Behavioral Ecology
doi:10.1093/beheco/arr146

Original Article

Sister clade comparisons reveal reduced maternal care behavior in social cobweb spiders

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Animals living in cooperative groups experience fundamentally different environments than their nonsocial relatives, potentially changing the strength of natural selection on some aspects of their behavior. Using a comparative approach, we examined a potential example of this phenomenon: an association between reduced levels of maternal care behavior and sociality in cobweb spiders. We compared 6 different measures of maternal care behavior between species from 2 independently derived social clades and subsocial species from sister clades. In natural nests, we measured the mean distance between egg sacs and the nearest female and the proportion of egg sacs being attended. In the lab, we measured a female's willingness to accept an egg sac, abandon her egg sac when disturbed, repair a damaged egg sac, and the speed at which a female reclaimed her egg sac when separated from it. Social species from both social clades scored significantly lower than subsocial species from sister clades on 6 and 4 of 6 of these assays of maternal care, respectively. We discuss alternative explanations of this pattern, including the potential role of relaxed natural selection in a social environment in permitting the evolution of a novel "low-parenting" phenotype. *Key words: Anelosimus*, cooperative breeding, evolution, maternal care, relaxed selection, social spider, sociality. *[Behav Ecol]*

INTRODUCTION

The evolution of group living and cooperation (sociality) carries with it manifold changes to the environmental context individuals are exposed to Wilson (1975). These can include a higher frequency of interaction with conspecifics, reduced predation (Elgar 1989; Beauchamp 2008), buffering of temperature changes (Willis and Brigham 2007), as well as increased food availability (Sonerud et al. 2001), mating opportunities (Bijleveld et al. 2010), and resting time (Pollard and Blumstein 2008). Whatever their specific nature, these changes can result in fundamentally different environments for individuals in species with different levels of sociality. This can in turn have profound consequences for the expression and evolution of their individual and collective behaviors. Indeed, many authors believe that differences in social context have the potential to explain a great deal of behavioral variation in nature—a major goal of both evolutionary biology and ecology (West-Eberhard 1983; Wcislo 2000; Keller 2009).

Sociality can influence behavior via 2 interacting processes: plasticity and genetic evolution. First, plastic behaviors that rely on cues modified by the social environment can be differentially expressed across social contexts. For example, it is well known that many animals will reduce their level of antipredatory behavior (e.g., vigilance) when in larger groups (Lima 1995). Similar facultative responses to changes in social context have been widely reported for various behaviors in disparate taxa, including mating behavior in primates and vinegar flies (Dufty et al. 2002; Krupp et al. 2008), foraging behavior in salmonids (Grand and Dill 1999), calling frequency in frogs (Chu et al. 1998), and dispersal behavior in sciurids (Toth and Robinson 2009).

Apart from affecting plastic traits, different levels of sociality can also alter selective regimes and permit the evolution of novel behavioral phenotypes. For example, it has been shown that communicative complexity and vocal repertoire size have evolved in concert with social complexity in primates (McComb and Semple 2005). The widely held evolutionary explanation for this pattern is that increased social complexity creates unique intragroup fitness challenges for primates for which certain novel behavioral phenotypes (in this case advanced communication and cognition abilities) are selectively advantageous (Dunbar and Shultz 2007). Such selection-altering effects arising out of social life are known as "indirect genetic effects" and/or "social selection" (West-Eberhard 1983; Queller 1992; Wolf et al. 1999, 2001; Wcsilo 2000; Bijma and Wade 2008; Wolf and Moore 2010).

Using the comparative method (Harvey and Pagel 1991), we explore the association between level of sociality and individual maternal care behaviors in social and subsocial cobweb spiders of the genus *Anelosimus* Simon (1891) (Araneae: Theridiidae). These spiders are an ideal system for studying this association as sociality (cooperative breeding, hunting, and nest building) has independently evolved at least 4 times in the genus and each social species has extant subsocial sister taxa (Agnarsson 2006; Agnarsson et al. 2006, 2007). This allows for multiple phylogenetically controlled comparisons of behavior between social and subsocial species from sister clades. Additionally, differences in level of sociality between *Anelosimus* species likely translate into acute environmental differences for individuals within social groups. Social *Anelosimus* live in nests of up to hundreds of individuals, build and share a communal living space, cooperatively hunt, and

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Received 17 February 2011; revised 19 July 2011; accepted 20 July 2011.

perform alloparental care (Avilés 1997; Lubin and Bilde 2007). In contrast, subsocial *Anelosimus* live alone in single-individual nests in which their offspring hatch, fledge, and eventually disperse (Avilés 1997). This profound difference in social context creates the potential for the expression and/or evolution of novel behavioral phenotypes.

In a previous study (Samuk K, Avilés L, unpublished data), we noticed that more social *Anelosimus* species appeared to exhibit lower levels of individual maternal care behaviors, an association that we here formally test. Lower levels of maternal care behavior might be associated with greater degrees of sociality because social species enjoy increased physical protection of egg sacs given their larger nests, dilution effects due to multiple egg sacs, group antipredator behaviors, and extensive alloparental care (Avilés 1997; Uetz and Hieber 1997). Together, these social factors are likely to ameliorate risks to egg sacs in social nests relative to subsocial ones (Uetz and Hieber 1997), thus relaxing selection for individual care behaviors. As a consequence, the benefits of a high level of maternal care behavior may be accordingly lower for social females than for subsocial ones. Assuming maternal care is costly (energetically or otherwise), we thus expect a facultative and/or evolutionary attenuation of these behaviors in social species.

