

Sociality level correlates with dispersal ability in spiders

Guadalupe Corcobado^{*1}, Miguel A. Rodríguez-Gironés¹, Jordi Moya-Laraño¹ and Leticia Avilés²

¹Department of Functional and Evolutionary Ecology, Estación Experimental de Zonas Áridas, Consejo Superior de Investigaciones Científicas, Carretera de Sacramento s/n La Cañada de San Urbano, C.P. 04120 Almería, Spain; and

²Biodiversity Research Centre, Department of Zoology, University of British Columbia, 6270 University Blvd, Vancouver BC V6T 1Z4, Canada

Summary

1. The evolution of sociality alters the genetic structure of populations, often leading to an increase in the level of inbreeding and a concomitant decrease in the ratio between the benefits and costs of dispersal.

2. The association between an absence of dispersal and sociality in spiders has so far been established indirectly from the age distribution of colonies, their genetic structure and their sex ratio. Using a functional and mechanistic approach, we investigated the dispersal tendencies and abilities of individuals of both sexes in species of spiders with different degrees of sociality. We predicted that dispersal tendencies and abilities would decrease when sociality increased.

3. In seven species of *Anelosimus* (Theridiidae), we tested whether there is a sharp transition between dispersing subsocial species and non-dispersing social ones, or whether dispersal ability decreases more gradually as level of sociality increases and whether both sexes are equally affected. Our assays measured the propensity and ability to bridge, a common aerial locomotion mode in spiders that is especially relevant during pre-mating dispersal.

4. We found that the tendency to disperse by bridging and, at least in males, the ability to disperse, significantly decrease as the level of sociality increases, and that this occurs without a pronounced threshold between subsocial and social species. Additionally, we detected a reduction of leg length relative to body size with increasing sociality and decreasing dispersal abilities in males, which may be mechanistically related to their reduced ability to bridge.

5. We propose that the loss of dispersal ability associated with the evolution of sociality in spiders, especially in males, could contribute to the maintenance of their inbred social systems by substantially increasing dispersal costs.

Key-words: *Anelosimus*, bridging, evolution of sociality, feedback mechanisms, social spiders, subsocial spiders

Introduction

Dispersal is an important trait in the life history of organisms (Johnson & Gaines 1990; Clobert *et al.* 2001). Dispersal contributes to the maintenance of genetic variability and the colonization of new potential habitats; it decreases the risk of inbreeding, intrasexual mate competition, or resource competition and affects metapopulation dynamics. Dispersal also has some important costs, including an associated increase in the risk of predation. Thus, the pattern of dispersal that maximizes expected fitness will depend on the ecological and social conditions experienced by individuals in a given environment (reviewed in Johnson & Gaines 1990).

Social spiders constitute an excellent system to study dispersal because of the association of this trait with different social and breeding systems (Bilde *et al.* 2005, 2007; Avilés & Bukowski 2006). In the more developed social spiders, non-territorial permanent-social according to the classification of Avilés (1997), that is, those in which individuals live together within a communal nest across their entire lifetime, mating tends to take place among siblings within a nest and budding female groups are believed to be responsible for colony foundation (Lubin & Robinson 1982; Vollrath 1982; Schneider *et al.* 2001; Johannesen *et al.* 2002, 2009b). These species thus exhibit high levels of inbreeding, highly female-biased sex ratios and a population structure where members of a colony are genetically nearly identical to one another and neighbouring colonies are often genetically related (Johannesen *et al.*

*Correspondence author. E-mail: gcorcobado@gmail.com

2002, 2009b; Agnarsson, Maddison & Aviles 2010). These species appear to lack a generalized pre-mating dispersal phase, as suggested by field observations of limited male dispersal (Lubin *et al.* 2009) and the observation that only large colonies give rise to dispersal events (Vollrath 1982; Schneider *et al.* 2001; Lubin & Robinson 1982). Subsocial spiders, non-territorial periodic-social according to the classification of Aviles (1997), that is, those in which individuals have a cooperative phase cohabiting within a communal nest followed by a solitary phase, on the other hand, show an intermediate degree of sociality, with colonies consisting of the offspring of a single female who cooperate during their early part of the live cycle, but disperse to live solitarily prior to mating. In these species, the maternal care phase is extended and juveniles live together in the natal nest after the mother dies. Because of their characteristic pre-mating dispersal phase, subsocial species are primarily outbred (e.g., Aviles 1997; Lubin & Bilde 2007), as reflected in their 1 : 1 sex ratios (reviewed in Lubin & Bilde 2007) and the presence of considerable genetic variability among neighbouring colonies compared with social species (Johannesen *et al.* 1998, 2002, 2009b; Johannesen & Lubin 1999, 2001; Agnarsson, Maddison & Aviles 2010). All these characteristics suggest that the benefits of dispersal probably outweigh dispersal costs for subsocial, but not for social spiders. Thus, there is evidence that social spiders live in environments where solitary dispersers suffer higher rates of predation (Henschel 1998) and newly established single female colonies seldom manage to succeed (Vollrath 1982; Bilde *et al.* 2007).

