2006. The Journal of Arachnology 34:399–421

SOCIAL BEHAVIOR IN AMBLYPYGIDS, AND A REASSESSMENT OF ARACHNID SOCIAL PATTERNS

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ABSTRACT. Aggregation, extended mother-offspring-sibling interactions, and complex social behaviors are extremely rare among arachnids. We report and quantify for the first time in Amblypygi prolonged mother-offspring-sibling associations, active aggregation, and frequent ‘‘amicable’’ (tolerant, nonaggressive) tactile interactions in two species: *Phrynus marginemaculatus* C.L. Koch 1840 (Phrynidae) and *Damon diadema* (Simon, 1876) (Phrynichidae). Sociality is characterized by frequent contact and tolerance, and infrequent agonism until sexual maturity in *D. diadema* and into adulthood in *P. marginemaculatus*. We experimentally examined potential benefits and costs affecting aggregation: risk of predation, preferred habitats and prey availability. Only increased predation risk decreased nearest-neighbor distances and increased maternal vigilance. Individuals aggregated on a variety of surface textures and locations that varied daily, rather than aggregating only on preferred microhabitats. Manipulation of prey abundance had no affect on the tendency to aggregate.

Patterns of parental care, duration of association, and the presence of social traits found in the most social taxa of non-spider arachnids are reviewed. Species in most arachnid orders have transient parental care with defense of eggs, a brief period of association with newly emerged young prior to independent foraging and explosive dispersal from the natal nest. More prolonged sociality, with long-term associations among mothers-offspring-siblings is rare and is only described in a few species in the Amblypygi, Scorpionida, Pseudoscorpionida, and Acari. All such species have subsocial origins, but current use of the term subsocial is overly broad and we propose a more restricted terminology for clarity.

Keywords: Whip spiders, aggregation, maternal care, ontogeny, predation risk, foraging

Sociality in arachnids is extremely rare. Here we report prolonged association between mothers and their immature offspring, active aggregation among siblings, and extensive social contact in two species of captive amblypygids, *Phrynus marginemaculatus* C.L. Koch 1840 (Phrynidae Blanchard) and *Damon diadema* (Simon 1876) (Family Phrynichidae), that differs from the solitary behavior previously described for amblypygid adults. Subsociality, or an association between mothers and their offspring or among siblings prior to reaching sexual maturity, has not been previously reported in the Amblypygi. Although arachnid sociality at all levels of complexity is uncommon, sociality has been applied to describe behaviors ranging from transient early parental care (Laniatores opilionids: Machado & Raimundo 2001; Machado 2002; Uropygids: Schmidt 2003), to ‘‘subsocial’’ mother-offspring-sibling associations that last for brief periods (spiders: Kim 2000; Schneider 1995; scorpions: Polis & Lourenco 1986), ‘‘subsocial’’ associations that last until sexual maturity (spider mites: Saito 1997; Mori & Saito 2005; amblypygids: this manuscript), to the complex multiple adult societies of the most social of the colonial and cooperative spiders (reviews in Buskirk 1981; Aviles 1997; Whitehouse & Lubin 2005) (see Tables 1–3 for details). Along with describing patterns of social interactions in amblypygids, we propose expanding and modernizing the definitions of subsociality to better interpret the social and evolutionary implications that allow these rare predatory species to successfully live in groups.

Beyond studies of the dramatic courtship and fighting behavior of adult amblypygids (Alexander 1962; Weygoldt & Hoffman 1995; Weygoldt 2000, 2002) relatively little work has been done on other aspects of amblypygid behavior. Most studies suggest that adult amblypygids are generally solitary and intolerant

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Table 1.—General patterns of early parental care for each arachnid order. Due to a lack of information, Palpigradi and Ricinulei were excluded. Where informative, T indicates the pattern is typical for the members of the order, C indicates that this is common among some Families, and R indicates that only a few rare species exhibit the alternate pattern. Numbers refer to citations in all three Tables: 1 = Avilés 1997; 2 = Brach 1978; 3 = Buskirk 1981; 4 = Cloudsley-Thompson 1977; 5 = Coddington et al. 1990; 6 = Evans 1998; 7 = Harvey 2003; 8 = Kim 2000; 9 = Kullmann 1972; 10 = Machado 2002; 11 Machado & Oliveira 1998; 12 = Machado & Raimundo 2001; 13 = Machado & Vasconcelos 1998; 14 = Mahsberg 2001; 15 = Mori & Saito 2005; 16 = Polis & Lourenco 1986; 17 = Polis & Sissom 1990; 18 = Punzo 1998; 19 = Ramachandra & Bali 1990; 20 = Rowland 1972; 21 = Rayor & Taylor 2006;

	Arachnid order			
Parental trait	Araneae	Amblypygi	Uropygi	Schizomida
Carry egg sac	C	T: 28	T: 19, 23	20
Live young				
Guard eggs	C			
Youngest instar carried	R	T: 28	T: 23	20
First mobile instar guarded	C	21	23	
No Association with 1st instar	C			
Association with 1–2 instars prior to explosive dispersal	R	T: 28	19, 23	7, 20

predators. No work has evaluated whether these traits are also characteristic of juvenile and subadult amblypygids. According to Weygoldt (2000) ