (http://www.r-project.org) to determine whether pairs of females collected from the same communal nest were more closely related than random pairs from the population. A null distribution was simulated using both the social and solitary relatedness estimates by randomly forming 40 pairs (with replacement) and calculating the average pairwise relatedness. This procedure was repeated 10 000 times. We then compared the average relatedness of our observed pairs to this distribution of 10 000 averages under the null hypothesis of no population structure, simulated by random pairings of individuals, with replacement drawn from the population. The fraction of simulation replicates possessing greater than the average relatedness of the observed set of pairs then represents a one-tailed P value for the data given the null hypothesis (Good 1994). We applied a second randomization to test whether social pairs tend to be more closely related than pairs of solitary females at similar spatial distance (see sampling above), we simulated the null hypothesis of no relationship between relatedness and social phenotype, while controlling for spatial distance. Here we kept pairs of females together, but randomly re-labelled them as social or solitary. For each of 10 000 replicates, we calculated the difference between the means, the difference between the medians and the test statistic (the maximum rank sum) for the Wilcoxon paired-sample test and compared the simulated distributions of these statistics to their observed values. Conventional t-tests or Wilcoxon tests were not appropriate because the distributions of relatedness were not symmetrical (Zar 1984).

Results

Genetic structure

The AMOVA showed the highest percentage of variation was explained among individuals within pairs (89.2%) with the lowest amount of variation explained between social and solitary groups (0.102%; Table 2). Thus,
there was no detectable population genetic differentiation between social and solitary phenotypes. However, there was significant variation among pairs (10.72%; Table 2), i.e. social individuals sharing a nest or solitary individuals in close proximity were more similar than expected by chance.

Characteristics of the five polymorphic loci used in the analysis of *A. studiosus* kinship patterns are detailed in Table 1. The di-nucleotide repeat markers offered between three and 22 alleles with an average of 12.4 alleles and a mean expected heterozygosity of 0.7195 (Table 1). Deviations from Hardy–Weinberg were evident, with four out of five showing heterozygote deficits overall (Table 1). Heterozygote deficit could be attributed to the presence of (i) null alleles; (ii) non-random mating; or (iii) population subdivision (Wahlund effect). Non-random mating (inbreeding) might be an expected outcome of kin selection and population subdivision is consistent with the AMOVA results. Nevertheless, to be conservative, we specified that these loci be analysed with null alleles assumed present in the maximum likelihood program ML-RELATE (Kalinowski et al. 2006).

**Relatedness**

The average pairwise relatedness for individuals in communal/social nests ranged from zero (unrelated) to 0.85 and had an average of 0.25 (n = 40 pairs). Solitary nests had pairwise estimate relatedness values ranging from zero (unrelated) to 0.71, with an average of 0.18 (n = 40 pairs). The social and solitary mean and median values were significantly different from random (Monte Carlo, 10 000 randomizations), indicating that spiders in the same nests (or in close proximity) are more closely related than random pairs of individuals in this population (Fig. 1).

The second randomization tested for significant differences between social pairs and solitary pairs of individuals. The proportion of randomizations with median difference greater than or equal to observed median difference (observed = 0.17) was *P* < 0.0434 and for the Wilcoxon paired test statistic (observed = 397.5) *P* = 0.0326. Therefore, social pairs are significantly more related than the solitary pairs in this population, although the difference is subtle (Fig. 2).

For social pairs, the mean relatedness of 0.247 (bootstrap 95% CI: 0.171–0.321) and median of 0.226 (0.110–0.320) are consistent with a half-sibling level of relatedness. Neither confidence interval overlaps 0.5, the expected relatedness of full siblings. For solitary pairs, the mean of 0.182 (0.110–0.253) and median of 0.08 (0.000–0.170) illustrate a right-skewed distribution where most pairs were unrelated.

