

EGGSAC RECOGNITION IN *LOXOSCELES GAUCHO* (ARANEAE, SICARIIDAE) AND THE EVOLUTION OF MATERNAL CARE IN SPIDERS

Hilton Ferreira Japyassú, Cátia Regina Macagnan and Irene Knysak: Laboratory of Arthropods, Butantan Institute, Av. Vital Brazil 1500, São Paulo—SP, 05503-900, BRAZIL

ABSTRACT. We report for the first time the existence of eggsac recognition and maternal care in *Loxosceles gaucho*. Spiders confronted simultaneously with their own and foreign eggsacs stay closer to their own eggsacs. This is unexpected since eggsac recognition should evolve among species with clumped distributions, high maternal investments and few breeding opportunities, features not present in this species. Despite this recognition, spiders with a single eggsac make no distinction between their own and foreign eggsacs: they adopt eggsacs from sympatric, conspecific females, and take care of them as their own. It seems that there is a readiness to perform maternal care that overrules the recognition system. We describe oviposition behavior and compare it with other descriptions in the literature. Seven behavioral characters related to eggsac building and/or guarding are mapped onto available phylogenies. Maternal care behaviors are quite conservative among spiders, useful for the grouping not only of families, but also of higher order ranks.

Keywords: Maternal care, offspring recognition, oviposition, evolution, Sicariidae, *Loxosceles gaucho*

Spiders show varying degrees of maternal care, from the building of an eggsac to oviposition at suitable sites (Suter et al. 1987; Christenson & Wenzl 1980), eggsac guarding (Pollard 1984; Richman & Jackson 1992; Castanho & Oliveira 1997), extended maternal care during the spiderlings' communal life (Morse 1992) including prey supply and regurgitation for feeding the young (Ito & Shinkai 1993; Evans 1998a; Li et al. 1999) and even extreme suicidal care (Evans et al. 1995; Schneider & Lubin 1997; Kim et al. 2000). Maternal care has positive fitness consequences, reducing predation on eggs (Fink 1987) and offspring (Fink 1986; Willey & Adler 1989; Morse 1992), or providing nutrition and consequently enhancing spiderling survival (Kullmann & Zimmermann 1974; Kim et al. 2000).

Spiders with extended maternal care should evolve offspring recognition systems to avoid exploitation by non-relatives. However, there is little evidence of kin recognition among spiders (Clark & Jackson 1994), perhaps because other conditions are necessary for the evolution of offspring discriminating systems. Evans (1998b) suggests that two of these con-

ditions are a high probability of encountering other conspecifics brood, and a low probability of future breeding opportunities.

Loxosceles gaucho Gertsch 1967 is a spider of medical importance whose bites cause necrotic lesions in humans (Jorge et al. 1991). Due to this medical importance, much of its biology is well documented (Rinaldi et al. 1997; Rinaldi & Stropa 1998). *Loxosceles* spp. are active at night, build simple or complex white silk sheet webs covering the substrate (Bücherl 1964), usually in small natural cavities (Bücherl 1962). Species in the genus do not fulfill any of the requirements for the evolution of kin recognition: they lay up to eight egg clutches from a single mating (Galiano 1967), and are solitary (Delgado 1966), showing a low probability of encountering unrelated offspring. In this paper we describe aspects of *L. gaucho* behavior, including oviposition, maternal care, and kin recognition. We also review the literature concerning these characters and discuss the results from a phylogenetic perspective.

METHODS

Sixty-three females (voucher specimens deposited at Butantan Institute, numbers 30064–

30069) were observed from mating to the emergence of the spiderlings (April–December 1999). Each spider was kept in a $30 \times 15 \times 20$ cm glass terrarium, under an external light–dark cycle, in the laboratory. Prey was offered three times/week, alternating between *Gryllus* sp. (Orthoptera), *Tenebrio molitor* larvae (Coleoptera), *Pycnocellus surinamensis* (Blattodea) and *Alphitobius pisceus* larvae (Coleoptera). Newborn *Gryllus* sp. and *Gryllobates sigilattus* (Orthoptera) were offered twice to the spiderlings five and ten days after their emergence from the eggsac. The observation period was terminated 15 days after the spiderlings emerged from the eggsac.

Experimental design.—Two experiments were conducted, one to test the existence of eggsac recognition by the mother ($n = 24$), and the other to evaluate the existence of maternal care and its fitness consequences ($n = 39$). In both cases, the mother was left five days with her own eggsac before it was removed for the beginning of the experimental treatment. The spiders spun a delicate covering sheet on the floor of the terraria, and attached the eggsacs into available folded pieces of cardboard paper, which served as retreats. In order to exchange eggsacs between spiders we removed these cardboard retreats from the terraria.

Eggsac recognition: Twenty-four females with eggsacs were divided into pairs, each pair with eggsacs built on the same day. In each pair, one female received back her own eggsac plus the one of the other female (herein considered the “foreign” eggsac). The second female in each pair was merely an eggsac donor.

Maternal care: The females were assigned to one of three experimental treatments, designed to evaluate the effect of maternal care on spiderling survival. Spiders in the “mother-with-own-offspring” group (own, $n = 14$) received back their own eggsac; this allowed the description of maternal care, and also functioned as a control for the other treatments. In the two remaining treatments, the females were divided into pairs, and each individual received the eggsac from the other in the pair; one female in the pair (adoption group) took care of the eggsac from her paired conspecific (adopt, $n = 13$) while the other was removed from the terraria (no-care

group), leaving the eggsac alone (ncare, $n = 12$).

Observational scheme.—In all the experimental treatments, the terraria were scanned three times a day (morning, afternoon and night), in three alternate days for each week, from mating to 15 days after the emergence of the offspring. We observed the relative position between spiders and eggsacs, and also the number of appendages touching the eggsac. If the spiders and/or offspring were in activity (ovipositing, foraging) the observational scheme changed to focal and ad libitum, that is, we focused on the active spider(s) until the end of the behavioral bout.

Comparative data.—The comparative information available in the literature allowed the description of 7 behavioral characters (Appendix 1). We mapped these characters onto the family cladogram proposed by Coddington & Levi (1991), modified at the araneid node by means of the cladogram proposed by Scharff & Coddington (1997); only unambiguous optimizations were discussed. We split the family Sicariidae in order to better analyze the genus *Loxosceles*; we also split the family Salticidae in order to distinguish the proposed primitive spartaeines (Jackson & Pollard 1996) from the other salticids.

RESULTS

Eggsac building.—Eggsac building occurred in four phases. First, the spider constructed a silken basal plate on the substrate. A few days later, she layed a gelatinous mass with the eggs on the basal plate, dried this mass by moving her palps and chelicerae, and finally layed a cover plate, composed of two superimposed silken layers. The observed time intervals within the whole reproductive period are presented in Table 1. The time interval from mating to eggsac building varies much more than the time of egg maturation.

