

Indiscriminate care of offspring predates the evolution of sociality in alloparenting social spiders

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Abstract Alloparental care—the care of other’s offspring—is a key aspect of sociality in many groups of animals. Understanding how this complex behavior arises requires identifying both the selective forces that may favor it, as well as characteristics of particular lineages that facilitate or hinder its evolution. One potential hindrance is the existence of discrimination against foreign offspring, an obstacle that would need to be overcome in order for alloparental care to evolve. In this study, we explored whether offspring discrimination may have constrained the evolution of alloparental care in social spiders in the genus *Anelosimus*. Social spiders are known for their cooperative behaviors, which include alloparental care. After quantitatively assessing the extent of alloparenting in the care of egg sacs in natural nests of these spiders, we investigated whether discrimination against foreign egg sacs existed in ancestral pre-social species in the genus. We did so by testing for discrimination between a female’s own and foreign egg sacs in three subsocial sister taxa of each social species investigated. We found no detectable evidence of discrimination in the care of egg sacs by female *Anelosimus*, regardless of level of sociality. We used these data, along with those from previous studies, to infer that a lack of discrimination is likely the ancestral state in the genus *Anelosimus*. This supports the idea that offspring discrimination was not a constraint on the evolution of alloparental care in social *Anelosimus* species. We discuss

the evolutionary implications of this finding, and suggest that lack of offspring discrimination may have eased the transition from solitary to cooperative breeding.

Keywords Alloparental care · Co-option · Adoption · Sociality · Maternal care · *Anelosimus*

Alloparental care, i.e., the care of other’s offspring, occurs widely among social animals. It encompasses phenomena such as sibling–sibling care in cooperatively breeding birds, allosuckling in sperm whales, and sterile care-giving castes in eusocial insects (Wilson 1975). Over the last 40 years, the importance and prevalence of this intriguing behavior has become increasingly apparent. Indeed, along with group living, alloparental care is considered one of the essential aspects of advanced sociality (Crespi and Yanega 1995; Burda et al. 2000). Hence, understanding the evolution of alloparental care is a key component in elucidating the evolution of cooperative living generally.

Documenting the occurrence of alloparental care is a first step in assessing its significance in any group of organisms. Once shown to occur, research can then move to exploring how such behaviors might have evolved (reviewed variously in Dugatkin 1997; Koenig and Dickinson 2004; Bergmüller et al. 2007; Clutton-Brock 2009). Understanding the evolution of alloparental care requires not only consideration of the extrinsic biotic and abiotic factors that may favor alloparenting, such as seasonality or high predation risk (Bergmüller et al. 2007; Clutton-Brock 2009), but also consideration of intrinsic characteristics of a species or group of species that may facilitate or hinder its evolution. Examples of the latter include the typical kin composition of social groups or the presence or absence of discrimination against foreign offspring. While extrinsic factors have been explored at length in the literature (e.g., Bergmüller et al. 2007; Clutton-Brock 2009 and references therein), the role of intrinsic factors other than relatedness has only recently begun to be explored (e.g., Hunt 1999; Toth et al. 2007).

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One intrinsic factor recently receiving attention is the degree of co-optability of parental care in a lineage (Jamieson and Craig 1987; Toth et al. 2007). Essentially, there may be certain characteristics of the parental care behavior of some species that allow them to more (or less) easily evolve alloparental care (Toth et al. 2007). Identifying such characteristics may thus aid in understanding why particular lineages evolve alloparental care more readily than others. One such characteristic is offspring discrimination. If an animal has evolved to reject offspring who are not its own, we would expect that an extra evolutionary step—the loss or attenuation of this discrimination—would be required for the evolution of alloparental care. Such discrimination is known to exist in many animal species, and hence could be an important constraint on the evolution of alloparental care (birds—Lefevre et al. 1998; ants—Shimoji et al. 2012; primates—Hammerschmidt and Fischer 1998; rodents—Phillips and Tang-Martinez 1998; amphibians—Gibbons et al. 2003). One way of examining how important such a constraint might be is to examine the association between alloparental care in contemporary species and the reconstructed ancestral state of offspring discrimination in their lineages. This requires a body of empirical data on discrimination, as well as a resolved phylogeny of the group.

Here, we assess quantitatively the presence of alloparental care in social spider species of the genus *Anelosimus* and investigate whether lack of discrimination between own and foreign offspring may have been the ancestral condition preceding the origin of this behavior in the genus. *Anelosimus* spiders lend themselves to an investigation of the association between a lack of offspring discrimination and alloparental care for two reasons. First, social species have independently evolved multiple times from within a clade of mostly subsocial species, with the latter resembling the ancestral species from which the social ones might have originated (Avilés 1997; Agnarsson et al. 2007). Second, there is a well-resolved phylogeny of the genus (Agnarsson 2006; Agnarsson et al. 2006, 2007) that can be used to infer ancestral behavioral states. In social species, individuals remain grouped as adults, cooperatively building, hunting, and likely performing alloparental care (Avilés 1997). In subsocial species, in contrast, adult females live alone in single-individual nests in which their offspring hatch, fledge, and eventually disperse (Avilés 1997).