We observed maternal care behaviors relevant to egg sac defense from predators, parasitoids and parasites, protection from physical damage and moisture, and thermoregulation (Austin 1985; Fink 1987; Gillespie 1990; Ruttan 1991; Foelix 1996). We compared 6 measures of such behaviors among species in 2 pairs of independently derived social and subsocial sister clades of *Anelosimus*. Overall, we found a strong trend for reduced maternal care behavior in social species relative to subsocial ones. We consider alternative explanations for this pattern, including relaxed natural selection, phenotypic plasticity, and an incidental association due to differences in the external environment of subsocial and social cobweb spiders. We argue that reduced individual maternal care behaviors in social spiders may result from changes in selective pressures emerging from larger nests and colonies, trade-offs between care-giving and communal activities, such as foraging and web repair in a communal setting as well as the presence of multiple caregivers.

MATERIALS AND METHODS

Study species

We selected 2 pairs of sister taxa comprising 6 species of cobweb spiders for our study. The first pair was the social species *Anelosimus guacamayos* Agnarsson (2006) and its subsocial sister species *Anelosimus elegans* Agnarsson 2006. The second pair was a simultaneous comparison between 2 members of a social clade, *Anelosimus domingo* Levi (1963) and *Anelosimus eximius* Simon (1891),versus 2 subsocial members of their sister clade, *Anelosimus baeza* Agnarsson (2006) and *Anelosimus cf. oritoyacu*, the latter being an undescribed subsocial species close to *Anelosimus oritoyacu* Agnarsson 2006. For the latter, we compared the 4 species as 2 groups because we cannot rule out the possibility that *A. domingo* and *A. eximius* share a single origin of sociality (Agnarsson 2006). Hence, independent comparisons for each social species would not be warranted.

We performed all laboratory and field measurements in June 2010 at the natural habitats of each of the 6 species at various sites in eastern Ecuador. In the Napo province, we studied *A. domingo* and *A. eximius* at the Estacion Biológica Jatun Sacha (lat 1.06°S, long 77.61°W, ~410 m elevation). Jatun Sacha consists of 2500 hectares of 70% primary rain forest and 30% regenerated secondary rain forest (Guevara and Avilés 2007). In the Quijos Canton of Napo, we studied *A. baeza* along the Tena-Quito road south of Baeza (lat 0.46°S, long 77.89°W, ~1900 m), *A. elegans* and *A. guacamayos* in the Reserva Ecólogica Antisana and the Parque Nacional Sumaco (lat 0.63°S–0.65°S, long 77.8°W, ~1800 m elevation). Both of these locations are situated in lower montane cloud forest (Neill 1999). Finally, in the Pichincha province, we studied *A. cf. oritoyacu* at the Bellavista Cloud Forest Reserve near Tandayapa (lat 0.016°S, long 78.68°W, ~ 2000 m elevation), which is composed mostly of undisturbed montane cloud forest.

Field measurements

In total, we located 61 *A. elegans*, 16 *A. guacamayos*, 38 *A. baeza*, 35 *A. cf. oritoyacu*, 5 *A. eximius*, and 3 *A. domingo* nests. In each nest, we measured 2 aspects of egg sac attendance behavior (a key component of maternal care, Gillespie 1990) for each of the 6 species in their natural nests. First, we measured the distances between egg sacs and the nearest adult female spider. In larger nests (>10 egg sacs), we selected a sample of egg sacs for this measurement using a transect method. To do this, we began by approximating a linear transect (calibrated with a measuring tape held outside the nest) along the longest axis of the nest, passing through the center of the nest and the 2 axes orthogonal to it; we then sampled the egg sac closest to the line at each 10-cm intervals.

Next, we counted the number of egg sacs being attended by females, that is, in contact with the female's body and the total number of egg sacs. We used these values to calculate the proportion of egg sacs being attended in each nest. Note that because disturbing the nest usually causes spiders to abandon egg sacs (Samuk K, personal observation), we could not exhaustively search for every egg sac in the innermost retreats of the nest. Hence, our estimates are somewhat biased toward visible egg sacs. All egg sacs included were nonetheless in the interior of the nest and were clearly intact and actively cared for by the spiders (e.g., they were not discarded, empty, moldy, or damaged, as is often the case with discarded egg sacs).

Laboratory assays

For our laboratory assays, we collected females from natural colonies using a drinking straw aspirator. Collected females were either clutching an egg sac, in physical contact with one, or at least within a 1 cm of one. These were thus females that were exhibiting maternal care behaviors and were for the most part in the nest's interior. In nests with more than one female, we again employed a transect method to select female/egg sac pairs to be collected—those closest to each 10 cm mark along the longest geometrically centered axis of the nest. In total, we collected 36 A. baeza and 37 A. cf. oritoyacu single females, to be compared against 34 A. eximius, from five colonies, and 37 A. domingo, from three colonies. For the second comparison, we collected 33 A. elegans single females and 44 A. guacamayos from sixteen colonies. Note that although we had no way of assessing the reproductive status of the females, clutching and proximity are themselves indicative of the post-egg sac laying stage (Samuk K, personal observation; Samuk K, Avilés L, unpublished data).