Social behaviour appears to be a derived character in spiders, evolved from subsocial-like ancestors, which in turn would be derived from solitary species with extended maternal care (Agnarsson 2006; Aviles 1997; Lubin & Bilde 2007; Johannesen *et al.* 1998; but see Agnarsson, Barrantes & May-Collado 2006). The loss of the pre-mating dispersal phase is therefore a key step in the transition from outbred subsocial to inbred social species. Comparing dispersal tendency and efficiency, as well as morphological adaptations to dispersal, can help us understand how the transition from one social system to another took place. Dispersal tendency and efficiency can be determined in the laboratory with experimental bridging trials (Corcobado *et al.* 2010). Morphological adaptations to dispersal can be inferred from measuring relative leg length to body size, because selection for efficient bridging is expected to lead to leg elongation (Moya-Laraño *et al.* 2008). Bridging is a common mode of spider locomotion that involves the production of a thread of silk that is pulled by the wind until it attaches to a nearby plant; after tensing, the spider crosses the line bridge hanging upside down from the silk (Moya-Laraño *et al.* 2008; Corcobado *et al.* 2010).

Our goal in this study is to determine the extent to which dispersal ability has been reduced in the transition from subsocial to social spiders, whether the transition between dispersing subsocial species and non-dispersing social species has been a sharp one or whether species with intermediate levels of sociality also exhibit intermediate abilities to disperse, and whether both sexes are equally affected. We do so by

focusing on the reduction of the function (i.e., the ability to disperse) and on the mechanisms involved (i.e. relationship between spider shape and dispersal). We explore these questions across species of the genus *Anelosimus* (Fig. 1), a genus that has become a model system to study the evolution of sociality in spiders given the multiple times it has given rise to social species (reviewed in Lubin & Bilde 2007). Here, we set out to test four specific predictions of the hypothesis of a loss of dispersal ability with increasing level of sociality in spiders. Because mating in social species takes place inside the maternal nest, we predict that as the degree of sociality increases, spiders should (i) decrease their propensity to disperse by bridging and (ii) become less efficient bridgers. The above two predictions refer to a behavioural trait (propensity) and the measurement of the ability to bridge (performance), respectively. Furthermore, because social spiders experience a reduced selective pressure for efficient bridging, we predict that (iii) the more social species should have relatively shorter legs in relation to their body size, thus being this decrease in relative leg length the mechanism responsible for the reduction of dispersal abilities, with this effect being (iv) stronger in males as in spiders males are, for the most part, the searching sex (Foelix 1996; but see Aisenberg, Viera & Costa 2007). Actually, selection favouring dispersal should be in general stronger in males than in females, and consequently, we would expect weaker effects of the previous predictions in the case of females.

To test these predictions, we performed experimental bridging trials in the laboratory using adult males and females



Fig. 1. Group of individuals of *Anelosimus eximius* cooperating in the capture of a big moth within their nest. Photograph taken by Guadalupe Corcobado in the rain forest in the Jatun Sacha Biological Stations, province of Napo, Ecuador.

of seven species of the genus *Anelosimus* that exhibit different degrees of sociality and analysed the data correcting for the non-independence because of common ancestry of species (Grafen 1989). As far as we know, the approach of looking experimentally at dispersal ability following a functional and mechanistic approach to understand the evolution and maintenance of sociality has not been considered so far.

Materials and methods

THE STUDY SYSTEM

The genus *Anelosimus* has become a model system to study sociality because it includes eight out of the 23 known social spider species and six out of 18 independent origins of sociality identified across spiders (Aviles 1997; Agnarsson 2006; Agnarsson *et al.* 2006; Agnarsson, Maddison & Aviles 2007; Lubin & Bilde 2007). *Anelosimus* species live in high vegetation where dispersal using silk is typical. Of the two modes of silk-dependent dispersal in spiders – ballooning, used for long-distance displacements, and bridging, for more localized dispersal (several metres) (Bonte *et al.* 2009) – we focus on the latter because species from the genus *Anelosimus* have been shown to be efficient bridgers (Moya-Laraño *et al.* 2008) and bridging seems to be the main mode used by *Anelosimus* in both natal and breeding dispersal (Aviles & Gelsey 1998; Powers & Aviles 2003; Klein, Bukowski & Aviles 2005). Natal dispersal occurs when individuals first leave the natal nest, while breeding dispersal is mainly used by subadult or adult males looking for receptive females to mate with. The transition from outbred subsocial to inbred social systems in spiders would have involved a suppression of both of these types of dispersal. In our study, we assessed the dispersal tendencies and abilities of adults of both sexes, which should be relevant for both natal and breeding dispersal as in the species we studied natal dispersal occurs late enough in the life cycle that a fraction of individuals only disperse as adults (e.g. Aviles & Gelsey 1998; Iturralde 2004; L. Avilés & G. Corcobado, unpublished data).