**Discussion**

Typically, cooperative social spiders are monomorphic for the social phenotype and exhibit high levels of

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**Table 1** Characteristics of the five polymorphic loci scored in *A. studiosus* with the primer sequence shown in addition to the most popular allele for the loci in the population (n = 200). Tm (°C) refers to optimizing annealing temperatures. *n* = number of individuals scored, *H*<sub>obs</sub> = observed heterozygote frequency, *H*<sub>exp</sub> = expected heterozygote frequency assuming Hardy–Weinberg equilibrium (HWE), and *P* refers to significance of deviation from HWE following Bonferroni Correction.

<table>
<thead>
<tr>
<th>Locus</th>
<th>Length of fragment (bp)</th>
<th>Number of alleles</th>
<th>Primer sequence (5’_3’)</th>
<th>Tm (°C)</th>
<th><em>N</em>&lt;sub&gt;ind&lt;/sub&gt;</th>
<th><em>H</em>&lt;sub&gt;obs&lt;/sub&gt;</th>
<th><em>H</em>&lt;sub&gt;exp&lt;/sub&gt;</th>
<th>Deviation <em>P</em>-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>C106</td>
<td>137</td>
<td>8</td>
<td>AAGCCAAAATGCTCTCTTT</td>
<td>56</td>
<td>137</td>
<td>0.533</td>
<td>0.646</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>GCTCAAGAAGCAGGTGATTC</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>D126</td>
<td>148</td>
<td>3</td>
<td>CATTCTGCCAAAAGTTG</td>
<td>56</td>
<td>148</td>
<td>0.635</td>
<td>0.452</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>GCAGTGTTGCTGCTGCTTT</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>B225</td>
<td>146</td>
<td>10</td>
<td>GGCCCTCAATGTAATCAAAGTTG</td>
<td>56</td>
<td>146</td>
<td>0.315</td>
<td>0.782</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>GCCGGCCACGTATATAAATG</td>
<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>D110</td>
<td>114</td>
<td>22</td>
<td>GGAGAAATCTGTGCAAATCTTG</td>
<td>57.3</td>
<td>114</td>
<td>0.395</td>
<td>0.844</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>GCCGGATTATACCTTATTAACCG</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>D112</td>
<td>120</td>
<td>19</td>
<td>ATTCGCCAGCTCTGATCTT</td>
<td>57.3</td>
<td>120</td>
<td>0.375</td>
<td>0.873</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>GCATTTAGATTCCACAGACACC</td>
<td></td>
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</tbody>
</table>

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**Table 2** AMOVA for social and solitary pair relatedness coefficients, *F* statistics and *P* values from Arlequin

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>d.f.</th>
<th>% of variation</th>
<th>Fixation index</th>
<th><em>P</em> value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Between social and solitary phenotypes</td>
<td>1</td>
<td>0.102</td>
<td><em>F</em>&lt;sub&gt;CT&lt;/sub&gt; = 0.001</td>
<td>0.335</td>
</tr>
<tr>
<td>Among pairs within phenotypes</td>
<td>78</td>
<td>10.722</td>
<td><em>F</em>&lt;sub&gt;SC&lt;/sub&gt; = 0.107</td>
<td>0.018</td>
</tr>
<tr>
<td>Within pairs</td>
<td>224</td>
<td>89.175</td>
<td><em>F</em>&lt;sub&gt;ST&lt;/sub&gt; = 0.108</td>
<td>0.017</td>
</tr>
</tbody>
</table>
inbreeding. Measures of within colony degrees of relat-

edness are on the order of full sibs or higher (Buskirk 1981; Roeloffs & Riechert 1988; Riechert & Roeloffs 1993; Aviles 1997; Lubin & Bilde 2007). In contrast, our AMOVA results indicate that A. studiosus populations are polymorphic for social and solitary phenotypes and our estimates of within-colony relatedness of social A. stud-

iosus were closer to the half-sib level on average. For these reasons, A. studiosus is an exemplary system in which to examine the forces shaping the evolution and maintenance of sociality.

The evolution of cooperative group behaviour can be explained by mutual benefit and/or increased inclusive fitness of cooperative genotypes (i.e. kin selection). Mutual benefits in A. studiosus include increased silk production with more females producing energetically expensive silk and shared brood care if a mother dies before her brood is old enough to care for themselves (Riechert & Jones 2008). Our results on the relatedness of A. studiosus are consistent with a role for kin selec-

tion in that cooperative females are more closely related than expected by chance and significantly more related than solitary female pairs with similar inter-individual distances. These results suggest that cooperative interac-

tions in A. studiosus are likely to benefit kin over and above the level expected by population structure alone.