We placed each field-collected female and egg sac in a plastic container ~11 cm in circumference and 6 cm in height. These containers had a raised inner circle, 8 cm in circumference and 0.3 cm high inset in their bases and were sealed with a perforated lid. We misted each container daily with water using a spray bottle. Before all trials, we removed all residual webbing in the container to standardize assay arenas across replicates. We conducted every assay described below within 1–4 days of collecting the egg sac and female under seminatural lighting conditions between 0800 and 2000 h. After experimentation,

we returned subsocial females and their egg sacs to vegetation similar to their original location of collection. For social species, we placed the spiders and egg sacs back into their original nests.

Assay 1: egg sac acceptance
To test for a female's willingness to accept an egg sac after being separated from it, we placed females and their egg sacs 1–2 cm apart. We then slowly rolled the egg sac toward the female using a paintbrush and recorded whether the female grabbed the egg sac using her mouthparts and/or pedipalps. We terminated the trial if the female did not immediately grasp the egg sac.

Assay 2: egg sac relinquishment
Our second assay was a test of the female's willingness to relinquish her egg sac when disturbed. We pursued females clutching egg sacs with a small paintbrush, lightly prodding them, and moving along with the spider as it retreated. We stopped when the female relinquished the egg sac or 3 min elapsed, whichever came first.

Assay 3: egg sac reclamation latency
Our third assay measured the latency to reclaiming an egg sac after being separated from it. This metric was meant to capture the extent of egg sac searching behavior (Opell 2001). To begin, we placed the female and her egg sac 6 body lengths apart. We then made 6 successive measurements of the distance between the egg sac and the female's cephalothorax at 15-min intervals followed by 7 successive observations at hour intervals, for a maximum of 13 observations over 8.5 h. We stopped measurements after 8.5 h or when the female first clutched the egg sac, whichever came first.

Assay 4: egg sac repair probability
Our final assay measured a female's willingness to repair a damaged egg sac. We first placed the female spiders in 2.0 ml natural self-standing tubes with o-ring caps (USA Scientific, Ocala, FL) with a section of dried leaf. Separately, we damaged the spider's egg sac by making a small hole in the outer casing and widening it with forceps. The final holes were typically ~3 mm in diameter. We placed the ripped egg sac into the tubes with the female and leaf and capped the tubes. After 8 h, we recorded whether the female had made any visible attempt to repair the egg sac. We defined a "visible attempt" as any combination of binding the hole shut with silk, folding the outer casing in on the hole, binding the open end of the egg sac to the leaf, and/or holding the egg sac shut using the mouthparts and chelicerae.

Statistical analyses

To compare assays between social and subsocial sister taxa, we used 3 different types of analyses (Table 1). First, for 4 of our 6 measures, we employed generalized linear mixed models (GLMMs). In each model, we included species as a fixed effect and colony identity as a random effect to avoid pseudoreplication. We fit each GLMM via penalized quasi-likelihood using the glmmPQL function in the MASS package in R (Venables and Ripley 2002; R Development Core Team 2009).

For the egg sac relinquishment experiment, we performed a "right-censored" mixed effects survival regression of relinquishment time with species as a fixed effect and source colony as random effect using the survreg function in R (Therneau and Lumley 2009). Note that "right-censored" indicates a replicate in which the event of interest (the egg sac being dropped by the female) did not happen during the duration of the experiment. For the egg sac reclamation experiment, which produced both interval censored (i.e., the event occurred some time during a given interval) and right-censored data, we calculated nonparametric maximum likelihood estimates (NPMLE) of reclamation time curves (Kaplan–Meier curves) using the icfit function in the interval package for R (Fay 2009). Note that for the latter, it was not possible to include the effect of colony in the model. We thus also repeated the analysis using standard survival regression (i.e., disregarding the interval structure) in which colony could be included as a random effect.

Note that there was no significant effect of time of day on the level of maternal care performed by females in any assays, and thus, time was not included as a cofactor in any of the models (significance of general additive model smoothing parameters; acceptance: $\chi^2 = 0.746$, $P = 0.388$, degrees of freedom [df] = 1.01, $n = 153$; repair: $\chi^2 = 4.508$, $P = 0.11$, df = 2.056, $n = 188$; relinquishment: $F = 0.036$, $P = 0.85$, df = 1, $n = 179$; reclamation: $F = 1.984$, $P = 0.065$, df = 6.418, $n = 206$).