Basal plate: The spider fixed dry threads onto the substrate with swinging movements of the abdomen. During the first part of the movement the spinnerets continuously touched the substrate; then they were lifted, describing an arch, just to touch the substrate again, then the movement was re-started in the opposite direction (Fig. 1a). This was repeated many times (Fig. 1b, c, d) until the spider made a small pause, changed the orientation of her body, and performed this whole pro-

Table 1.—Mean time lag (in days) between distinct behaviors performed by the mothers, from mating to the hatching of the spiderlings. Sample size, standard deviation and range are also shown.

First/Second event	<i>n</i>	Mean (days)	SD	Range
Mating/basal plate	19	47.4	18.0	24–82
Mating/egg mass (and cover plate)	70	59.6	28.1	21–120
Basal plate/egg mass (and cover plate)	19	1.7	1.4	0–5
Egg mass (and cover plate)/hatching	36	56.7	6.5	45–68

cedure over and over (Fig. 1d) to the completion of a circular sheet with a diameter of approximately 2 cm.

Egg mass: The spider stayed close to the basal plate for approximately two days, at which time she layed the egg mass onto it (Table 1). Initially, she layed a brownish gelatinous mass on the basal plate. This was done with the cephalotorax directed upwards. The spider repeatedly touched this mass with the palps, then with the chelicerae, ventral cephalotorax and ventral abdomen, always in this sequence. Next she layed the eggs in the mass, with a series of rhythmic leg I and II flexions (in one episode we counted 55 flexions); then she paused, rotated the body axis, and repeated this procedure several times (never more than ten times), gradually reducing the frequency of the rhythmic flexions and enlarging the pauses. At the end of this phase, the eggs were clearly visible through the gelatinous mass.

Desiccation: The spider handled the egg mass with the palps and paused with the chelicerae on the eggs for some minutes. Then she rotated and performed this same sequence until a full 360° rotation was completed. In the meantime, the gelatinous mass disappeared, exposing the conically arranged eggs.

Cover plate: Three distinct sequences of movements compose this last eggsac building phase (Fig. 2). First the spider attached silk at two points near the boundary of the basal plate (open dots, Fig. 2a) and at one point over the egg mass (closed dot, Fig. 2a); this small three-attachments cycle was repeated as the spider rotated on the eggsac (Fig. 2b, c, d); at the end of each cycle the spider paused and touched the egg mass with her palps. After a 360° rotation the spider sometimes repeated the whole procedure in the opposite direction. In the next sequence of movements, the spider fixed several times at opposite sides of the boundary of the basal plate (Fig. 3a, b); she

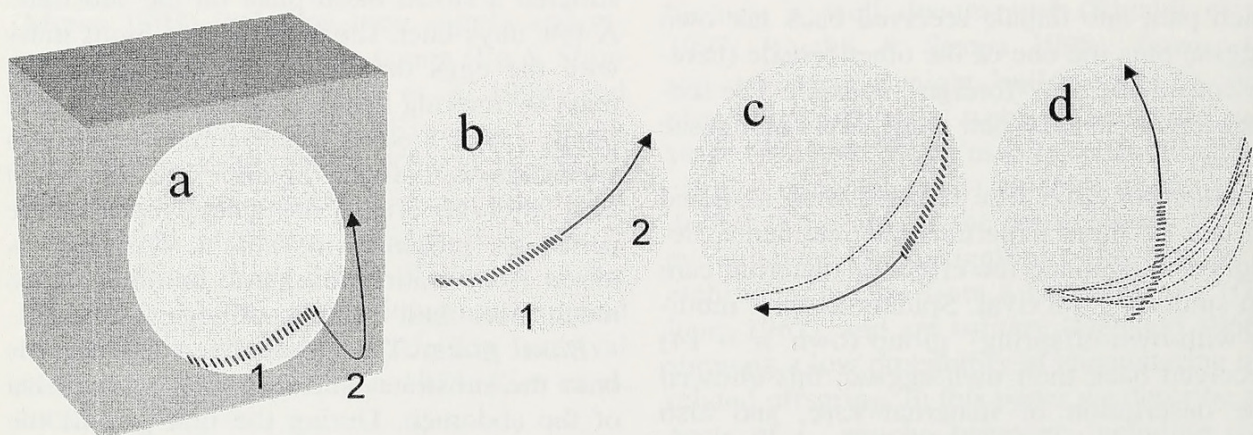


Figure 1.—Building of the basal plate. The spider lays threads (continuous and interrupted black lines) onto the vertical substrate (dark gray). These threads will eventually compose the basal plate (light gray). The spider touches the substrate continuously with the spinnerets during the first part of each movement (1) and then raises the abdomen (2) to touch the substrate again only at the end of the movement (a). These movements are shown in the remaining diagrams without perspective; threads laid in previous movements are depicted as dotted lines; threads currently being laid are shown as in b. After various back and forth movements (c, d) the spider changes the orientation of her body and begins a new back and forth series.

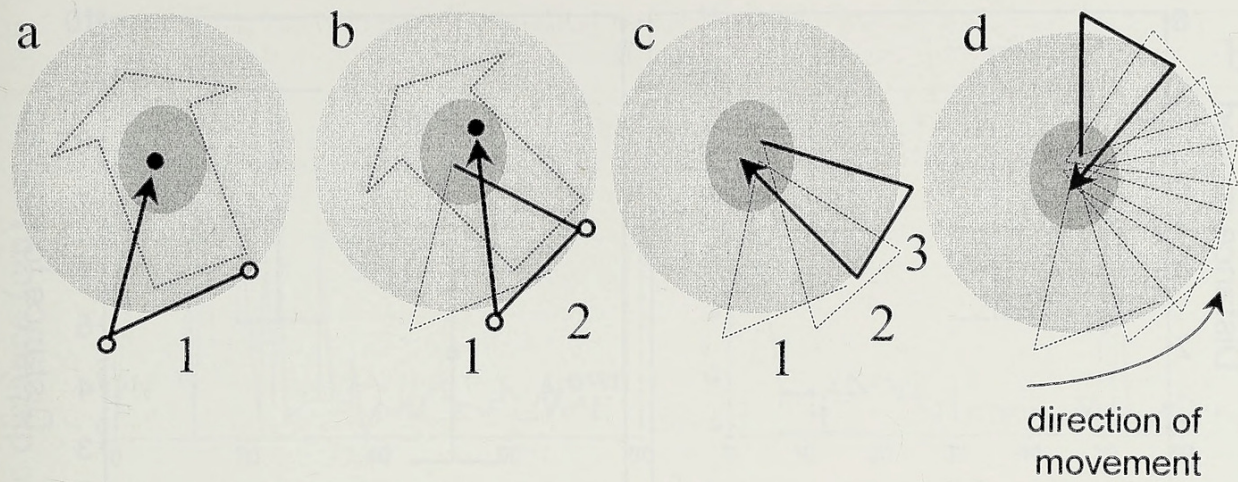


Figure 2.—Building of the first cover plate sheet. The spider lays threads over the basal plate (light gray) and egg mass (dark gray). The large dotted arrow represents the spider body axis (the arrow head is the cephalothorax). The building of this sheet involves the repetition of one same series of movements (1, 2, & 3 in a, b, & c) while rotating the body axis around the whole structure (d); at each movement the spider attaches the current thread in three points, two at the periphery of the basal plate (open dots in a and b), and one over the egg mass (black dot). Dotted lines indicate previous series of movements, and continuous lines indicate current series of movements.

then rotated to initiate a new bout of lateral fixations (Fig. 3c). Small variations in these movements are depicted at Fig. 3d. The spider then increased the amplitude of these lateral fixations, and occasionally scraped the ventral side of her cephalothorax and abdomen with her hind legs, possibly leaving hairs on the silken tissue. Sometimes the spider added small pieces of debris to the cover plate.