We collected males and females of seven different species of the genus *Anelosimus* (Theridiidae) (Fig. 2), four social – *A. domingo* Levi, *A. eximius* Keyserling, *A. guacamayos* Agnarsson, *A. oritoyacu* Agnarsson and three subsocial – *A. baeza* Agnarsson, *A. elegans* Agnarsson, and *A. studiosus* Hentz, according to the classification of (Aviles 1997; Lubin & Bilde 2007). We did not include any solitary species, because all species of the genus *Anelosimus* found hitherto in Ecuador are either social or subsocial (Agnarsson *et al.* 2006). The

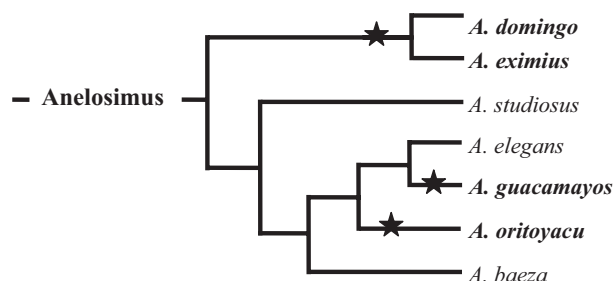


Fig. 2. Phylogeny of the spiders used for the comparative analyses based in previous published phylogenies of the genus *Anelosimus* (Agnarsson 2006; Agnarsson, Maddison & Aviles 2007). Boldface font, social species; Normal font, subsocial species. The stars indicate independent origins of sociality.

samples were collected in the provinces of Napo and Pichincha, in Ecuador (Fig 2; see Tables S1 and S2 for details, Supporting information).

BRIDGING TRIALS

We kept spiders in jars until testing, which always occurred within 48 h of collection. Trials were performed in local makeshift laboratories and always at room temperature (range = 13.7–24.1 °C; Mean = 20.07 °C, SD = 2.46 °C). We followed the methods described in Corcobado *et al.* (2010) to induce bridging in the laboratory. We placed the spider on the top of a 27-cm-high wire stand, located between a blowing fan (3 m away) and a plant (30 cm away), so that the air directed towards the plant any silk released by the spider. Air speed at the top of the stand was 0.6–0.8 m s⁻¹. If spiders had not started bridging 2 min after their release, we tried to induce them to bridge by poking them gently with a paint brush. Trials were finished either when the spider reached the plant after a successful bridging or 8 min after we first poked them. We recorded the result of the trial, the number of poking events until the spider started bridging, and bridging speed (i.e., once the spider started walking upside down hanging from the silk line, the distance covered in a continuous transect – without perceptible stops – divided by the time required to cover that distance). Time was measured from recordings in a JVC EVERIO GZ-MG575 video camera, while the distance covered was measured *in situ* using measuring tape to 0.1 cm precision. For those spiders (29 out of 241) that failed to bridge in the first trial, we ran a second trial, leaving spiders at least 2 h to recover between trials. Of these 29 spiders, 17 finally bridged.

After the trials, all spiders were frozen and taken to the laboratory to be weighed. In a previous study, we verified that there was no difference in weight between living and frozen spiders (Corcobado *et al.* 2010). All spiders were preserved in 70% ETOH after weighing. We measured the size of specimens under a dissection microscope. All animals were measured by the same observer – GC – with high intra-observer repeatability ($R = 0.94$; $P < 0.001$; $n = 20$). We measured body size as carapace width (CW) and first tibia length (TIL) as an estimate of leg length.

STATISTICAL ANALYSES

Comparative analysis

To correct for non-independence because of common ancestry of species (Grafen 1989), we performed Generalized Least Squares analyses (GLS) using the package PHYLOGR, as implemented in R (Diaz-Uriarte & Garland 2009). Analyses were based on the phylogeny of Agnarsson, Maddison & Aviles (2007). Because branch lengths are unknown for this phylogeny, we assigned all branches the same arbitrary value of one. Phylogenetic distance matrices were calculated using the PDTREE procedure within the statistical package PDAP (Garland, Harvey & Ives 1992) and imported into PHYLOGR. Figure 2 shows the phylogeny of our sample of species. To compare males and females, we added to each tip one more node with two branches, representing the two sexes. So, in our tree for the comparative analyses, we had average values for males and females of each species at the tips.

Selecting the final model

For each of the analyses, we first identified all the predictor variables that had been reported to affect the response variable and ran a GLS including all of them. Sex (females = 1, males = 0) and its interactions with other independent variables were introduced in the initial

model. Starting with the higher order interactions, we then performed backward removal of the interaction terms that were furthest away from significance ($P > 0.30$). To graphically display the results of each predictor in the final model, we used partial regression plots (Moya-Laraño & Corcobado 2008).

Testing prediction (i): across spider taxa, the propensity to bridge decreases as the degree of sociality increases

We studied the tendency of the spiders to disperse by bridging through two dependent variables. First, for each sex and species, we calculated the proportion of individuals that bridged without needing stimulation (bridging propensity). Second, for each sex and species, we recorded the average number of stimulations needed to persuade them to bridge. In both cases, the initial models included as predictors body size (CW), which is negatively related to the tendency to bridge (Corcobado *et al.* 2010), level of sociality, sex and the interaction of sex with the other two variables. After removing non-significant terms, the final models included CW and sociality level for the response variable bridging propensity, and sex and sociality level for the response variable number of stimulations.