Using each analysis framework above, we performed the following comparisons: *A. guacamayos* versus *A. elegans*; *A. eximius* and *A. domingo* versus *A. baeza* and *A. cf. oritoyacu*. We computed GLMM comparisons by fitting pairwise models for each comparison, with one group modeled as the intercept term

Table 1
Statistical model information and results for contrasts between 2 pairs of social and subsocial sister clades of cobweb spiders

			Contrast (H_0: social–subsocial = 0)							
			(*Anelosimus eximius*, *A. domingo*)–(*A. baeza*, *A. cf. oritoyacu*)				*A. guacamayos*–*A. elegans*			
Measurement	Analysis	Error function	Estimate	df_1, df_2	SE	*P* value	Estimate	df_1, df_2	SE	*P* value
Female distance	GLMM	Gamma (log)	0.43	80, 80	0.09	**<0.00001**	0.42	46, 64	0.16	**0.011**
Attendance	GLMM	Binomial (logit)	−1.36	80, 80	0.40	**0.001**	−1.54	46, 64	0.47	**0.002**
Acceptance	GLMM	Binomial (logit)	−3.79	82, 82	0.82	**0.00002**	−1.47	53, 28	0.50	**0.007**
Repair	GLMM	Binomial (logit)	−1.80	73, 73	0.77	**0.02**	0.19	45, 45	0.49	0.70
Relinquishment	survreg	Weibull (identity)	−170.77	82, 82	9.9	**<0.00001**	−55.93	38, 32	10.39	**<0.00001**
Reclamation	survNPMLE[a]	N/A	5.66[b]	69, 67	—	**<0.00001**	1.69[b]	38, 32	—	0.09

Each row contains model information for 1 of 6 measures of maternal care behavior. Estimates and standard errors (SEs) correspond to parameters of the difference between social and subsocial species. Bold *P* values signify significance at the $\alpha = 0.05$ level.

[a] Nonparametric maximum likelihood estimate of survival.

[b] Logrank test *Z*-score.

and the other group as a standard model parameter. For comparison of survival regression parameters, we similarly fit pairwise survival models, with one group modeled as an intercept term and the other as a regression parameter. Finally, we compared NPMLE estimates of survival time using the logrank test. Unless otherwise stated, all comparisons were 2-tailed and employed an α of 0.05.

RESULTS

Field measurements

As a group, the social species *A. eximius* and *A. domingo* had significantly higher average egg sac to nearest female distances than the subsocial species *A. baeza* and *A. cf. oritoyacu* (Figure 1A, Table 1). The social species *A. guacamayos* also had significantly higher average egg sac to nearest female distances than the subsocial species *A. elegans* (Figure 1A, Table 1).

There was a similar pattern for the related measure of proportion of egg sacs attended in the nest: Nests of *A. eximius* and *A. domingo* had significantly lower proportions of guarded egg sacs than nests of *A. baeza* and *A. cf. oritoyacu* (Figure 1B, Table 1), as did nests of *A. guacamayos* relative to those of *A. elegans* (Figure 1B, Table 1).

Egg sac acceptance

Females of *A. eximius* and *A. domingo* had significantly lower probabilities of accepting egg sacs versus *A. baeza* and *A. cf. oritoyacu* (Figure 2A, Table 1). Similarly, *A. guacamayos* females had significantly lower probabilities of accepting egg sacs versus *A. elegans* (Figure 2A, Table 1).

Egg sac relinquishment

When under simulated threat, females of *A. eximius* and *A. domingo* relinquished their egg sac significantly sooner on average compared with females of *A. baeza* and *A. cf. oritoyacu* (Figure 3A, Table 1). *Anelosimus guacamayos* females also released their egg sacs significantly sooner on average than *A. elegans* females (Figure 3B, Table 1).

Egg sac reclamation latency

When separated from their egg sacs, *A. eximius* and *A. domingo* females took significantly longer than *A. baeza* and *A. cf. oritoyacu* females to reclaim their egg sacs (Figure 3C, Table 1). In contrast, there was no significant difference in reclamation time between *A. guacamayos* and *A. elegans* (Figure 3D, Table 1). We could not include colony as a random effect in these interval survival models but found no significant effect of source colony identity on reclamation time (logrank k-sample test: *A. eximius*, $\chi^2 = 7.58$, $P = 0.11$, $n = 36$; *A. domingo*, $\chi^2 = 3.89$, $P = 0.14$, $n = 30$; *A. guacamayos*, $\chi^2 = 16.5$, $P = 0.12$, $n = 38$). Using standard survival regression, which allows control of colony identity, we found the same pattern for *A. eximius* and *A. domingo* ($Z = -5.93$, $n = 70$, $P < 0.0001$), although in contrast to the interval survival analyses, *A. guacamayos* also had significantly longer reclamation times than its subsocial sister species ($Z = -2.56$, $P = 0.01$, $n = 70$).

Egg sac repair probability

Anelosimus eximius and *A. domingo* females were significantly less likely to repair a damaged egg sac compared with *A. baeza* and *A. cf. oritoyacu* females (Figure 2B, Table 1). There was, however, no significant difference in the probability of egg sac repair between females of *A. guacamayos* and *A. elegans* (Figure 2B, Table 1).

DISCUSSION

We found reduced levels of maternal care behavior by females of every social species relative to their subsocial sister taxa. This was true of all 6 measures for *A. eximius* and *A. domingo* and 4 of 6 measures for *A. guacamayos*. Hence, our data support the hypothesis that increased level of sociality is associated with reduced individual maternal care behavior.