Mother-offspring interactions.—The female interacted in various ways with her egg-sac. She repaired it, adding lines to the whole

structure. She sometimes repositioned it and, in one case, even brought back the egg mass (which had fallen on the terrarium floor) to its original place, adding a new cover plate. A few days before the emergence of the spiderlings the mother made an aperture in the egg-sac and began to knock persistently at the cover plate, hitting at it with the tip of her forelegs (as if signaling to the spiderlings the appropriate moment to emerge); in one case we witnessed the mother holding the aperture while the spiderlings abandoned the eggsac.

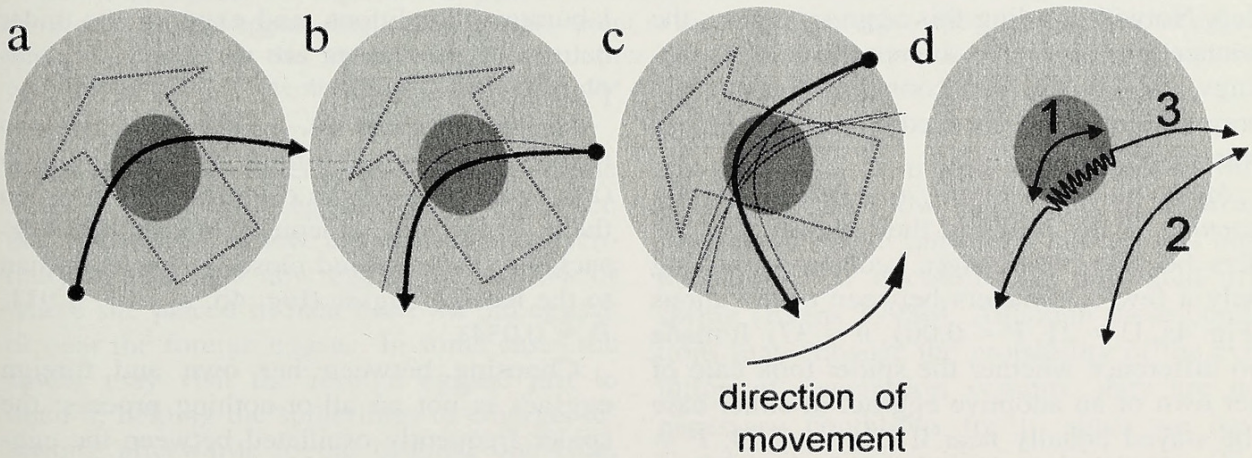


Figure 3.—Building of the second cover plate sheet. The spider makes various back and forth movements (a & b) before changing the body axis to restart this same series in another position (c). These back and forth movements may vary as to the fixation points (d), which can occur near the egg mass (1) or outside the basal plate (2); sometimes the spider slows down the movement while passing over the egg mass and attaches variously onto it (3).

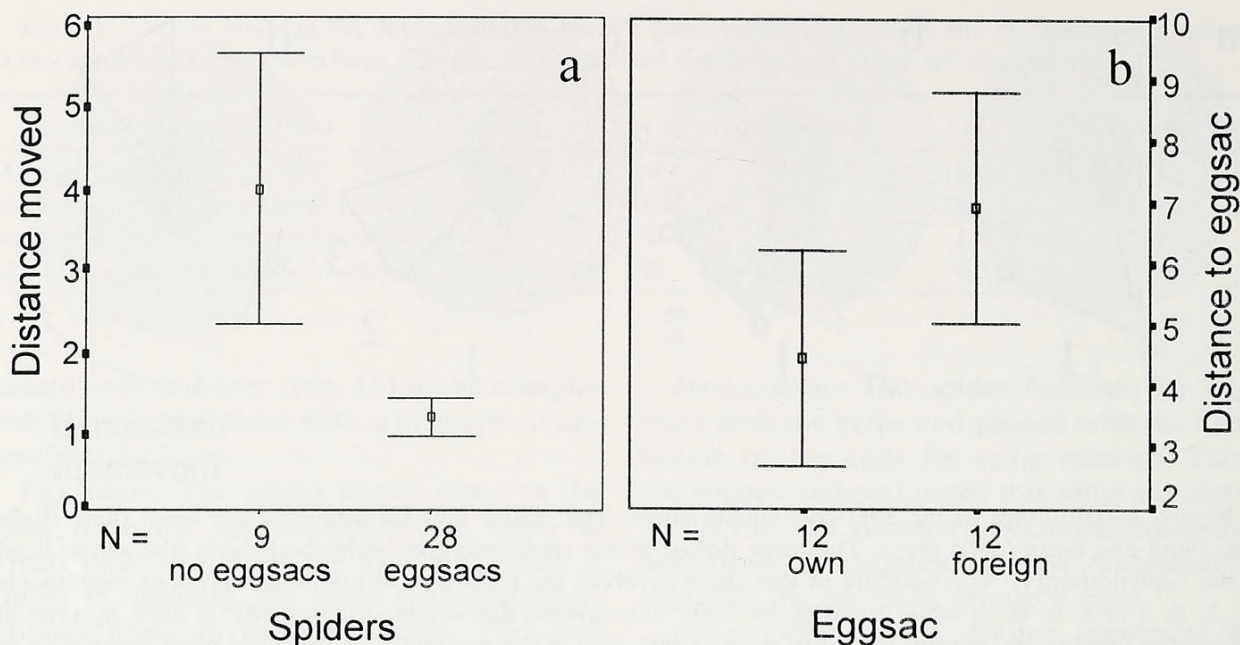


Figure 4.—Maternal displacement and eggsac recognition. Spiders without eggsacs move for larger distances than spiders with eggsacs (cm, mean \pm 2SE; 4a). Spiders with eggsacs stay nearer to their own than to foreign eggsacs (cm, mean \pm 2SE; 4b).

The female appeared to compete with her offspring for food. Jerking the web repeatedly with her front legs, she appeared to signal to the spiderlings her precedence over a prey item; she also actively pushed nearby spiderlings, or even departed carrying the prey item. Despite that, some spiderlings fed along with the mother.

Offspring-offspring conflicts over prey usually resulted in a behavioral arms race: first they elevated their forelegs, next they beat each others cephalothorax with these legs, and finally they bit each other until one of them fled. Notwithstanding this aggressiveness, the winner often accepted the approach of its siblings after he/she had consumed part of the prey, so that collective feeding among siblings was frequent.