While alloparental care is thought to occur in ~11 species of permanently social spiders, most reports of its occurrence, including most studies of *Anelosimus* (Christenson 1984; Furey 1998, but see Jones et al. 2007), are largely qualitative or anecdotal (Lubin and Bilde 2007 and references therein). Focusing on the alloparental care of egg sacs—silken structures that contain the entire clutch of a single female (Foelix 1996), we had two objectives in this study. First, we set out to confirm the occurrence of alloparental care in several social *Anelosimus* species using a quantitative measure that makes it possible to assess variability among species. Secondly, we

aimed to determine whether lack of discrimination between own and foreign offspring may have preceded the origin of alloparental care in the genus. We did this by assessing offspring discrimination in subsocial species related to the social ones included in this study and by compiling data from the literature on other *Anelosimus* (Furey 1998; Avilés and Salazar 1999; Avilés and Purcell 2011) and other theridiids outside the genus (Grinsted et al. 2012).

Methods

Study species

We focused on the ‘eximius’ clade of the genus *Anelosimus* (Agnarsson 2012), which contains five social species, representing four to five independent origins of this social system (see subclade in Fig. 3). We selected six species from this subclade for study: three subsocial species—*Anelosimus elegans*, *Anelosimus cf. oritoyacu*, and *Anelosimus baeza*—and the three permanently social species—*Anelosimus guacamayos*, *Anelosimus domingo*, and *Anelosimus eximius*. Of these, *A. guacamayos* appears to exhibit a lower level of sociality than the other two, as females of this species tend to live in smaller colonies and, more frequently than the other two species, also in single female nests (Avilés et al. 2007; Avilés and Harwood 2012). For our measures of alloparental care in the wild, we collected data on all six species. For our assays of offspring discrimination in the laboratory, we focused on the subsocial *A. elegans* and its social sister species *A. guacamayos* and the subsocial *A. baeza* chosen as a subsocial representative from a clade sister to that to which the social *A. eximius* belongs to.

Field sites

We performed our work at four field sites in eastern Ecuador. We studied *A. eximius* and *A. domingo* at the Jatun Sacha Biological Station (lowland rainforest, 400 m elevation, 1.06°S, 77.61°W), *A. guacamayos* and *A. elegans* in the Reserva Ecológica Antisana and Parque Nacional Sumaco (cloudforest, 1,840 m elevation, 0.64°S, 77.8°W), *A. baeza* at the Yanayacu Biological Station (cloudforest, 2,200 m elevation, 0.60°S, 77.89°W), and *A. cf. oritoyacu* at the Bellavista Cloudforest Reserve near Tandayapa (2,000 m elevation, 0.016°S, 78.68°W). *A. cf. oritoyacu* is a presently undescribed species, morphologically close to the social *A. oritoyacu* (Avilés and Purcell 2011), but clearly subsocial, as its colonies contain a single adult female and her offspring (L. Avilés, unpublished data).

Field assays of alloparental care

Our first objective was to confirm the existence and quantitatively estimate the extent of alloparental care in *Anelosimus*

species. This requires the selection of maternal care behaviors to study. One of the most important forms of maternal care offered by spiders involves clutching the egg sac in order to move it around the nest, away from predators and parasites, under cover, etc. (Gillespie 1990; Foelix 1996). Eventually, females also facilitate the exit of the spiderlings from the egg sac by opening it and also feed the spiderlings by regurgitation (Viera et al. 2007). These care behaviors, particularly those that occur at the egg sac stage, are necessary for the survival of the offspring (Gillespie 1990). Of these behaviors, the act of guarding or clutching the egg sac is likely the most universal form of maternal care in spiders. It is also the easiest to assay in the field, particularly since marking and tracking individual spiderlings can be difficult. Thus, focusing on egg sac care behaviors, we measured the extent of alloparental care as the probability of observing a different individual clutching an egg sac in a subsequent observation—hereafter referred to as “switching probability”. This also provides, by extension, the probability that the same individual will remain with the same egg sac between subsequent observations (“remaining probability”), also an informative quantity.

We located and marked colonies of each species (social and subsocial) that contained females clutching egg sacs. Due to methodological constraints, we could not mark every female in nests with more than 10 females. We thus subsampled larger nests using a transect method: for each 10-cm mark along the longest, geometrically centered axis of the colony, we selected the closest female clutching an egg sac. We removed these females and their clutched egg sac from the nest using a drinking-straw aspirator, and marked them with matching acrylic paint marks. After the paint had dried, we replaced the female and her egg sac at the approximate site of their removal.