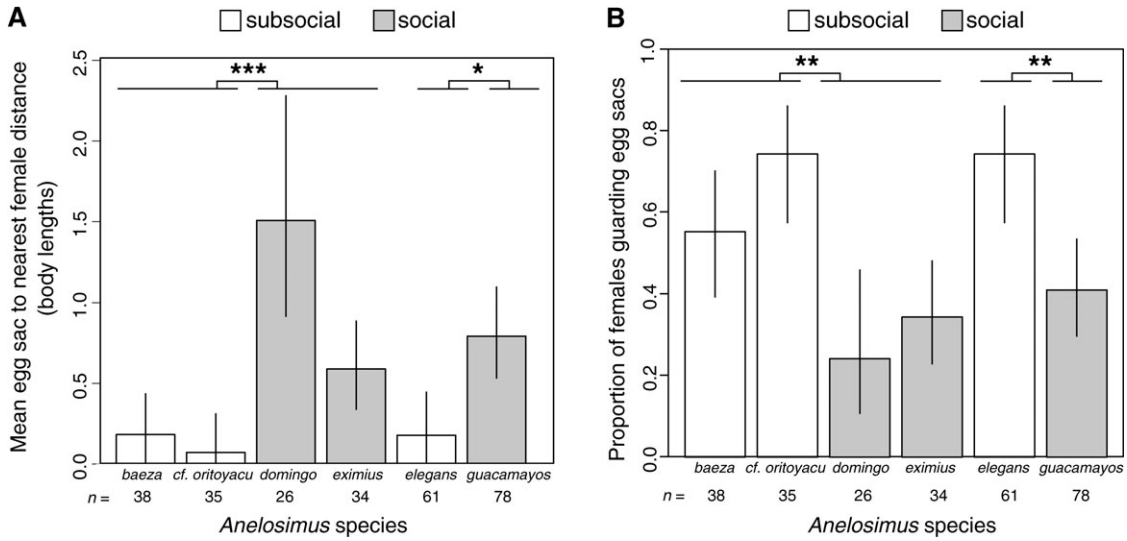

Figure 1
Two metrics of maternal care measured in natural nests of 6 species of *Anelosimus*. (A) Distance from egg sacs to the nearest adult female spider; (B) Proportion of egg sacs guarded by female spiders; White and gray bars represent subsocial and social species, respectively. Bar heights and 95% confidence intervals are derived from back-transformed generalized linear model estimates. Braced horizontal lines above groups represent statistical comparisons performed as part of the generalized linear model contrast structure (see Table 1 for full details). Significance codes: $*P < 0.05$, $**P < 0.001$, and $***P < 0.0001$. Sample sizes are indicated below each species label.

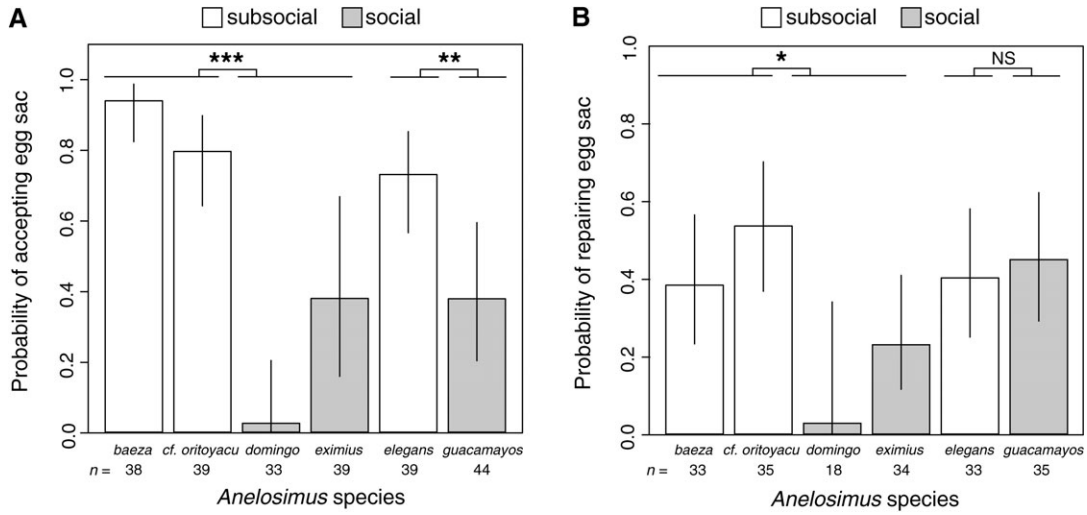

Figure 2
A) Probability female spiders of 6 *Anelosimus* species will accept an egg sac when presented with one under laboratory conditions; (B) Probability female spiders of 6 *Anelosimus* species will repair a damaged egg sac over 8 h under laboratory conditions. White and gray bars represent subsocial and social species, respectively. Bar heights and 95% confidence intervals are derived from generalized linear model estimates, back-transformed into proportions or probabilities. Braced horizontal lines above groups represent generalized linear model parameter contrasts (see text for statistical details). Sample sizes for each species are indicated under their respective labels. Significance codes: $*P < 0.05$, $**P < 0.005$, and $***P < 0.0005$. Sample sizes are indicated below each species label.