Maternal investment and fitness consequences: After building their eggsac the spiders became much more sedentary, moving only a few centimeters between observations (Fig. 4a, $U = 21$, $P < 0.001$, $n = 37$). It made no difference whether the spider took care of her own or an adoptive eggsac: in either case she stayed equally near it ($Z = -.679$, $P = 0.497$, $n = 27$). Furthermore, the females in the *own* group did not differ in any aspect of maternal care from the ones in the adopt group, either in the number of legs touching the eggsac ($Z = -.776$, $P = 0.438$, $n = 27$)

or in the frequency ($Z = -1.165$, $P = 0.244$, $n = 27$) or amplitude ($Z = -.437$, $P = 0.662$, $n = 27$) of their movements in the terrarium.

There was no significant influence of the presence and kind of maternal care on the frequency of successful eggsacs ($\chi^2 = .559$, $P = 0.756$, $n = 39$). Spiderlings in all treatments (*own*, *adopt* and *ncare*) did not differ, on the time of emergence from the eggsac ($\chi^2 = .991$, $P = 0.609$, $n = 28$) or on their total weight ($\chi^2 = .941$, $P = 0.625$, $n = 27$) or survival rate ($\chi^2 = 1.260$, $P = 0.533$, $n = 33$). This may be due to the absence of enemies in laboratory conditions, and experiments under natural environments are necessary to complement these results.

Eggsac recognition.—Although *L. gaucho* treated her own and foreign eggsacs similarly (as shown above), she discriminated between them. When simultaneously offered two eggsacs the spider stayed closer to her own than to the foreign eggsac (Fig. 4b; $t_{2,22} = -1.911$, $P = 0.034$).

Choosing between her own and foreign eggsacs is not an all-or-nothing process: the spider frequently oscillated between the eggsacs for a variable period before settling for one or the other (Fig. 5a, c). Many factors seem to interfere in this process. The spider is able to detect eggsac viability: if one of the eggsacs is not viable ($n = 4$), the spider usu-

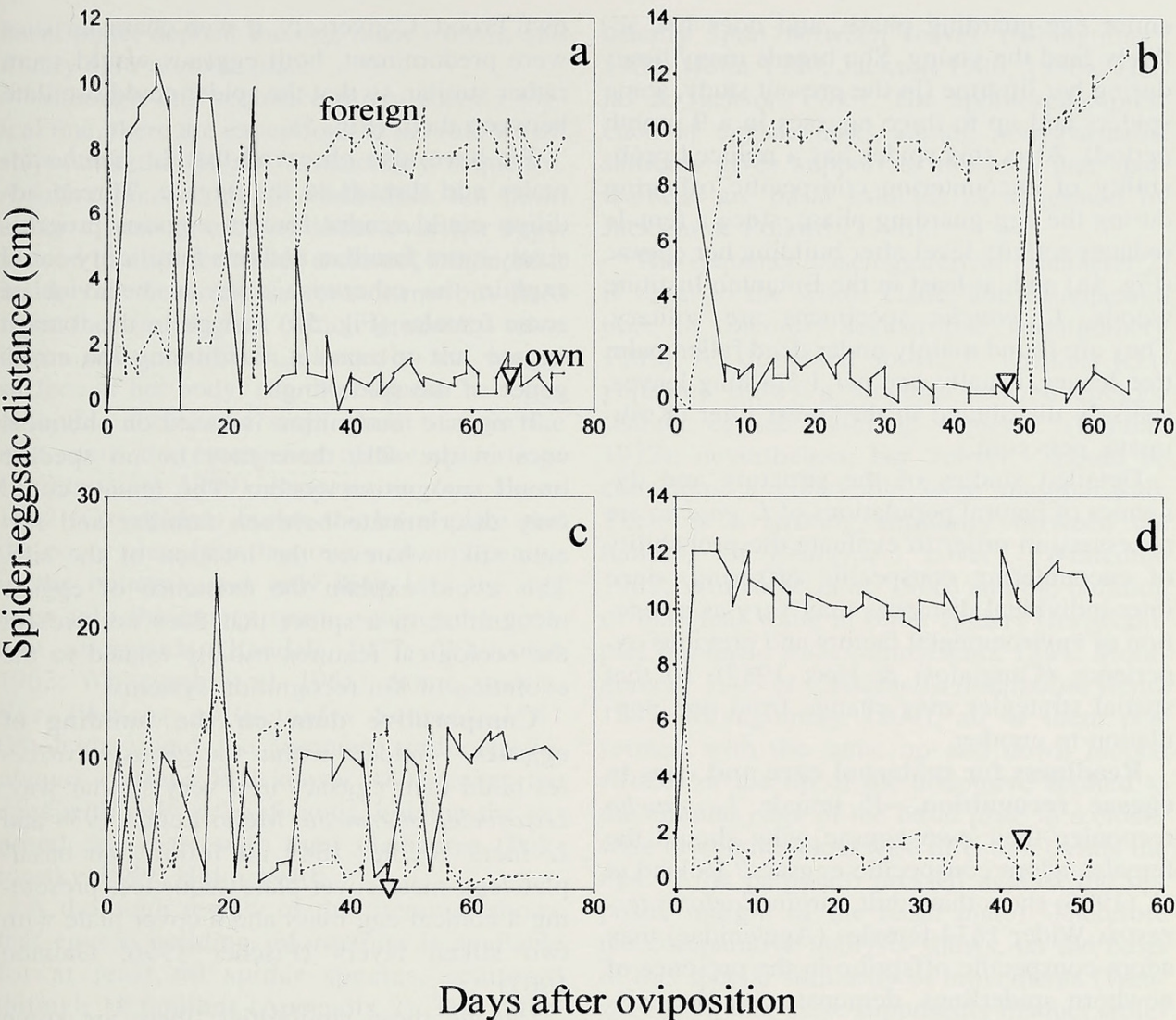


Figure 5.—Oscillations between own and foreign eggsacs. Exposed to her own and a foreign eggsac, the mother frequently oscillated between them, staying sometimes nearer to her own eggsac, and sometimes nearer to the foreign eggsac. The figure depicts the displacement of four spiders (a, b, c, d) in the eggsac recognition experiment. The distance between the spider and each of the eggsacs in the terrarium is shown throughout the experimental period. Continuous line = distance to own eggsac; dotted line = distance to foreign eggsac. Light gray triangles point to the moment of the oviposition of a second eggsac by the mother (from this moment on there are three eggsacs into the terraria); if the triangle is placed onto the dotted line, the new eggsac is close to the foreign eggsac, and vice versa.

ally chooses the other ($n = 3$), even if the other is the foreign eggsac (Fig. 5d). When the spider lays a new eggsac, she preferentially attends this new eggsac, regardless of where she placed it: near her own old eggsac or near the foreign eggsac. In some cases the spider may visit the foreign eggsac just to open it, helping the spiderlings to emerge, returning afterwards to the original one (Fig. 5b).