Testing prediction (ii): across spider taxa, the ability to disperse by bridging decreases as the degree of sociality increases

We analysed the ability of the spiders to bridge by including bridging speed as the dependent variable in the model. Bridging speed for a given spider was recorded during a continuous bout of running upside down. The predictor variables introduced in the initial model were TIIL and the residuals of CW (because CW and TIIL were highly correlated we used the residuals of CW on TIIL to get a measurement of size independent of leg length), room temperature during the bridging trial, level of sociality, sex and all the interactions between sex and the remaining independent variables. Theory predicts that leg length controlled for body size should be positively related to bridging speed, as it has been found across instars in a different species of *Anelosimus* than the ones used here (Moya-Laraño *et al.* 2008). We included room temperature in the initial model because it varied among experimental trials and temperature may positively affect speed (e.g. Bauwens *et al.* 1995). However, because the number of variables was high relative to the number of cases, this model had low statistical power. We thus ran the analysis for males and females separately. Body size and temperature were the only variables retained in the final model for females, while the final model for males included leg length, temperature and sociality level.

Testing predictions (iii) and (iv): across taxa, body shape become less fit to bridging (shorter legs relative to their body size) as the degree of sociality increases and this effect is more pronounced in males than in females

To test these hypotheses, we analysed the relationship between leg length (TIIL) and body size (CW) across the different species of *Anelosimus* using log-transformed variables. Thus, the response variable was TIIL (log-transformed), and the initial model included CW (log-transformed), level of sociality, sex and the interactions between sex and the other predictors. The final model included CW (log-transformed), sex, sociality level and the interaction between sex and sociality level.

Rank of sociality

In addition to categorizing the species as social or subsocial (Aviles 1997; Lubin & Bilde 2007), and to accommodate the fact that within each of the above two categories there is a gradation in level of sociality (Aviles *et al.* 2007; Riechert & Jones 2008), we constructed a continuous variable ranking with our seven species from least (assigned a value of 1) to most (assigned a value of 7) social. We established the ranking *a priori* based on a combined assessment of the median dispersal instar and the proportion of nests with more than one adult female (see Tables S1 and S2, Supporting Information), with species that dispersed later in their life cycle and had a greater proportion of nests with multiple adult females deemed to have a higher sociality rank (Purcell & Aviles 2007). According to this criterion, in decreasing order of sociality, our study species were ranked as: *A. domingo* 7; *A. eximius* 6; *A. oritoyacu* 5; *A. guacamayos* 4; *A. baeza* 3; *A. elegans* 2; *A. studiosus* 1. We note that this ranking is not intended to replace the discrete social categories, which are quite useful for most purposes, but simply to capture the heterogeneity that is present within categories and the fact that some species are intermediate in their level of sociality (e.g. Aviles *et al.* 2007; Riechert & Jones 2008). Likewise, the ranking along a continuous scale does not imply that sociality evolved gradually in the genus; it is entirely possible that various species achieved their sociality level independently in a single sharp transition from a solitary or subsocial ancestor and yet ended up in different positions on a sociality scale. Given a position on such a scale, we then ask whether dispersal ability adjusts to that level so that the resulting relationship between sociality and dispersal ability is continuous across categories or abrupt between subsocial and social.

The ranking is based on previous published data and some unpublished data (see footnote to Table S1 for references, Supporting information). The instar composition of newly established nests was used to infer the dispersal instar for each of the species, as individuals in newly established nests would represent recent dispersers. Newly established nests are identified in the field mapping all existing nests in an area and noting subsequent appearances of new nests. The number of nests containing groups of females was determined from the same records given the total number of adult females (single vs. multiple) present in the colonies (L. Avilés and G. Harwood manuscript in preparation). As different populations of the same species may differ in their level of sociality depending on the habitat in which they occur (Purcell & Aviles 2007), for our ranking we only used the information on the same subset of populations which matched the ones included in our study. While in seasonal species the stage of the colonies at the time of a survey may affect the proportion of nests with solitary females, this is usually not an issue for species in Ecuador, where seasons are not pronounced and colonies of all stages tend to be present throughout the year. We note, nonetheless, that the ranking of *A. oritoyacu* should be considered preliminary, as this is a recently discovered species for which little is known (Aviles & Purcell 2011).