Interestingly, for nearly every assay, the magnitude of the difference between *A. guacamayos* and *A. elegans* was approximately one half of the magnitude of the difference between *A. eximius*/*A. domingo* and *A. baeza*/*A. cf. oritoyacu*. In other words, *A. guacamayos* exhibited a more subsocial-like maternal care profile than *A. eximius* and *A. domingo*. This matches our

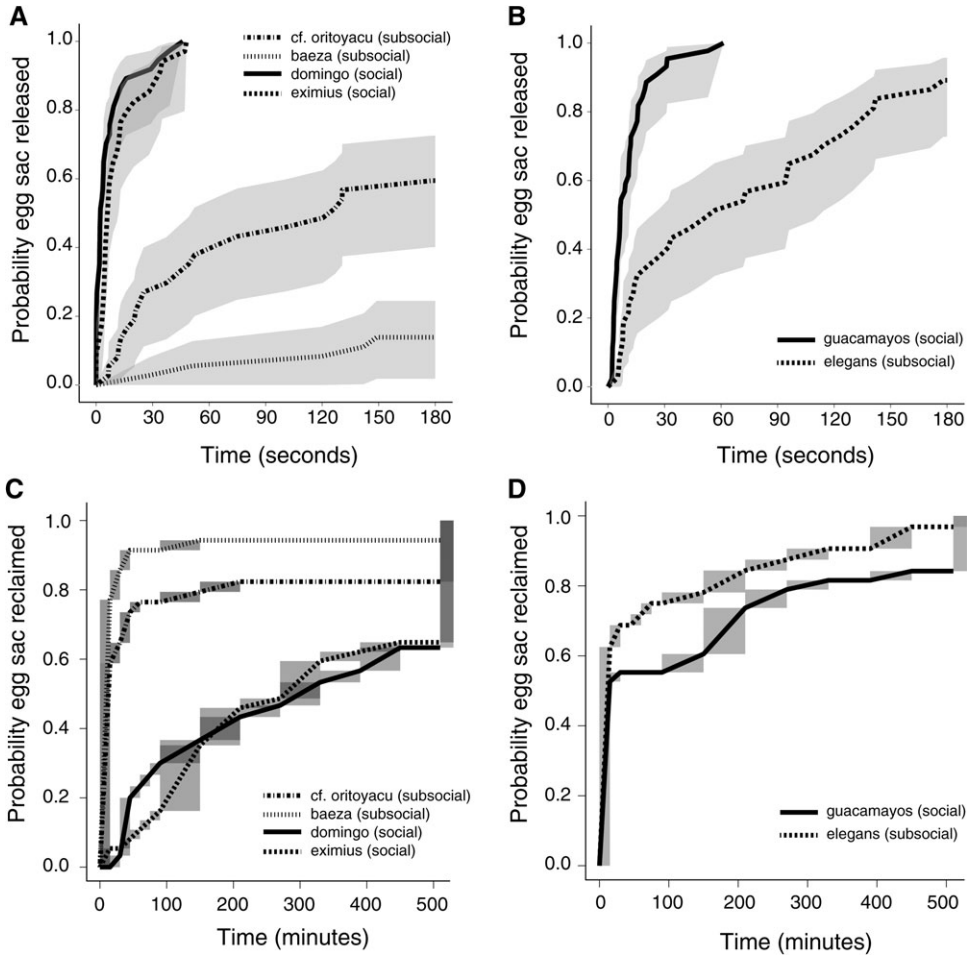

Figure 3
Survival plots of the results of 2 laboratory assays of maternal care for females of 6 species of *Anelosimus*. (AB) Probability female spiders dropped their egg sac when being pursued over 180 s, (CD) Probability female spiders located their egg sac over 510 min after being separated from it. Fitted lines represent smoothed Kaplan–Meier and gray outlines denote 95% confidence intervals. Note that observations in CD were made at intervals versus continuously in AB, which results in rectangular confidence intervals when fitted by NPMLE. Darker gray areas signify areas of overlap between confidence intervals. Survival plots have been inverted and separated into the 2 contrast groups for clarity.

expectations about the role of degree of sociality in shaping behavior, as *A. guacamayos* appears to exhibit a lower level of sociality than the lowland social species (Avilés et al. 2007). Specifically, *A. guacamayos* colonies are 1 to 2 orders of magnitude smaller, have greater interindividual distance among females within nests, and have a significantly greater proportion of nests with solitary females compared with *A. eximius* (Avilés et al. 2007). It is also worth noting that *A. guacamayos* and *A. elegans* diverged more recently than *A. eximius*/*A. domingo* and *A. baeza*/*A. cf. oritoyacu* (Agnarsson et al. 2010). A longer history of divergent social environments could result in more evolutionary divergence in maternal care behavior. This could further explain the discrepancy between *A. guacamayos* and *A. eximius*/*A. domingo*.

Finally, there was some evidence of *A. domingo* exhibiting more extreme reduced maternal care behaviors than *A. eximius* (e.g., trends in Figures 1A,B and 2A,B). This again is consistent with differences in level of sociality: *A. domingo* are known to cooperate more in prey capture (Guevara and Avilés 2011) and, compared with *A. eximius*, their colonies may be more likely to propagate by fission rather than by the dispersal of single females (Avilés L, personal observation).

Potential causes of reduced maternal care

Perhaps, the largest question our results raise is: what biological process is responsible for the reduction in maternal care we observed in social cobweb spider species? There are a number of viable alternatives. First, our results could be indicative of a facultative reduction of maternal care in response to the presence of "helpers" (alloparents). This behavior, dubbed "load-lightening" by Brown et al. (1978), has been widely reported for various cooperatively breeding birds (reviewed in Crick 1992; Heinsohn 2004). In the case of birds, parents with helpers spend less time caring for their offspring and more time self-feeding, assumingly increasing their survival and future breeding (Crick 1992; Cockburn 1998).