DISCUSSION

There are few reports of kin recognition among spiders, and it has been suggested that

this recognition is more likely to appear within species that show high levels of maternal investment, breed only once and present high probability of encountering unrelated offspring (Evans 1998b). Although these conditions may enhance the probability of the evolution of recognition systems, they are not necessary conditions for it, since we have found eggsac recognition in *L. gaucho* (Fig. 4b), a species that does not meet these requirements. *L. gaucho* does not show high levels of maternal investment: the female maintains foraging activities throughout the

entire egg-guarding phase, and does not actively feed the young. She breeds many times during her lifetime (in the present study, some spiders laid up to three eggsacs in a 9 month period). Also, this spider has a reduced probability of encountering conspecific offspring during the egg-guarding phase, since a female reduces activity level after building her eggsac (Fig. 4a) and, at least in the Butantan Institute woods, *L. gaucho* specimens are solitary. They are found mainly under dead fallen palm tree leaves, usually one per 1.5m long leaves, sparsely distributed in the forest litter (Kashimata, pers.com.).

Detailed studies of the structure and dynamics of natural populations of *L. gaucho* are necessary in order to evaluate the probability of encountering conspecific offspring, since inter-individual distances may vary as a function of environmental factors and previous experience (Cangialosi & Uetz 1987), so that spatial strategies may change from one population to another.

Readiness for maternal care and cues to eggsac recognition.—If female *L. gaucho* recognize their own eggsac, why should the females adopt conspecific eggsacs? Roland et al. (1996) show that adult, virgin *Coelotes terrestris* Wider 1834 females (Agelenidae) may adopt conspecific offspring in the presence of newborn spiderlings, demonstrating the existence of a readiness to provide maternal care. This readiness could explain adoption by *L. gaucho* females of a single foreign eggsac (adopt group).

Nevertheless, this readiness could not explain adoption in the group of females with two eggsacs: they should always prefer their own brood. They should not oscillate between their own and foreign eggsacs (cf. Fig. 5). Clark & Jackson (1994) showed that *Portia labiata* Thorell 1887 (Salticidae) recognizes her offspring based not only on cues from the eggsac (possibly chemical cues in the silk), but also on cues from the web itself: spiders in foreign webs destroy foreign eggsacs more frequently than spiders in their own webs. It seems from our data that web characteristics are not only important factors in the recognition system, but that they are more important than eggsac factors. If eggsac characteristics were predominant factors in maternal care decisions, *L. gaucho*, confronted with her own and foreign eggsacs, should always prefer her

own brood. Conversely, if web characteristics were predominant, both eggsacs would seem rather similar, so that the spider could oscillate between them (Fig. 5).

We have also observed that *L. gaucho* females add threads to the eggsac. Thread addition could render foreign eggsacs progressively more familiar, and this familiarity could explain the otherwise aberrant behavior of some females (Fig. 5b) that go to the foreign eggsac just to open it, facilitating the emergence of the spiderlings.

If eggsac recognition is based on chemical cues in the silk, there may be no specific brood recognition system. The female could only discriminate between familiar and foreign silk, whatever the location of the silk. This could explain the existence of eggsac recognition in a spider that does not present the ecological features usually related to the evolution of kin recognition systems.

Comparative data on the building of eggsacs.—Spiders within the genus *Loxosceles* build their eggsacs in a very similar way. *Loxosceles intermedia* Mello-Leitão 1934 and *L. laeta* Nicolet 1849 all follow the basal-plate/egg-mass/cover-plate sequence, presenting a conical egg mass and a cover plate with two silken layers (Fischer 1996; Galiano 1967).

Despite these similarities, there are some differences between species. For example, this is the first report of a *Loxosceles* species that scrapes her ventral abdomen and cephalothorax while building the last layer of the cover plate. Also, *L. rufipes* Lucas 1834 stays inside an eggsac nest during the egg-guarding phase (Delgado 1966); a similar structure has been observed in some *L. intermedia* (Fischer 1996), but not in *L. laeta* or *L. gaucho*. The building of eggsacs by *L. intermedia* has been described in some detail, and it differs from *L. gaucho* in two additional aspects: she builds the basal plate with movements similar to the building of the first cover plate layer in *L. gaucho* (Fig. 2); besides this, *L. intermedia* lays the egg mass right after the building of the basal plate (cf. Table 1).

Eggsac building has been described for many spider species, but the descriptions vary strongly as to the details included. Despite this variation, the literature reveals a consistent behavioral sequence pattern: most spiders spin a

basal plate, deposit the egg mass over it, and finally spin a cover plate.

Although this sequence might seem a logical one, there are exceptions to the rule which show that this is not a necessary sequence. *Ariadna bicolor* Hentz 1842 does not build either a base or a cover sheet over her eggs; instead this spider builds a closed, silken nest; inside this nest, she secretes a mucous fluid from the oral region, which gradually turns into a gelatinous sheet adhered to the ventral surface of her body; she then deposit her eggs onto this sheet, and stays close to it in the nest, until the emergence of the spiderlings (Montgomery 1909). *Peucetia viridans* Hentz 1832 (Oxyopidae) builds the basal plate and the cover plate (this last one with an opening in the bottom), and only then lays the egg mass into the empty space, sealing the aperture afterwards (Randall 1977; Whitcomb 1962; Whitcomb et al. 1966). Some spiders, like *Pholcus opilionoides* Schrank 1781 (Pholcidae) and the jumping spider *Heliophantus cupreus* Walckenaer 1802 cover the eggs with only a few threads, holding the exposed egg mass with their chelicerae (Pokrowsky 1899; Holm 1940).

A thorough review of the literature shows that eggsac building information is available for at least 60 spider species, scattered through 18 families (Appendix 2). This information was mapped onto available cladograms (Coddington & Levi 1991; Scharff & Coddington 1997) to evaluate the evolution of the behavioral characters.

Evolution of maternal behavior.—The selected behavioral characters (Appendix 1) are quite conservative. Most of them are plesiomorphic within Opisthothelae spiders (Fig. 6), and were subsequently lost or modified in some groups (see discussion below). To our knowledge, there is no information on maternal behavior of liphistiids (Mesothelae), the outgroup of Opisthothelae, which prevents any generalization of the present analysis to Araneae.

Eggsac nests (character 1) have appeared independently at least three times (*Ariadna bicolor*—Segestriidae, gnaphosids, and among non-spartaeinae salticids, Fig. 6). Structurally, gnaphosid nests are similar to the ones of *A. bicolor* (a silken tube closed all around) and different from salticid nests, which are composed of two interconnected silken sheets,

usually spun between leaves (Montgomery 1909; Holm 1940; Jackson 1986, 1990a; Halas & Jackson 1986). The apomorphic presence of eggsac nests among non-spartaeinae salticids gives support to the idea that spartaeinae are basal salticids as suggested by Jackson & Pollard (1996).