We followed two approaches to check the robustness of our results given possible uncertainty in the exact ranking of species such as *A. oritoyacu*. First, we repeated all the analyses considering sociality as a categorical variable with two levels (social = 1; subsocial = 0). Because most results were qualitatively similar, we only report those that differ from the continuous case. We also conducted a sensitivity analysis to check the robustness of our results to small changes in the sociality ranking. There are $7! = 5040$ possible ways of ranking our seven species. If one analysis is conducted with two different, arbitrary rankings, the results will differ. We expect that the difference between the results of the analyses with the two rankings will increase with the distance between the rankings. We therefore repeated our

statistical analyses with all 5040 possible rankings and checked how quickly results (P values and regression coefficients) changed with the distance to our original ranking. In doing so, we used as a measure of distance the minimum number of swaps required to go from our original ranking to an alternative one, where a swap is defined as the permutation of two species with consecutive rankings (say *A. eximius* and *A. oritoyacu*). If a statistically significant result became non-significant after a single random swap, the conclusion drawn from the analysis would be extremely sensitive to the particular sociality ranking hypothesized. In other words, the robustness of our results will increase with the number of swaps required to turn a significant result into a non-significant one.

Gradual vs. sharp relationship between dispersal ability and sociality level

For those analyses in which sociality appears as a continuous variable, we fitted phylogenetically corrected linear regression models to the data. In these analyses, a significant effect of sociality can be obtained if there is a linear relationship between sociality and dispersal ability, or if there is a sharp transition, with two clouds of points at substantially different dispersal ability levels, one corresponding to the social and the other to the subsocial species. In this latter scenario, the results of the analyses should change little if the order of species is changed within each group. Thus, to test whether there are sharp differences between the dispersal ability of subsocial and social species, with little within-group variability, we repeated all analyses for each of the 144 rank permutations that assign ranks 1–3 to the subsocial species and ranks 4–7 to the social species (thus keeping subsocial and social species apart) and checked the number of permutations for which sociality remained significant. The lower the number of permutations leading to a significant effect of sociality, the worse would be the fit of the sharp-transition model to the data.

Results

All species we tested proved to be good bridgers, in agreement with previous results obtained from another species in the genus *Anelosimus* (Moya-Laraño *et al.* 2008) and with the general relationship between spider body size and bridging ability across taxa (Corcobado *et al.* 2010; Rodríguez-Girones, Corcobado & Moya-Laraño 2010). Across species, the proportion of individuals who bridged at the end of the trials for each species ranged from 75 to 100% in females and from 86 to 100% in males. Nevertheless, we observed strong differences among species in the tendency to bridge.

PREDICTION (I): THE PROPENSITY TO DISPERSE BY BRIDGING DECREASES WITH THE LEVEL OF SOCIALITY

Our results were consistent with the prediction that the tendency to disperse by bridging decreases as the level of sociality increases. Level of sociality was the only variable that had a significant effect on the proportion of spiders that bridged without stimulation ($t(11) = -2.42$, $P = 0.034$) (Fig. 3, see Appendix S1, Supporting information), with no differences between males and females. Similar results were obtained when we measured the tendency to bridge as the mean number of stimulations needed to persuade spiders to bridge:

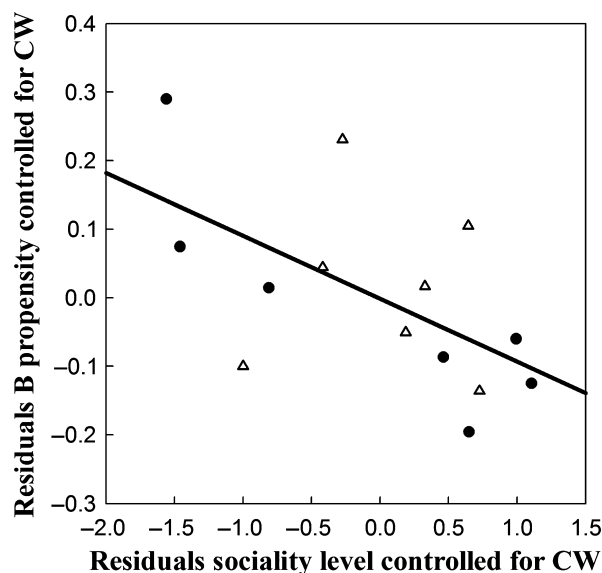


Fig. 3. Partial relationship between bridging propensity and the level of sociality. Partial regression plot where the response and the predictor variable of interest are both controlled for the rest of the independent variables that were retained in the final selected model. The Y -axis shows residuals of bridging propensity (bp) controlled for carapace width (CW); the X -axis shows residuals of social level controlled for CW. Males are represented by black circles and females by empty triangles.

the more social species needed on average a larger number of stimulations to bridge ($t(11) = 2.27$, $P = 0.044$). In this case, however, a significant effect of sex was also detected, with females needing more stimulations to bridge than males ($t(11) = 2.46$, $P = 0.032$) (see Appendix S1, Supporting information).