However, evidence suggests that load-lightening may not be the explanation for the reduction in maternal care we observed. In a previous laboratory study, we reared gravid subsocial and social females in isolation for a period of 1 month. Despite these spiders being free of social interactions and any "help stimulus," we recovered the same pattern and magnitude of reduced care in the social species relative to their subsocial relatives (Samuk K, Avilés L, unpublished data). Thus, it seems that in the timeframe of our previous study, cobweb spiders do not facultatively adjust their maternal care in response to social context.

Apart from the social environment, maternal care behavior could also be facultatively adjusted to match the level of predation/parasitism perceived by female cobweb spiders (a major source of egg sac loss, Foelix 1996). However, during both this study and our previous study, we incidentally excluded predators and parasites from the experimental females. This exclusion lasted 1–2 days in this study and ~30 days in our previous study. Yet, we still recovered levels of maternal care behavior similar to our field estimates for both subsocial and social females (Figure 1, Samuk K, Avilés L, unpublished data). These observations suggest that the observed reduction of maternal care behavior in social *Anelosimus* is likely a fixed species trait and not a result of plasticity.

If we accept that maternal care behavior is not a plastic trait in *Anelosimus*, the pattern we observed could be the result of divergent natural selection caused by different external environments. Such selection would need to somehow favor "low parenting" behavioral phenotypes in social species, but not in subsocial species. This could occur if, for example, social species tend to live in areas with lower levels of predation. However, species in one of the social–subsocial pairs, *A. guacamayos* and *A. elegans*, are currently sympatric and have likely been so in the past (Avilés et al. 2007). Hence, their comparison has mostly controlled for differences in the external environment, currently and through evolutionary time. If the reduction in maternal care behavior were the result of extrinsic selection, we would have expected to observe similar levels of maternal care in *A. guacamayos* and *A. elegans*, which we did not (Figures 1–3).

The case for the other group of species is more complex: *A. eximus* and *A. domingo* are found in the lowland rain forest (~400 m elevation), whereas *A. baeza* and *A. cf. oritoyacu* are found in mid to high elevation cloud forest (~1600–2000 m elevation). Clearly, there are major environmental differences between these habitats. However, it is almost certain that nearly all of these differences would actually "increase" the risk to egg sacs of social species and thus favor "higher" levels of maternal care in social females. For example, we know that in the lowland rain forest, there is much greater potential for predation on social spiders by ants, birds, and wasps (Olson 1994; Rahbek 1997; Avilés et al. 2007; Purcell and Avilés 2007). Furthermore, there is far more physical disturbance in the form of debris, rain, and tree falls (Rahbek 1997; Purcell and Avilés 2007). Indeed, in their transplant study of *A. baeza* to the lowland rain forest, Purcell and Avilés (2008) found that *A. baeza* failed to establish due to high rates of rainfall and intense predation by ants. Thus, it seems overall unlikely that externally imposed selection explains the reduction in maternal care we observed. Note that a similar argument could be made for externally driven facultative reductions in maternal care.

Relaxed natural selection

Given that external environmental pressures do not appear to explain this pattern, we suggest that a relaxation of natural selection on maternal care behavior coincident with increased sociality is the most promising alternative explanation. There are several lines of evidence that support this idea. First, the reduction in maternal care we observed appears to have convergently evolved in each social species. Such independent convergent evolution of phenotypes under similar environments (social environments in this case) is generally agreed to be preliminary evidence of selection (Endler 1986). Secondly, studies of other spider species suggest that there is strong potential for a relaxation of selection on maternal care in social groups. For example, work in colonial *Metepeira* spp. and social *Stegodyphus dumicola* spiders suggests that egg sacs experience less predation in social versus subsocial nests (reviewed in Uetz and Hieber 1997; Henschel 1998). The amount of maternal care egg sacs need to prevent mortality also appears to be far lower in group-living species than in solitary ones (Uetz and Hieber 1997; Henschel 1998). This reduction in egg sac risk is ostensibly due to dilution effects, a larger denser nest, and possibly group active-antipredatory behaviors in social nests (Uetz and Hieber 1997; Henschel 1998). Social *Anelosimus* enjoy all these protective features and are also known to extensively alloparent (Samuk K, unpublished data, Avilés 1997). So, it seems reasonable to assume that egg sacs in social *Anelosimus* nests experience at least as much of a reduction in risk as do egg sacs in *Metepeira* and *Stegodyhpus* nests. Such a reduction in risk to egg sacs could easily result in a relaxation of natural selection on maternal care behavior in social *Anelosimus*. A notable exception to these patterns is the increased incidence of egg sac parasites in larger *A. eximius* nests (Avilés and Tufiño 1998), which makes the relaxed care of egg sacs observed somewhat paradoxical.

Interestingly, in a recent study, Jones et al. (2010) found that social morphs of the socially polymorphic cobweb spider *Anelosimus studiosus* had lower reproductive success in single-female colonies than did subsocial morphs. They interpret this difference as evidence of a fitness cost associated with decreased activity level and aggressiveness in the social morphs when in solitary nests. This is further evidence that the strength of natural selection can be ameliorated by social context in cobweb spiders generally.