The sequence base/eggs/cover (character 2) is basal to the whole clade, and disappeared once (*A. bicolor*, Segestriidae, Montgomery 1909). As discussed above, *P. viridans* (Oxyopidae) shows a singular base/cover/eggs/sealing eggsac building sequence (Randall 1977); nevertheless, her “cover” should be considered a remarkable, large marginal wall. There is a striking similarity between the building of *Peucetia*’ “cover” (Whitcomb 1962; Whitcomb et al. 1966) and the building of marginal walls in other spiders (for example, *Rabidosa punctulata* Hentz 1844, Montgomery 1903 or *Castianeira longipalpa* Hentz 1847, Montgomery 1909), all of them performed with the same up and down looped strokes of the tip of the abdomen, applied to the circular edge of the basal plate in a clockwise or counter-clockwise direction (while the tips of the palps are pressed against the opposite margin of the basal plate). Therefore the comparative analysis shows, on the basis of this special similarity of movements (Wenzel 1992), that these supposedly distinct structures are indeed the same, homologous structures, distinct only in size.

The use of a silken sheet as a base for the cocoon (character 3) is the plesiomorphic state of this character among Opisthothelae. On this silken sheet there can sometimes exist a cushionlike mat of silk, which can be more or less pronounced in different species. Theridiids have discarded the sheet to oviposit directly onto this cushionlike mat of silk (Montgomery 1903), a putative synapomorphy to the family. Unfortunately the available descriptions do not allow a clear distinction between a single-sheet basal plate and one with both the single-sheet and the mat of silk. Detailed observations are necessary to split this state and further analyze the evolution of this character.

The presence of a marginal wall surrounding the basal plate (character 4) is also plesiomorphic for Opisthothelae, but this character disappeared independently at least 5 times (Fig. 6). The marginal wall is extremely

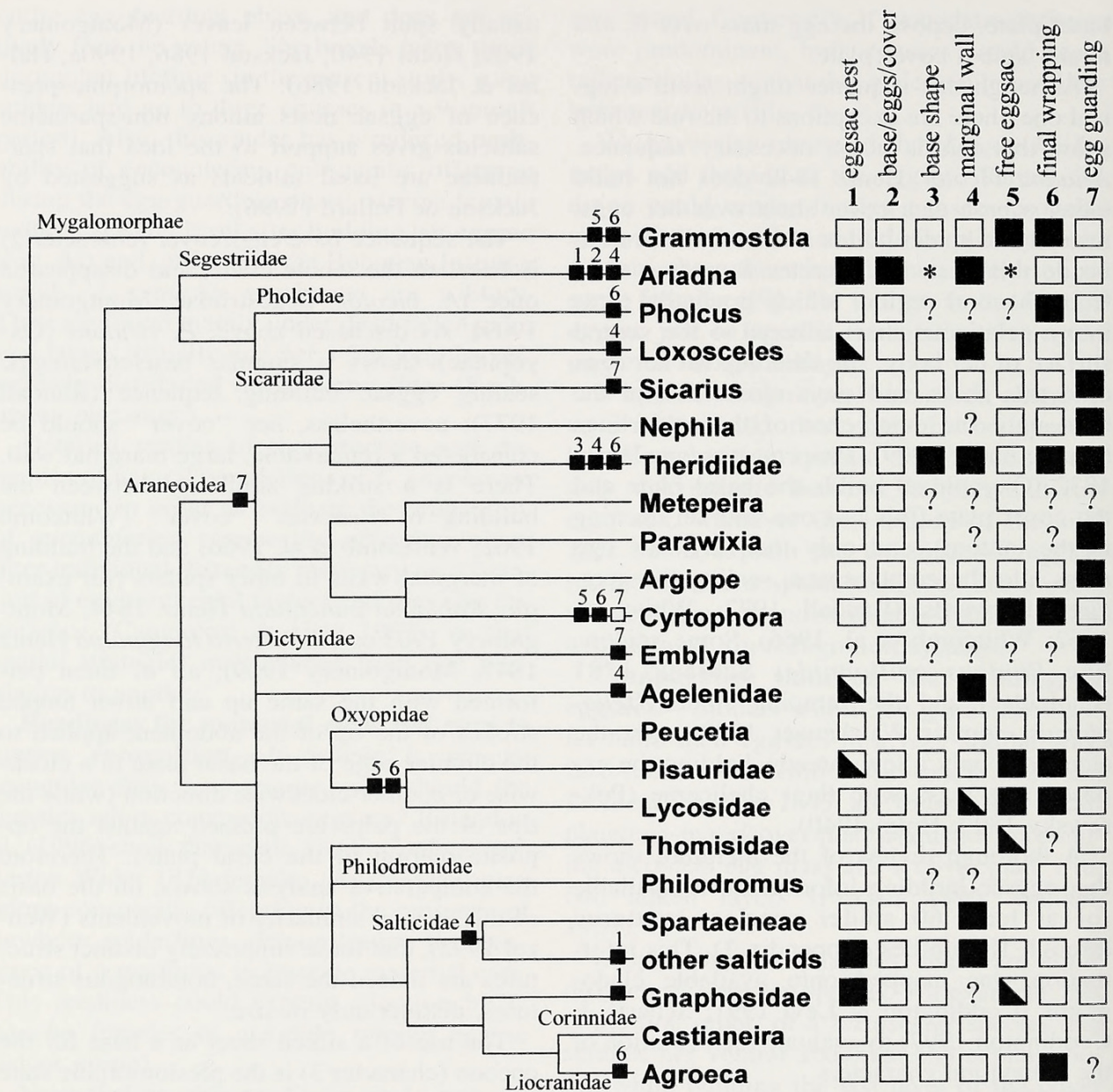


Figure 6.—Probable evolution of maternal behavioral characters among Opisthothelae. Data on Appendix 2 were mapped onto the family cladogram proposed by Coddington & Levi (1991), modified at the araneid node by means of the cladogram proposed by Scharff & Coddington (1997). ■ = synapomorphy; □ = plesiomorphy or reversion; ◐ = polymorphism; “?” = unknown; “*” = nonapplicable.

variable in size, ranging from 1.5 cm high in *P. viridans* (Randall 1977) to a subtle, almost imperceptible ridge in *Schizocosa crassipes* Walckenaer 1837 (Montgomery 1903). In this last case, some authors may have simply overlooked this delicate feature, and it is possible that more careful observations will reveal its existence in many more taxa, thus reducing the level of homoplasy in this character.

After covering the eggsac, some spiders detach it from the substrate (character 5) and wrap it all around (character 6). These char-

acters have appeared simultaneously and independently in three taxa: among mygalomorph spiders [they also occur in *Vitalius sorocabae* Mello-Leitão 1923 (HFJ, pers.obs.)], in *Cyrtophora moluccensis* Doleschall 1857, and at the node Pisauridae plus Lycosidae (Bücherl 1951; Berry 1983; Montgomery 1903, 1909). If a spider detaches the eggsac from the substrate, she will also wrap it afterwards, but the reverse is not true: theridiids and liocranids (*Agroeca brunnea* Blackwall 1833) wrap the eggsac while it is still

hanging from the upper substrate (Montgomery 1903; Ewing 1918; Bonnet 1935; Holm 1940).