Following marking, we returned to each colony approximately nine times over 3 days, distributed equally over morning (0600–1200), afternoon (1300–1600), and evening (1800–2300) observation periods. For each marked egg sac we were able to locate, we recorded whether it was being clutched and the identity of the female clutching it (her paint mark color, “unmarked”, or no female). After removing ambiguous observations, i.e., those in which either the egg sac or female were unmarked, we calculated the proportion of observations in which the egg sac and female identities remained the same as the previous observation (“remain”), changed identities (“switch”), or transitioned from having a female (marked or not) to no female (“abandon”). This method captures a snapshot of alloparental care in the nest and is conservative in its estimate of “true” switching rate (see simulation in [Supplementary material](#)). Every switch in egg sac or female identity we observed involved the female departing from the egg sac she was caring for, encountering a new egg sac and resuming care behavior.

Note that we performed our egg sac switching assay in nests of social species, which typically contain multiple females and egg sacs, and nests of subsocial species, which typically contain a single female and egg sac. We did this for a number of reasons. First, switching between egg sacs or females is not completely out of the question for subsocial females nesting close to one another (e.g., on the same plant, which is sometimes the case). These females may become separated from their egg sacs during prey capture events or when dropping out of their nests in response to threats and must then re-locate their egg sac and resume care (K. Samuk and L. Avilés, personal observations). Secondly, this allows us to control for the effect of paint marks on the egg sac care behavior of females (we also systematically tested for this effect in laboratory experiments, see Table S1). Finally, it allowed us to directly determine the extent of care provided to an egg sac in social and subsocial nests.

Offspring discrimination

Our second objective was to determine whether lack of offspring discrimination was ancestral to the social *Anelosimus* species we studied. We operationally defined lack of offspring discrimination as providing the same level of care for a foreign egg sac and one’s own egg sac.

Rearing protocol

Because we needed to be certain of maternity, in the case of social species we collected female spiders that appeared gravid (i.e., had swollen abdomens with darkened sagittal spots) (52 *A. guacamayos* and 40 *A. eximius* females from 12 and seven independent colonies, respectively) and reared them until they produced egg sacs. In the case of the subsocial species, where the risk of maternity confusion is minimal to none, we collected females and their egg sacs from their individual nests (32 *A. elegans* and 58 *A. baeza*). We deposited these spiders in cylindrical plastic containers with a height of 5.5 cm and a circumference of 11 cm. Each container contained a ~0.2-cm-wide by 10-cm-long twig placed diagonally, and two 9×3 cm leaves obtained from various plant species we observed *Anelosimus* spp. nesting on. Leaves were placed over and under the twig, forming a retreat and nesting substrate. Containers were topped with perforated plastic lids with approximately eight 0.1 cm holes/cm².

We opened each container daily, cleared it of detritus and fungus, and administered a fine misting of water from a spray bottle. Every other day, we fed spiders insects sized approximately one half their body length (0.2–0.8 cm, depending on the species). Insects were primarily small dipterans, lepidopterans, orthopterans, and homopterans. We captured insects using a blacklight projected on a hanging sheet or by sweep-netting grassy areas. After ~30 days

of feeding, the following number of females produced egg sacs: 21/32 *A. elegans*, 24/58 *A. baeza*, 32/52 *A. guacamayos*, and 11/40 *A. eximius*. All of these females were entered into the experiment described below.

Offspring discrimination assay

We performed our egg sac care assays by presenting the spiders with either their own or a foreign egg sac. We chose to present spiders with single egg sacs in separate trials rather than both sacs simultaneously because this best mimics the way females would encounter egg sacs in the wild. Subsocial spiders only care for a single egg sac, while roving females in social nests typically encounter egg sacs one at a time (K. Samuk, personal observation).

We began our assay by removing egg sacs from females entering the experiment. In most cases, this involved separating the egg sac from the spider by gently gripping it with FeatherWeight forceps (BioQuip products, CA, USA) and jiggling it free of the spider's mouthparts. After a 10-min cool-down period, we presented females with their own egg sac or the egg sac of a conspecific (separately collected from field colonies at least 500 m away). To control for possible treatment order effects, we randomly chose half of the females to receive their own egg sac first, and the other half to receive the egg sac of a conspecific first. We repeated the assay described below at least 48 h later with the opposite type of egg sac (own or conspecific, whichever the female had not yet received). Egg sacs were used only once for each experiment and returned to their nest of origin after use.

We presented egg sacs to the females by placing them in the geometric center of the nest. We regarded this as a suitably natural way for a female to encounter and choose to care for an egg sac. We returned to each container at 11 observation times: immediately after introduction, then at three half-hour-long intervals between 0.5 and 1.5 h, 6-h-long intervals between 2.5 and 7.5 h, and a final observation at 24 h after introduction. Based on a pilot study, this observation schedule allowed us to best capture the time course of the care decision.