PREDICTION (II): THE ABILITY TO DISPERSE BY BRIDGING DECREASES WITH THE LEVEL OF SOCIALITY

We used bridging speed (i.e. the speed at which the spider ran upside down hanging from the silk line) as a proxy for the ability to disperse. The initial analyses showed very different patterns between the sexes, so we analysed males and females separately. In males, bridging speed increased with leg length ($t(3) = 19.04$, $P < 0.001$) and decreased with sociality level ($t(3) = -6.43$, $P = 0.008$). We also detected a significant effect of temperature ($t(3) = 4.98$, $P = 0.016$). Thus, after controlling for temperature and leg length, the males of the more social spiders bridged at lower speed, and once we controlled for temperature and level of sociality, males with longer legs bridged at higher speed (Fig. 4, see Appendix S1, Supporting information). Although body size was not included in the selected model, leg length was still significant in the full model that also included body size (leg length, $t(2) = 13.57$, $P = 0.005$), revealing that the observed pattern is probably influenced by the relative length of the leg controlled for body size, rather than by absolute leg length. None of the variables tested had significant effects on the bridging speed of females in analyses with sociality as a

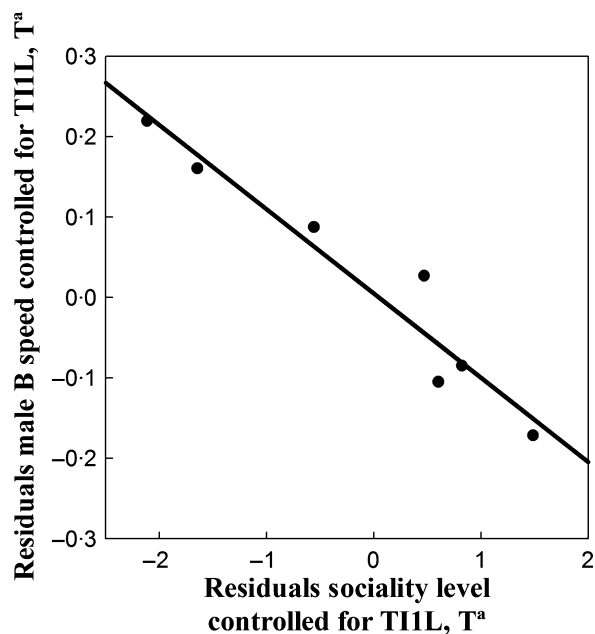


Fig. 4. Partial relationship between male bridging speed and level of sociality. Partial regression plot where the response and the predictor variable of interest are both controlled for the rest of the independent variables that were retained in the final selected model. The Y-axis shows residuals of bridging speed (bp) controlled for tibia length (T11L) and average bridging temperature (T^a); the X-axis shows residuals of social level controlled for T11L and T^a .

continuous variable (see Appendix S1, Supporting information). However, with sociality as a categorical variable, social females bridged more slowly than subsocial ones ($t(4) = -3.96$, $P = 0.017$), suggesting that there is a nonlinear relationship between sociality and bridging ability in females; there was also a trend in females for bridging speed to increase with tibia length ($t(4) = 2.45$, $P = 0.070$).

PREDICTIONS (III) AND (IV): MORE SOCIAL SPECIES HAVE RELATIVELY SHORTER LEGS IN RELATION TO THEIR BODY SIZE, WITH THIS EFFECT BEING STRONGER IN MALES THAN IN FEMALES

There was a significant interaction between sex and sociality level ($t(9) = 2.89$, $P = 0.018$) on the relationship between leg length and body size for males and females of different species. Leg length (relative to body size) increased with the level of sociality in females and decreased in males (see Appendix S1, Supporting information).

SENSITIVITY ANALYSIS

Our results were robust to small changes in the ranking of sociality level. Generally, the effect of level of sociality [or its interaction with sex, in predictions (iii) and (iv)] remained statistically significant when we made one or two random swaps in the sociality ranking, and became marginally non-significant after three random swaps (see Appendix S2, Supporting information). Meanwhile, the effect of sociality level on male

bridging speed (prediction ii), became marginally non-significant after two random swaps (see Appendix S2, Supporting information). It follows that our conclusions are unlikely to change if further data alter the sociality ranking we have used, as the results will only change if 2–3 out of seven positions are misplaced, which is itself highly unlikely to occur.

GRADUAL VS. SHARP RELATIONSHIP BETWEEN DISPERSAL ABILITY AND SOCIALITY LEVEL

There was little support for the sharp-transition model. When we reanalysed the data changing the relative order of subsocial and social species, but keeping these two groups apart, sociality (or its interaction with sex) was only significant in 31 (bridging propensity), 28 (number of stimulations), 22 (relative leg length) and 28 (male bridging speed) of the 144 possible permutations. Such low values are incompatible with the hypothesis that there are sharp differences between the dispersal ability of subsocial and social species, with little within-group variability.

Discussion

We found that the degree of sociality in spiders correlates with changes in dispersal propensity, dispersal performance and morphological traits affecting dispersal ability. Although the association between sociality and absence of dispersal in spiders had been established in the past from data on the age structure of colonies and their genetic structure and sex ratios (Aviles 1997; Lubin & Bilde 2007 and references therein), no previous study had directly measured dispersal behaviour using a functional and mechanistic approach as performed here. In this study, we provide the first direct evidence that the propensity and, more importantly, the ability to disperse in spiders decrease as level of sociality increases, as we had predicted.