Although egg guarding (character 7) is a plesiomorphic behavior for Opisthothelae, it has been lost at least three times, and its absence is a putative synapomorphy for a large group of families, the araneoids. These web building spiders may place the eggsac either far from or near their web, sometimes even at the periphery of the trap, but usually do not maintain close, persistent contact with it as other spiders do (Montgomery 1903; Bonnet 1925, 1935; Austin & Anderson 1978; Gobbi et al. 1979). Since uloborids, the outgroup of araneoids (Griswold et al. 1998), still preserve the plesiomorphic egg guarding behavior [*Miagrammopes animotus* Chickering 1968 guards her eggsac until the emergence of the spiderlings (Opell 2001)], it is possible that this behavior has been lost at the araneoid node.

This analysis reveals that maternal behavioral characters are conservative among Opisthothelae, useful for the grouping not only of families, but also of higher order ranks, such as araneoids and Pisauridae plus Lycosidae. It is surprising that behavioral characters, frequently considered labile features to be avoided in phylogenetic contexts (Atz 1970; Brown 1975), present such a conservative evolutionary pattern. Nevertheless, the hypotheses herein discussed about the evolution of behavioral characters are based on a still scattered database: many families are not included in the analysis, or are represented by just a few species. Furthermore, it must be clear that such hypotheses are always just as good as the phylogenies they rely on, because changes in the cladistic structure entail changes in the evolutionary hypotheses (Ryan 1995). Maternal behaviors have proved to be useful at the phylogenetic level, but much work is necessary to gather enough information for a comprehensive analysis within Araneae.

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APPENDIX 1.

Description of behavioral characters and definition of character states.

Character 1. Nest for the eggsac: (0) absent; (1) present. There is considerable structural variation among nests; as a rule they are built before eggsac construction, and they are larger than the female. Salticids usually present open nests, with one to many ways out; gnaphosids and segestriids build closed nests, and stay in them until the emergence of the spiderlings. Despite the variations in nest structure, all of them had at least an upper and a lower substrate, usually made up of silken sheets [but see Jackson (1986) for a nest almost without silk, between two leaves, built by the spider *Thiana demissa* Thorell 1892].

Character 2. General eggsac building sequence: base/oviposition/cover; (0) absent; (1) present. This is a widespread character: the spider starts building a base silken sheet, deposits the eggs onto it and builds a silken cover sheet onto the egg mass. This character was scored as present if these three steps were all present, and were performed in this order, notwithstanding the existence of intermediate steps, like the building of a silken wall (see below) onto the base, before egg-laying.

Character 3. Shape of the base: (0) silken sheet, sometimes with a cushionlike mat of curled strands of silk; (1) cushionlike mat of curled strands of silk. Most spiders present the single sheet state of the character.

Character 4. Marginal wall: (0) absent; (1) present. After building the basal plate, some spiders spin at its perimeter a wall of curled loops of silk. This is built with up and down movements of the abdomen, while the spider slowly rotates her body and touches the opposite side of the basal plate with the tip of the palpi. This silken wall can be a clearly visible structure (as in *Sicarius* sp., Levi & Levi 1969), but it is sometimes rather difficult to see. We only scored this character as present when explicitly described by the author or clearly distinguishable in pictures or photographs.

Character 5. Free eggsac from substrate: (0) no; (1) yes. After building the cover plate, some spiders remove the whole structure from the substrate with legs I and/or chelicerae. Species that have the eggsac firmly adhered to the substrate pull the basal plate from the substrate with legs I. Species that hang the eggsac from the web merely cut the suspension threads with the chelicerae. Once the eggsac has been removed from the substrate, the spider handles it freely with legs II, III and IV.

Character 6. Final eggsac wrapping: (0) absent; (1) present. After covering the eggmass with a sheet of threads (cover plate), some spiders envelop the whole structure (basal plate included) with a final silken protection. Note that the cover plate never enwraps the whole structure, but is built over the basal plate and eggmass. This behavior may be somewhat simplified in some taxa, as is the case for *Pardosa lapidicina* Emerton 1885, which wraps only the junction between the cover and the basal plate (Eason 1969).

Character 7. Eggsac guarding: (0) absent; (1) present. This behavior varies strongly, for the spider may carry the eggsac on the chelicerae (like pholcids), on the spinnerets (like lycosids) or may not carry it at all, in which case she may stay continuously in touch with it until the emergence of the spiderlings, or even make foraging trips and then return to the eggsac. For the sake of simplicity, and due to the incompleteness of many descriptions, we decided to score all these instances merely as the presence of eggsac guarding behavior.

APPENDIX 2.

Matrix of spider species versus characters for maternal behaviors.

If the species name has changed, the old name is also cited. Only species for which there is information on at least 2 characters were included. Data were compiled based mainly on original descriptions and, in a few cases on informative illustrations. Character 1 = eggsac nest; character 2 = base/eggs/cover building sequence; character 3 = base shape; character 4 = marginal wall; character 5 = free eggsac from substrate; character 6 = final wrapping; character 7 = eggsac guarding. See Appendix 1 for character descriptions and definitions of states. "?" = unknown; "*" = nonapplicable; "v" = polymorphism.