At each observation time, we measured the distance between the egg sac and female, whether the egg sac was under cover (not visible from directly above), and whether the female was caring for the egg sac (clutching it with her palps/chelicerae). These metrics and the combinations of them described below were designed to capture the general protective functions (anti-predatory/parasite/fungus and thermoregulatory) of spider egg sac care described by Foelix (1996).

We used a linear modeling approach to test for the effects of egg maternity on five dimensions of maternal care derived from our experiment: (i) probability of accepting the egg sac, (ii) latency to accepting the egg sac, (iii) mean egg sac–female distance, (iv) proportion of observations in which the female

was exhibiting care behavior, and (v) proportion of observations in which the egg sac was under cover. Because metrics (ii)–(v) required egg sac acceptance to occur, we only analyzed these responses for females who had accepted both their own and foreign egg sac presented to them in separate trials (~90 % of the females). While metric (i) was aimed at detecting offspring discrimination in an all-or-nothing sense, responses (ii)–(v) were aimed at detecting more subtle differences in maternal care provided to each sac.

We transformed responses (ii)–(v) to ensure normality of model residuals (see Table 1 for transformations), which were then assessed visually using a normal quantile plot. Because the response for variable (i) was binary, we used a mixed-effects logistic regression in lieu of standard mixed-effects regression for this analysis.

For each response variable, we fit generalized linear mixed effects models using the lme and lmer functions in the lme4 package in R (Development Core Team 2008; Bates et al. 2011). Because it was not standardized per se in the experiment, initial egg to female distance was included in all models (i.e., its effect on the response was removed prior to fitting the treatment effect). We also included the effect of species as the first term in every model to account for between-species variance in the absolute amount of care provided to egg sacs. Finally, each model included two random effects: source nest identity (to address potential non-independence of related females from the same nest) and female identity nested in source nest identity to account for repeated measures. Thus, each model followed the general formula of: care behavior=species+initial egg sac distance+egg maternity+source nest ID/female ID (random effects), where “/” implies nesting. We used ANOVA (responses ii–v) or likelihood ratio tests (response i) to assess the significance of the fixed effects of the various models.

Ancestral state reconstruction

We inferred the ancestral state of discrimination/no discrimination in *Anelosimus* using maximum parsimony, i.e., the ancestral behavioral trait is that which requires the fewest changes to produce the distribution of contemporary behaviors. To do this, we combined the data from our discrimination and alloparental care assays along with the data from four published studies, three on other *Anelosimus* species (Furey 1998; Avilés and Salazar 1999; Avilés and Purcell 2011) and another on two Theridiids outside *Anelosimus* (Grinsted et al. 2012). Using the phylogeny from Agnarsson et al. 2007, we scored *Anelosimus* species as lacking discrimination based on (i) whether they had been directly assayed for discrimination (this study—*A. elegans*, *A. baeza*, *A. guacamayos*, and *A. eximius*; Furey 1998—*A. studiosus*; Grinsted et al. 2012—*Chickua negra* and *Chickua* sp.) or (ii) whether field observations suggested a lack of discrimination, i.e., females caring for grouped egg

Table 1 Likelihood ratio tests (acceptance probability) and *F* tests (all other responses) of fixed effects derived from generalized linear mixed effect models of four measures of maternal care in experimental *Anelosimus* females

Response	Acceptance probability			Acceptance latency			Distance			Prop. time caring			Prop. time covered		
	–	Binomial		Reciprocal			Box–Cox			Arcsine $\sqrt{\quad}$			Arcsine $\sqrt{\quad}$		
Distribution		Source/individual		Gaussian			Gaussian			Gaussian			Gaussian		
Random effects:				Source/individual			Source/individual			Source/individual			Source/individual		
Fixed effects	<i>df</i>	χ^2	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>
Species	6	21.05	<0.001	44	114.47	<0.001	21	74.04	<0.001	21	254.68	<0.001	21	44.26	<0.001
Initial distance	7	1.79	0.18	41	8.73	0.005	89	20.17	<0.001	89	10.12	0.002	89	2.08	0.15
Treatment	8	0.38	0.54	41	0.32	0.57	89	0.47	0.49	89	0.97	0.33	89	0.44	0.51

Slashes between random effects indicate nestedness of the second term in the first. “Prop.” indicates a proportional measurement, i.e., the proportion of observational periods in which the behavior was observed. See text for analysis details

sacs laid by several different females (*Anelosimus rupununi*, Avilés and Salazar 1999) or marked females switching between marked egg sacs (*A. oritoyacu*, Avilés and Purcell 2011). Because there was only one observed state—no discrimination, we inferred the most parsimonious ancestral state by inspection.