First, we found that the tendency to disperse by bridging was significantly and negatively correlated with level of sociality for both males and females. This result was observed regardless of whether the tendency to disperse was measured as the number of individuals who bridged without stimulation (Fig. 3) or as the mean number of stimulations applied to persuade the spiders to bridge (see Appendix S1, Supporting information). Secondly, at least for males, the sex that is mainly responsible for mate searching in spiders (Foelix 1996), we found that dispersal ability (bridging speed) decreased as level of sociality increased (Fig. 4, see Appendix S1, Supporting information). This pattern was also confirmed when we analysed sociality as a categorical variable (social vs. subsocial). For females, we found a reduced ability to bridge related to sociality when we used sociality as a categorical variable, but not when sociality was treated as continuous. It thus appears that not only the tendency, but also the ability to disperse, at least in males, decreased in the transition from outbred subsocial to inbred social systems in spiders. Interestingly, the extent of the reduction in the tendency and ability to disperse parallels the degree of sociality attained by the var-

ious species, as there was no pronounced threshold between the traditionally considered subsocial and social species: although we found qualitatively similar results when sociality was treated as a continuous or dichotomous variable, there was little support for the sharp-transition model.

Patterns associated with the decreased ability to bridge with increasing sociality differed between the sexes. In males, the decrease in bridging ability was associated with a change in body shape, with the more social species having relatively shorter legs, that is, a body shape less fitted for bridging (Moya-Laraño *et al.* 2008). Conversely, none of the tested variables significantly explained bridging ability in females when sociality was evaluated through a continuous ranking even though social females did bridge more slowly than subsocial ones when sociality was treated as a categorical variable, and females of the more social species had longer legs (see Appendix S1, Supporting information). These patterns may reflect different selective pressures acting on dispersal abilities and leg length in males and females, probably as a result of differences in their activities pre-, during, and post-dispersal (see Bonte *et al.* 2011 for a review of dispersal costs at different phases of the life cycle).

In web-building spiders, males are the main sex responsible of mate searching (Foelix 1996) and thus selection should favour pre-mating dispersal much more strongly in this sex. Accordingly, after controlling for temperature and level of sociality, bridging ability was positively and strongly correlated with leg length in males, (see Appendix S1, Supporting information), in agreement with pendulum mechanics, which predicts a positive relationship between bridging speed and relative leg length after controlling for body size (Moya-Laraño *et al.* 2008). In social species, however, there is no longer an incentive for males to leave the natal nest in search of mates as co-nesting females no longer disperse upon reaching reproductive maturity and relatively large distances separate nests likely to contain unrelated females (Johannesen & Lubin 2001; Johannesen *et al.* 2002, 2009b; Smith *et al.* 2009). The reduction in leg length in social males could then reflect a trade-off with their ability to move within the maternal nest (Bonte *et al.* 2011), that is, individuals with relatively longer legs would be more efficient dispersing by bridging, but would be clumsy moving standing on their legs within the nest (Moya-Laraño *et al.* 2008).

Conversely, females of the more social species have longer legs (see Appendix S1, Supporting information). Although females in the social species may disperse to establish new nests when their colonies have reached a large size (Lubin & Robinson 1982; Vollrath 1982; Johannesen *et al.* 1998, 2002, 2009b; Schneider *et al.* 2001), we find it unlikely that their disproportionately long legs are related to improved dispersal ability, for two reasons. First, females decrease their tendency to disperse by bridging as level of sociality increases (Fig. 3, see Appendix S1, Supporting information). Second, and most importantly, we found no relationship between female leg length and bridging speed when we considered sociality as a continuous variable (see Appendix S1, Supporting information). More likely, an elongation of relative leg length in

females may be advantageous in behaviours related to their communal life style, such as re-building the web or silk-wrapping prey. Both these behaviours are important in the lowland wet tropical environments where social *Anelosimus* species occur. Here, strong rains require constant maintenance of webs (Purcell & Aviles 2008), which, relative to the body size of the spiders, may be orders of magnitude larger than in subsocial species. Likewise, efficient silk-wrapping of prey is important as social spiders have in their habitats access to much larger prey compared with non-social species at higher elevations or latitudes (Guevara & Aviles 2007; Powers & Aviles 2007). Males, on the other hand, have limited participation in communal activities (reviewed in Lubin & Bilde 2007), making selection pressures on communal-related traits weak. Thus, social males are simultaneously released from the parallel needs of dispersing and nest repair and prey wrapping, while social females must retain a high nest repair and prey wrapping capabilities, thus potentially explaining why relative leg length decreases in males, but increases in females, as level of sociality increases.