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Species (previous name, if changed)	Family	1	2	3	4	5	6	7	Reference
<i>Agelena labyrinthica</i> Clerck 1757	Agelenidea	1	1	0	?	0	0	1	Warburton 1891
<i>Tegenaria domestica</i> Clerck 1757 (<i>T. derhami</i>)	Agelenidae	0	1	0	0	0	0	0	Montgomery 1903
<i>Araneus quadratus</i> Clerck 1757	Araneidae	0	1	0	1	?	1	?	Crome 1956
<i>Argiope bruennichi</i> Scopoli 1772	Araneidae	0	1	0	1	0	0	0	Bonnet 1925
<i>Cyrtophora moluccensis</i> Doleschall 1857	Araneidae	0	1	0	1	1	1	1	Berry 1983
<i>Larinioides cornutus</i> Clerck 1757 (<i>Epeira strix</i>)	Araneidae	0	1	0	?	?	?	?	Emerton 1877
<i>Metepeira labyrinthica</i> Hentz 1847 (<i>Epeira labyrinthica</i>)	Araneidae	0	1	?	?	?	?	?	Montgomery 1903
<i>Prewixia bistrata</i> Rengger 1836 (<i>Eriophora bistrata</i>)	Araneidae	0	1	0	?	0	?	?	Gobbi et al 1979
<i>Castianeira longipalpa</i> Hentz 1847 (<i>Geotrecha pinnata</i>)	Corinnidae	0	1	1	1	0	0	1	Montgomery 1909
<i>Emblina sublata</i> Hentz 1850 (<i>Dytina volupis</i>)	Dictynidae	?	1	?	?	?	?	0	Montgomery 1903
<i>Drassodes neglectus</i> Keyserling 1887	Gnaphosidae	1	1	?	?	1	?	1	Montgomery 1909
<i>Sergiolus capulatus</i> Walckenaer 1837 (<i>Poecilochroa variegata</i>)	Gnaphosidae	1	1	?	?	0	0	1	Montgomery 1909
<i>Zelotes ater</i> Hentz 1832 (<i>Herpyllus ater</i>)	Gnaphosidae	1	1	0	?	?	?	1	Emerton 1877
<i>Agroeca burnea</i> Blackwall 1833	Liocranidae	0	1	0	1	0	1	?	Holm 1940
<i>Pardosa amentata</i> Clerck 1757	Lycosidae	0	1	0	?	1	1	1	Montgomery 1903
<i>P. lapidicina</i> Emerton 1885	Lycosidae	0	1	0	1	1	1	1	Eason 1969
<i>P. milvina</i> Hentz 1844 (<i>P. nigropalpis</i>)	Lycosidae	0	1	0	0	1	1	1	Montgomery 1903
<i>Rabidosa punctulata</i> Hentz 1844 (<i>L. punctulata</i>)	Lycosidae	0	1	0	1	1	1	?	Montgomery 1903
<i>Schizocosa ocreata</i> Hentz 1844 (<i>L. ocreata</i>)	Lycosidae	0	1	0	1	1	1	1	Montgomery 1903
<i>S. avida</i> Walckenaer 1837 (<i>L. lepida</i>)	Lycosidae	0	1	0	1	1	1	1	Montgomery 1903
<i>S. crassipes</i> Walckenaer 1837 (<i>Lycosa stonei</i>)	Lycosidae	0	1	0	1	1	1	1	Montgomery 1903
<i>Peuceetia viridans</i> Hentz 1832	Oxyopidae	0	1	0	1	0	0	1	Whitcomb 1962;
									Whitcomb et al. 1966
<i>Philodromus aureolus</i> Clerck 1757	Philodromidae	0	1	?	?	0	0	1	Montgomery 1903
<i>Pholcus opilionoides</i> Schrank 1781	Pholcidae	0	1	?	?	?	?	1	Pokrowsky 1899
<i>Dolomedes fimbriatus</i> Clerck 1757	Pisauridae	1	1	0	1	?	?	?	Pappenheim 1903 (apud Montgomery 1909)
<i>Pisaurina mira</i> Walckenaer 1837	Pisauridae	v	1	0	?	1	1	1	Montgomery 1909
<i>Heliophanus cupreus</i> Walckenaer 1802	Salticidae	1	?	?	?	?	?	1	Holm 1940
<i>Marpissa muscosa</i> Clerck 1757 (<i>M. rumpffii</i>)	Salticidae	1	1	0	?	0	?	1	Holm 1940
<i>Phidippus purpuratus</i> Keyserling 1885	Salticidae	1	1	?	?	0	0	1	Montgomery 1909
<i>Thiania demissa</i> Thorell 1892	Salticidae	1	1	0	?	?	0	0	Jackson 1986

Appendix 2.—Continued.

Species (previous name, if changed)	Family	1	2	3	4	5	6	7	Reference
<i>Thiania</i> sp.	Salticidae	1	1	0	?	0	0	1	Jackson 1986
<i>Brettus cingulatus</i> Thorell 1895	Salticidae	0	1	0	0	0	0	1	Jackson & Hallas 1986a
<i>Cocalus gibbosus</i> Wanless 1981	Salticidae	0	1	0	?	0	0	1	Jackson 190b
<i>Cyrbia algerina</i> Lucas 1846	Salticidae	?	1	0	0	0	0	?	Jackson & Hallas 1986a
<i>Gelotia</i> sp.	Salticidae	0	1	0	?	0	0	1	Jackson 1900c
<i>Portia fimbriata</i> Doleschall 1859	Salticidae	0	1	0	0	0	0	1	Jackson & Hallas 1986b
<i>Portia labiata</i> Thorell 1887	Salticidae	0	1	0	0	0	0	1	Jackson & Hallas 1986b
<i>Asemonea murphyae</i> Wanless 1980 (<i>A. murphyi</i>)	Salticidae	1	1	0	?	0	0	1	Jackson 1990a
<i>Asemonea tenuipes</i> Cambridge 1869	Salticidae	1	?	0	?	0	0	1	Hallas & Jackson 1986
<i>Goleba puella</i> Simon 1885	Salticidae	1	1	0	?	0	0	1	Jackson 1990a
<i>Lyssomanes patens</i> Peckham & Peckham 1896	Salticidae	1	1	0	?	0	0	1	Jackson 1990a
<i>Lyssomanes</i> sp. 1	Salticidae	1	1	0	?	0	0	1	Jackson 1990a
<i>Lyssomanes</i> sp. 2	Salticidae	1	1	0	?	0	0	1	Jackson 1990a
<i>Lyssomanes viridis</i> Walckenaer 1837	Salticidae	1	1	0	0	0	0	1	Hallas & Jackson 1986
<i>Onomastus nigricaudus</i> Simon 1900 (<i>O. nigricauda</i>)	Salticidae	1	1	0	?	0	0	1	Jackson 1990a
<i>Tomocyrba holmi</i> Prószyński & Zabka 1983 (<i>Onomastus holmi</i>)	Salticidae	1	1	0	?	0	0	1	Jackson 1990a
<i>Ariadna bicolor</i> Hentz 1842	Segestriidae	1	0	*	0	*	0	1	Montgomery 1909
<i>Loxosceles gaucho</i> Gertsch 1967	Sicariidae	0	1	0	0	0	0	1	Present paper
<i>L. intermedia</i> Mello-Leitão 1934	Sicariidae	0	1	0	0	0	0	1	Fischer 1996
<i>L. laeta</i> Nicolet 1849	Sicariidae	0	1	0	0	0	0	1	Galiano 1967
<i>L. rufipes</i> Lucas 1834	Sicariidae	1	?	?	?	?	?	1	Delgado 1966
<i>Sicarius</i> sp. 1	Sicariidae	0	1	0	1	0	0	0	Levi & Levi 1969
<i>Nephila edulis</i> Labillardiere 1799	Tetragnathidae	0	1	0	?	0	0	0	Austin & Anderson 1978
<i>Grammostola actaeon</i> Pocock 1903	Theraphosidae	0	1	0	1	1	1	1	Bücherl 1951
<i>Grammostola mollicoma</i> Ausserer 1875 (<i>G. longimana</i>)	Theraphosidae	0	1	0	1	1	1	1	Bücherl 1951
<i>Achaeranea tepidariorum</i> Koch 1841 (<i>Theridion tepidariorum</i>)	Theridiidae	0	1	1	0	0	1	0	Montgomery 1903; Ewing 1918; Bonnet 1935
<i>Enoplognatha marmorata</i> Hentz 1850 (<i>Steatoda marmorata</i>)	Theridiidae	0	1	?	?	?	?	?	Montgomery 1903
<i>Latrodectus mactans</i> Fabricius 1775	Theridiidae	0	1	?	?	0	?	?	Montgomery 1907
<i>Steatoda triangulosa</i> Walckenaer 1802 (<i>Teutana triangulosa</i>)	Theridiidae	0	1	1	0	0	1	0	Montgomery 1903
<i>Thomisus onustus</i> Walckenaer 1805	Thomisidae	0	1	0	1	1	?	1	Fabre 1823
<i>Xysticus ferox</i> Hentz 1847 (<i>Xysticus stomachosus</i>)	Thomisidae	0	1	?	?	0	?	1	Montgomery 1903



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