Results

Alloparental care

In total, in the four species studied we observed 723 informative egg-sac transition events (Fig. 1). With the exception of one *A. cf. oritoyacu* female who abandoned her egg sac during the observation period, all subsocial females (*A. elegans*, *A. baeza*, and *A. cf. oritoyacu*) and all solitary *A. guacamayos* females remained with their egg sacs during the entire observation period (Fig. 1). *A. guacamayos* females in multi-female nests remained with the same egg sac ~72 % of the time. In extreme contrast, *A. eximius* and *A. domingo* females remained with the same egg sac in only ~3 % of meaningful observations (Fig. 1). Both of these differences were highly significant (two-sample test for equality of proportions with Yates’ continuity correction—*A. domingo* vs. *A. guacamayos* $\chi^2=27.44$, *df*=1, *p*<<0.001; *A. eximius* vs. *A. guacamayos* $\chi^2=35.66$, *df*=1, *p*<<0.001).

We observed high probabilities of female egg sac switching behavior in all three social species (Fig. 1). Interestingly, *A. domingo* and *A. eximius* females switched egg sacs approximately five (61 %) and six (70 %) times more often than *A. guacamayos* females in multi-female nests (12 %, Fig. 1). Both of these differences were highly significant (symmetrical to comparison of switching rate above). Surprisingly, egg sacs in *A. domingo* and *A. eximius* nests were found without females caring for them approximately 34 % and 25 % of the time, in contrast with only 2 % of the time in multi-females nests of *A. guacamayos* (as above, *A. domingo* vs. *A. guacamayos* $\chi^2=17.65$, *df*=1, *p*<<0.001; *A. eximius* vs. *A. guacamayos* $\chi^2=4.35$, *df*=1, *p*=0.037).

Offspring discrimination

After accounting for between-species differences and the effect of initial egg sac to female distance, there was no significant difference in the acceptance probability (Table 1) or level of care provided by female *Anelosimus* to their own egg and foreign egg sacs (Table 1, Fig. 2). There was no preference for own vs. foreign egg sacs among females who did not accept both egg sacs (Table 1, acceptance probability). For females that accepted both egg sacs (~90 % of females), there was no difference in acceptance latency, female distance to the egg sac, proportion of time the egg sac was cared for, and proportion of

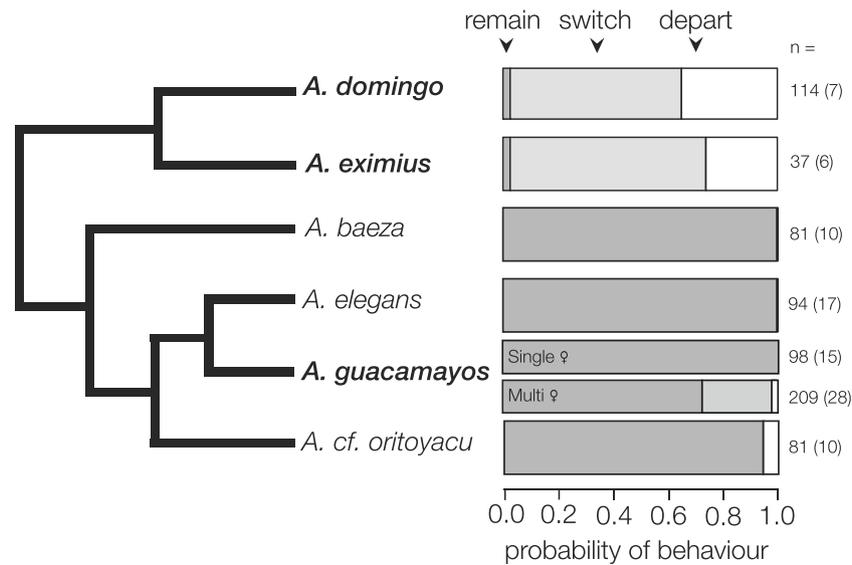


Fig. 1 The extent of alloparental care in six species of cobweb spiders (*Anelosimus* spp.). Stacked bars represent species-wide average probabilities of observing each indicated behavior in subsequent observations of an egg sac. Behaviors: “Remain”—the identity of the female caring for an egg sac remains the same; “Switch”—the identity of the female caring for an egg sac changes; “Depart”—the female previously caring for the egg sac departs and no other female takes her place (i.e.,

a lone egg sac). *A. guacamayos* data are divided into observations of single female nests and multi-female nests. Sample sizes indicate the total number of observations summed across all egg sacs, with the number of nests in parentheses. Social species are shown in bold. The phylogenetic position of *A. cf. oritoyacu*, which is an undescribed species, was inferred based on its close morphological similarity of *A. oritoyacu* (author 2, unpublished data)

time the egg sac remained under cover. No two-way interaction effects (species \times treatment, species \times initial distance, and initial distance \times treatment) were significant in any of the five models and were hence removed prior to ANOVA or likelihood ratio tests (Crawley 2002).