Naturally, more information is needed to assess whether socially mediated relaxed natural selection in *Anelosimus* is indeed a cause of the pattern we observed. For one, analysis of more sister clade pairs is needed to further support this evolutionary association. Secondly, one could directly test if egg sacs are indeed at lower risk in social nests than in subsocial ones (i.e., attempt to link sociality with fitness directly). Third, the effect of early-life social environment on later-life maternal care behavior could be explored by repeating our assays on social and subsocial females reared from egg sacs "in isolation" in the lab. Together, these experiments would help flesh out the selective forces involved in driving the pattern, the differential costs and benefits of maternal care behavior across social contexts and the role of plasticity in driving this pattern.

If relaxed natural selection is indeed the mechanism driving this pattern, our results have interesting implications. First, for each maternal care metric we studied, we found consistent reductions in "mean" trait values in social versus subsocial species, rather than, for example, an increase in trait "variance" with no shift in mean ("classic" relaxed natural selection, Lahti et al. 2009). This result is suggestive of one specific type of relaxed selection, vestigialization (Fong et al. 1995; Lahti et al. 2009). This implies that there may be an evolutionary trade-off involving maternal care behavior in social species. One possibility is that in social nests, females who spend most of their time guarding are using up time that could be used for capturing prey or maintaining the web (i.e., paying a lost opportunity cost). Hence, natural selection may favor social females who spend less time with their egg sacs, and more time foraging, consistent with the Whitehouse and Lubin (2005) suggestion that social spider colonies are primarily foraging societies. Extra time spent foraging/maintaining the web may then translate into increased fitness, either directly through production of a second egg sac or indirectly via fitness benefits to close kin. Thus, a partial emancipation from egg sac defense may be one of the manifold selective benefits of sociality, all else being equal.

Correlated behaviors

There is one further mechanism that could act in concert with relaxed natural selection or underlie the pattern we observed: among-behavior trait correlations. It is widely appreciated that among-trait correlations arising via pleiotropy, genetic linkage, etc. can lead to correlated evolutionary responses (Lande and Arnold 1983; Brodie et al. 1995). Because the evolution of sociality typically involves changes in many different classes of behavior, among-behavior correlations have likely played a role in the behavioral evolution in social animals (Wcislo 2000; Pruitt et al. 2010). In terms of the present study, it could be the case that reduced maternal care evolved as a correlated by-product of the evolution of some other behavior. For instance, Pruitt et al. (2010) have shown that social morphs of the socially polymorphic spider *A. studiosus* tend to have low levels of both aggressiveness and activity per se. Conceivably, thus, the level of maternal care behavior provided by a spider with generally lower activity levels may be less vigorous and of lower quality.

Significance

Along with increasing our knowledge of social and behavioral evolution in spiders, our findings point to the importance of changes in the social environment in the evolutionary process. Theoretical discussion of this topic is widespread (e.g., Wolf and Moore 2010) yet empirical examples are, to our knowledge, relatively rare (but see Blumstein and Armitage 1998; Devillard et al. 2004). This dearth is quite surprising, as increasing levels of social complexity are widely recognized as extremely important transitions in the history of life (Maynard Smith and Szathmáry 1997). One of the most interesting aspects of this transition is that traits evolved in previous social contexts are thrust into what are often completely different selective landscapes. Along with the present study, examples of this phenomenon (in the broad sense) include the changes in cellular traits coincident with the evolution of multicellularity, and the exportation of genes from the mitochondrial to nuclear genome after endosymbiosis was established. Another intriguing parallel with our study is the "social brain" hypothesis from the primate literature, which suggests that the unique abilities of the primate (and human) brain are attributable to adaptation to complex social environments, that is, a change of selection in concert with sociality (Dunbar and Shultz 2007). Whatever the system, understanding how traits evolve and interact during and after the transition to a higher level of complexity is fundamental to our understanding of the evolution of complex organisms generally. Further studies of this process are badly needed.

CONCLUSION

In this study, we have shown that 3 social cobweb spiders display lower levels of maternal care behavior relative to subsocial species from sister clades. Based on this and a number of supporting facts, this may be the result of relaxed natural selection on maternal care behavior. This relaxation of selection could have occurred as a result of a reduced risk to egg sacs and amelioration of environmental stressors in the more social species. Our study represents a starting point for further investigation into the understudied role of social complexity in behavioural evolution.

FUNDING

Natural Sciences and Engineering Research Council(NSERC) of Canada Discovery (261354-2008 RGPI to L.A.). K.S. was additionally supported by an NSERC Canada Graduate Scholarship (Master's) award (2009–2010). E.L. was supported by an NSERC Undergraduate Student Research award (2010).

We would like to thank the staff of the corporation "Sociedad para la Investigación y el Monitoreo de la Biodiversidad Ecuatoriana" (SIMBIOE) and the El Ministerio del Ambiente de Ecuador for assistance with logistics and obtaining permits. The associates of Reserva Ecólogica Antisana, Estacion Biológica Jatun Sacha, and Bellavista Cloud forest Reserve all provided fantastic general assistance and field support. Maurico Vega also provided valuable field assistance. The Avilés Lab, Maxence Salomon, and Katherine Ostevik provided helpful discussion and suggestions on the manuscript.

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