It is known that some factors such as starvation, density, sex ratio or silk limitation can affect dispersal (e.g. Perrin & Mazalov 2000; Poethke & Hovestadt 2002; Bonte, Lukac & Lens 2008; Biedermann, Klepzig & Taborsky 2011). Consequently, it could be argued that because we evaluated dispersal abilities in spiders directly captured from the field, among-species differences in spider condition could at least partially explain differences in dispersal abilities across different species, thus interfering with the conclusion of this work. Several arguments, however, support the conclusion that sociality, rather than body condition, is what explains differences in dispersal abilities across species. First, the study includes two pairs of species with different grades of sociality coexisting in the same location and, thus, sharing the same environmental conditions – *A. guacamayos* and *A. elegans* coexist in the Cocodrilos area, and *A. eximius* and *A. domingo* coexist in the Jatun Sacha area. Secondly, to get a representative sample of individuals of each species from a particular location, we collected a maximum of two individuals of each colony and we put special attention to collect individuals from colonies of different sizes. Thirdly, we found that in the case of males body condition, that is, residuals of body mass on body size, did not have a consistent effect on any of our response variables within species. For females, we found a significant but non-consistent relationship within species for the response variable number of stimulations only. Importantly, the sign and magnitude of the relationship between body condition and number of stimulations did not covary with sociality level (see Appendix S3, Supporting information). Hence, particularly in males, our results cannot be explained by possible among-individuals differences in feeding status.

We would like to point out that our study is only relevant to relative short-distance dispersal mediated by bridging. In the context of social spiders, this kind of displacements characterizes the pre-mating phase in subsocial species (Aviles & Gelsey 1998; Lubin, Hennicke & Schneider 1998;

Powers & Aviles 2003; Li & Kuan 2006) and is one of the main mechanisms whose suppression is responsible for the transition from subsocial to social systems in spiders (interindividual tolerance being the other). Although there is evidence for long-distance dispersal probably mediated by ballooning in *Stegodyphus* (Schneider *et al.* 2001; Johannesen *et al.* 2005, 2009a), another spider genus with multiple origins of sociality, such mechanism has not been documented for *Anelosimus*. It would be interesting to test in the future whether the pattern of a reduced ability to disperse by bridging is also found in relation to long-distance dispersal and whether a pattern of loss of dispersal ability with level of sociality is found in other taxa, such as *Stegodyphus*, where species with different degrees of sociality and multiple origins of sociality occur (Kraus & Kraus 1990; Johannesen *et al.* 2007). It would also be interesting to explore dispersal abilities in subadults, which in subsocial species constitute a sizeable fraction of individuals involved in natal dispersal and thus in the termination of the social phase (Aviles & Gelsey 1998; Lubin, Hennicke & Schneider 1998; Li & Kuan 2006).

Consideration of the costs of dispersal at different stages of the life cycle (Bonte *et al.* 2011) can help us to understand the reduction in the tendencies and abilities to disperse in male and female spiders as level of sociality increases. The proposed explanation for individuals of the more social species giving up dispersal relies on the high costs of dispersal and benefits of group living in the environments where social spiders inhabit, which would have selected for females that remain grouped and for philopatric males (Bilde *et al.* 2007; Aviles & Purcell, in press). Our results offer an interesting new contribution in this aspect. Morphological and behavioural changes that result in a diminished ability to disperse (e.g. reduced relative leg length in males) would be a response to the costs of developing and maintaining structures or behaviours that facilitate dispersal. The resulting diminished ability to disperse would then exacerbate dispersal costs and decrease the survival probability of dispersers, establishing a negative feedback on the propensity to emigrate from colonies. Under this scenario, the benefits of remaining in the natal group would likely overcome those of dispersal under a broader range of environmental conditions. Selection favouring the origin of sociality and inbreeding in these spider systems could thus differ from the mechanisms that maintain it. Most researchers agree that sociality in spiders has evolved as a result of costs of dispersal and benefits of group living under particular environmental conditions (reviewed in refs. Aviles 1997; Lubin & Bilde 2007); we propose that the decrease in dispersal ability concomitant with the achievement of sociality introduces a positive feedback loop, contributing to the maintenance of sociality and high levels of inbreeding once they are achieved.

In other social arthropods, reduced dispersal abilities have been detected in females and/or males of some social insects (e.g. Hölldobler & Wilson 1990; Danforth 1991). Frequently, these reduced dispersal abilities are linked to sharp morphological changes involving the emergence of wingless morphs (e.g. Danforth 1991; Peeters & Ito 2001; Yamauchi *et al.*

2001). Interestingly, our results show that reduced dispersal abilities may also be associated with more subtle morphological changes, such as a reduction of relative leg length, which in wingless organisms, such as spiders, may contribute to maintaining their inbred social systems. A lack of dispersal and the benefits of communal life, on the other hand, could minimize environmental stress to the individuals of the colony leading to low inbreeding depression (Fox & Reed 2011). From a more general point of view, our results highlight the importance of evaluating possible feedback mechanisms between morphology and behaviour to understand the evolution of phenotypic traits, such as dispersal (Bonte *et al.* 2011 and reference therein).

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Supporting Information

Additional supporting information may be found in the online version of this article.

Appendix S1. Full statistic tables of the main results exposed in this manuscript.

Appendix S2. Results of the sensitive analyses to assess the robustness of our ranking of sociality.

Appendix S3. Results of the effect of body condition at individual level.

Table S1. Details about origin of species.

Table S2. Summary of data used in the analyses.

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