Both species and initial distance were significant predictors of most discrimination assay responses (Table 1). Note that the full model accounts for the variation explained by these factors before testing for the effect of egg identity (i.e., they were treated as nuisance variables and statistically controlled for).

Ancestral state of discrimination

There was no (statistically detectable) evidence of kin discrimination in any of the *Anelosimus* species included in our combined dataset ($n=10$ species) (Fig. 3). Thus, based on maximum parsimony, the most likely ancestral behavioral state in *Anelosimus* is a lack of discrimination (zero state changes required).

Discussion

In our field assays, we found that switching between egg sacs was present in the three permanently social *Anelosimus* species we examined, but at substantially different levels: *A. eximius* and *A. domingo* females switched frequently between

egg sacs, while group-living *A. guacamayos* females switched considerably less often. In our experimental assay of egg sac discrimination, no species, regardless of level of sociality, exhibited a difference in how females treated their own egg sac and that of a conspecific. Thus, there is no statistical evidence of egg sac discrimination in these species. These results, combined with previous studies, reveal that a lack of offspring discrimination is the most parsimonious ancestral state for *Anelosimus* and possibly other Theridiids (e.g., Grinsted et al. 2012).

Patterns of alloparental care in *Anelosimus*

Our field estimates of alloparental care produced a number of interesting patterns. For one, the extent of alloparental care differed significantly between *A. guacamayos* and *A. eximius/A. domingo* (Fig. 1). This is consistent with the suggestion that *A. guacamayos* is generally less social than *A. eximius* and *A. domingo* (Aviles et al. 2007; Avilés and Harwood 2012). Specifically, *A. guacamayos* females are known to be more likely to establish solitary nests, form smaller colonies, and, when in groups, to show a certain degree of territoriality by physically spacing themselves and their egg sacs within the nests (Aviles et al. 2007; Avilés and Harwood 2012). We also found that social species often leave their egg sacs unguarded for large periods of time, whereas subsocial species generally do not (Fig. 1). This is consistent with findings in another study that social species