Although social pairs were more closely related than solitary pairs, solitary pairs were also more closely related than expected by chance (Fig. 1). This suggests that the intrinsically low dispersal of A. studiosus females might pre-dispose these spiders to the evolution of cooperation because interactions are, by default, more likely to involve relatives. Dispersal of A. studiosus females is known to average less than 1 m (Riechert & Jones 2008) and this alone might explain spatial genetic structure on the scale of our 100 m transects. However, the relatedness of social pairs is even greater than that of solitary pairs at the same distance, indicating that the benefits of cooperation are likely to benefit kin over and above the level expected based on population viscosity alone.

The range of social behaviour exhibited by A. studio-

sus, with a higher frequency of multi-female nests present at cold-water sites than warm-water sites (Jones et al. 2007), suggests that environmental factors maintain behavioural trait variation beyond the indirect benefits conferred by increased relatedness among females within multi-female nests. Direct benefits from cooperation include the sharing of the costs of silk production, which benefits individuals by being able to share the energetic costs of maintaining webs for prey capture and antipredatory benefits (Aviles 1997; Crespi & Choe 1997; Uetz et al. 2002; Lubin & Bilde 2007; Yip et al. 2008). Additionally, in harsh environ-

ments, where dispersal is constrained and the probability of reproduction is low, energetic benefits might
be gained by living in groups (Lubin & Bilde 2007). For example, the brood fostering model proposed by Jones et al. (2007) explains variation in the level of sociality based on a modified fitness return strategy (Strassman & Queller 1989) in which females ‘hedge their bets’ (Soucy 2002) against dying before her brood reaches maturity.

Male vagility and multiple paternity are two factors that might explain the lower relatedness values observed in *A. studiosus* compared to that in the tropical social spider species. Male *A. studiosus* mature earlier than females and leave the natal nest in search of females with a preference for social females exhibited by males from both subsocial and social mothers (Pruitt & Riechert 2009). The strong female biased sex ratios of the tropical social spiders reflect the fact that males stay in the natal nest and mate with sibs (reviewed in Riechert & Roeloffs 1993). Because *A. studiosus* females will accept males as long as 8 days after an initial successful copulation (Sarah I. Duncan, personal observation), this too might lead to mating with multiple males. This decreases the average relatedness of the offspring.

This study was aimed at evaluating whether kin selection might contribute to the evolution and maintenance of cooperative behaviour in a social spider. Our estimates of pairwise relatedness support a role for kin selection in that social pairs tend to be more closely related than solitary pairs. However, solitary pairs (at similar inter-individual distances) are also more closely related than expected in a panmictic population, indicating that low dispersal could facilitate the evolution of cooperation in this group of spiders. In addition, relatedness in *A. studiosus* is considerably lower than that reported for non-polymorphic social spiders in the tropics. This difference might reflect differences in the costs and benefits involved in social behaviour or might indicate that the extreme degree of kinship and inbreeding observed in some tropical colonies is a secondary effect of colonial behaviour in those systems. *Anelosimus studiosus* presents a unique opportunity to examine the evolution of cooperative behaviour in its early stages because sociality exists as a polymorphism within populations and both environmental and genetic factors might contribute to the current distribution of phenotypes.

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References


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S. Duncan studied genetic structure in socially polymorphic spiders for her MS thesis and is interested in behavior and conservation genetics. S. Riechert's work is at the interface between behavior, ecology and evolutionary biology and involves the extent to which populations are at adaptive equilibria with respect to their physical and biotic environments. B. Fitzpatrick's major interests are in genetics and biogeography of speciation, the importance of local adaptation for both evolution and conservation management, and invasion biology. J. Fordyce's interests are the underlying processes responsible for the evolution of behavioral, ecological, physiological and morphological discontinuities in nature, and how these processes might ultimately affect reproductive isolation.