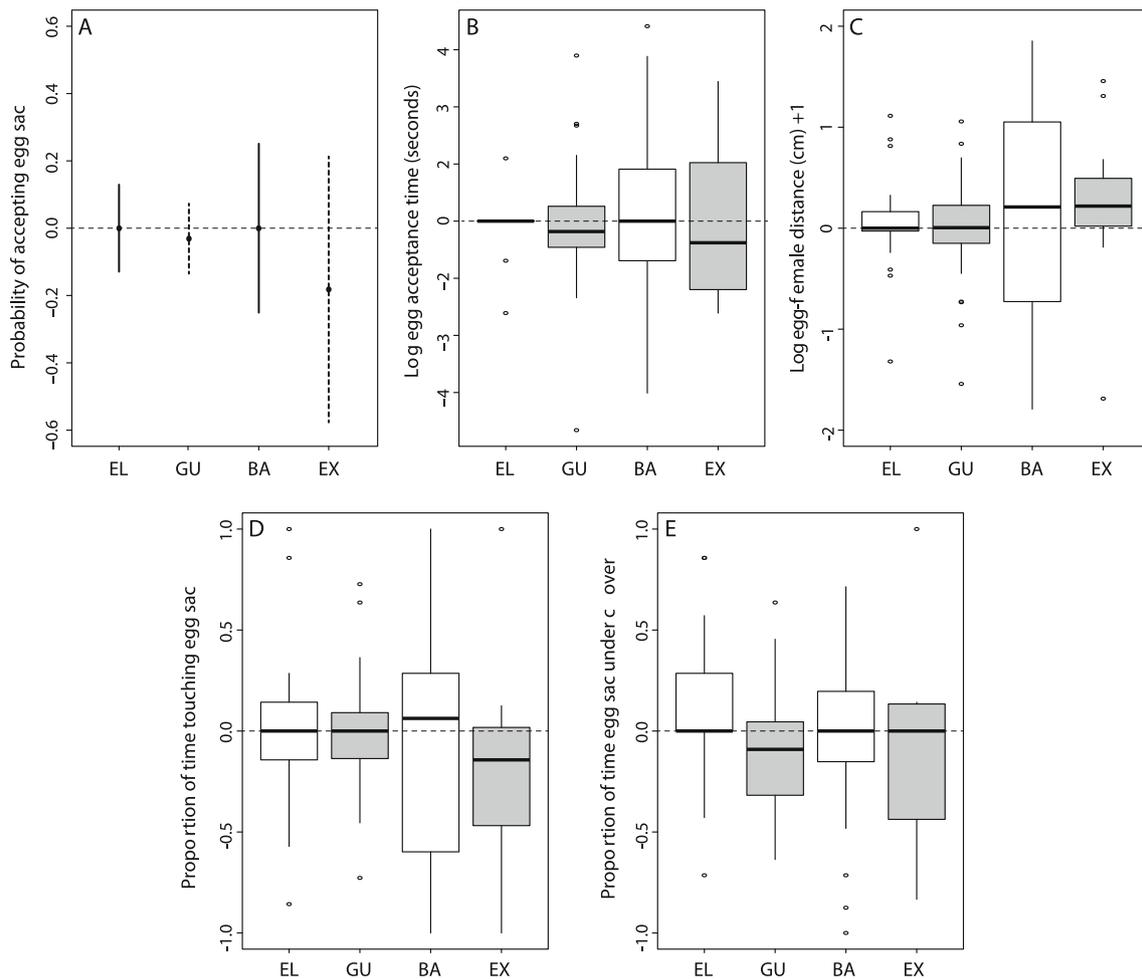


Fig. 2 Dot plot (a) and boxplots (b–d) of differences in the level of five care behaviors provided by *Anelosimus* females to their own versus foreign egg sacs. Dependent axes display the level of care behavior females provided to their own egg sac minus the level provided to a foreign egg sac in a different trial. Horizontal dotted lines indicate the expected score when there is no difference in egg

sac care. Species labels correspond to *EL*—*A. elegans*, *GU*—*A. guacamayos*, *BA*—*A. baeza*, and *EX*—*A. eximius*. Error bars in (a) represent 95 % confidence intervals. Dashed lines (a) and shaded boxes (b–e) indicate social species. Solid lines (a) and white boxes (b–e) indicate subsocial species

exhibit reduced maternal care behaviors relative to subsocial ones (Samuk et al. 2011).

Our measures of alloparental care, however, did not capture the relative amount of time females in the social colonies allocate to their own vs. the egg sacs of others, as we were unable to explicitly identify which egg sacs belonged to which females in the field surveys of the social species. Maternity for a given egg sac can only be definitively assigned if the female spins the sac in isolation, as in our experiment, or if egg sacs and females are destructively sampled for genetic analysis. Nonetheless, because egg sacs contain the eggs of a single female, any degree of switching is directly indicative of alloparental care, in particular with the extensive amount of switching taking place in *A. eximius/domingo*. This is less clear in the case of *A. guacamayos* (Fig. 3), where we do not know if the small amount of switching observed in the multi-female nests is due to females remaining longer with

their own egg sacs or simply infrequent (but unbiased) egg sac switching.

The role of offspring discrimination

Our ancestral state reconstruction suggests that the ancient subsocial spiders from which modern social spiders evolved probably did not display offspring discrimination. Hence, this trait did not need to be overcome in order for social species to evolve alloparental care. However, this leaves the question of why alloparental care was not selected against (and is currently maintained) in *Anelosimus*. The likely answer is that alloparental care may be broadly adaptive in *Anelosimus*. Studies by Jones et al. (2007) and Jones and Riechert (2008) have shown that the presence of surrogate caregivers is adaptive when there is a high probability that a mother will die before her offspring are self-sufficient (Gadagkar 1990).

Fig. 3 The phylogenetic distributions of offspring discrimination and sociality in *Anelosimus* and *Chickua*. *Solid dots* on the tree nodes represent ancestral states of offspring discrimination inferred by maximum parsimony (sociality ancestral states not shown). Branches with *dashed lines* represent taxa not included in the study. The “*Method*” column refers to the technique used to infer offspring discrimination: either experimentally presenting foreign egg sacs (assay) or by direct in-nest observation of egg sac switching (observation). Social taxa are indicated by *boldface* species names



Further, social *Anelosimus* species obligately inbreed and have high intra-colony relatedness, implying that most “foreign” offspring that females encounter in their nests are actually close kin (Avilés 1997; Agnarsson et al. 2010). Thus, there is scope for females to readily obtain indirect fitness via alloparenting.

Interestingly, a lack of parental discrimination as an ancestral condition opens up the opportunity for alloparental care to emerge as soon as females have access to egg sacs other than their own in the context of group living. With no “waiting time” for alloparental care to evolve, any benefits resulting from alloparental care could then compensate for negative aspects of group life, such as increased competition or parasitism. This could in turn facilitate the evolution of group living by shallowing or eliminating a potential “fitness valley” between subsocial and social life (sensu Jones et al. 2010). We thus suggest that a lack of discrimination against foreign egg sacs (this study), along with the extended maternal care behavior characteristic of the genus (Agnarsson et al. 2007), may have potentiated *Anelosimus* lineages to evolve permanent social behavior under particular ecological conditions (similarly discussed in Saffre et al. 1997). This may help explain the unusually frequent evolution of social behavior (and alloparental care) in this genus: four to six of 18 known independent origins of permanent social behavior in spiders (Agnarsson et al. 2006).

More generally, our results mesh well with the ideas discussed by Hunt (1999) that suites of pre-existing traits (and specifically maternal care behavior) can predispose lineages to evolve complex social behavior. For example, there is

good evidence from studies of paper wasps that sterile “nurse” workers behaviorally and neurochemically recapitulate previously evolved maternal care behaviors when caring for non-descendant offspring (Toth et al. 2007). While *Anelosimus* do not have sterile worker castes, the conceptual similarities between this result and the present study are worth noting.

Indiscriminate parental care: counter-intuitive?

The absence of offspring discrimination in species that raise their offspring in relative isolation (e.g. subsocial *Anelosimus*) should not be taken as surprising. Because these species are unlikely to encounter foreign offspring in the wild, they probably do not experience selection for offspring discrimination (Wisenden 1999). In fact, there should probably be selection against traits that risk rejection of one’s own offspring—potentially true of any rudimentary discrimination system (Tella et al. 1997). Hence, we expect that a lack of strong offspring discrimination is probably not uncommon among solitary/subsocial animals.

In contrast, we expect the opposite for species where unrelated families may be grouped in colonies and thus frequently encounter foreign offspring (Cullen 1957), as appears to be the case for many colonial birds (Seddon and van Heezik 1993; Lefevre et al. 1998). This suggests that a subsocial route to group living (a loss of dispersal behavior resulting in kinship structure and population viscosity) may impose fewer constraints on the evolution of alloparental care than a colonial (or parasocial) route

(Wilson 1975). Accordingly, other species of social spiders likely to also exhibit alloparental care (e.g., *Stegodyphus dumicola*) have also evolved sociality via the subsocial route (Schneider 2002; Salomon and Lubin 2007).

It should be noted that both discriminate and indiscriminate care (especially of egg sacs) has been reported for various species of spiders. To our knowledge, there are a total of five studies, in addition to this one, to have examined offspring recognition in spiders. A lack of offspring discrimination has been shown in three solitary species: *Loxosceles gaucho* (Sicariidae; Japyassú et al. 2003), *Miagrammopes animotus* (Uloboridae; Opell 2001), and *Pardosa milvina* (Lycosidae; Culley et al. 2010). In contrast, discrimination against foreign offspring has been observed in the subsocial spider *Diaea ergandros* (Thomisidae) (Evans 1998) and, under some circumstances, in the social *S. dumicola* (Eresidae) (Kurpick 2002, but see Schneider 2002). In the case of the *D. ergandros*, females accept foreign offspring into the nest, but provide less care to them than they do to their own offspring (Evans 1998). Interestingly, *S. dumicola* females refuse to guard foreign egg sacs, but allow foreign offspring to devour them via matrophagy (Kurpick 2002; Schneider 2002). In any case, although lack of discrimination is likely to be widespread in spiders, further data are needed to determine whether *Anelosimus* are exceptional in this regard.

Future work

Understanding why certain lineages are host to more social species than others is a major goal of behavioral ecology and evolutionary biology. Our results contribute towards this goal by providing the starting point of a larger investigation into the role of parental discrimination in hindering or facilitating the evolution of alloparental care and sociality. This will require additional data on discrimination in both alloparenting and non-alloparenting species and their relatives, both in spiders and other taxa. In the case of social spiders, the obvious next step is to expand the assay to other genera and families, particularly those that contain no social species. If offspring discrimination constrains the evolution of sociality/alloparental care, we might expect sociality-poor lineages to exhibit offspring discrimination more often. With sufficient data, we should eventually be able to test for a statistical association between indiscriminate care and the number of alloparenting species in a lineage. Finally, direct measurements of the costs and benefits of alloparental care, both for the parents and the offspring, will greatly advance our understanding of the evolution of alloparental care in *Anelosimus*.

Conclusion

We have shown that alloparental care in social *Anelosimus* is pervasive and variable between species. Between-species

variance in alloparental care may be a result of differences in the level of social behavior (probability of solitary nesting; inter-individual spacing). We have also demonstrated that a lack of offspring discrimination is likely the ancestral state for social *Anelosimus*. Hence, offspring discrimination did not constrain the evolution of alloparental care in this genus. Indeed, it is possible that indiscriminate care may have facilitated the evolution of alloparental care by allowing it to be expressed immediately, coincident with the origin of group living. This would allow alloparental care to be immediately “tested” by natural selection, rather than having to wait for sufficient mutation/recombination to modify an existing offspring recognition system. Taken in a phylogenetic context, our results suggest that the unusually frequent evolution of social behavior in *Anelosimus* may partly be explained by the co-optive potential of preexisting behavioral traits.

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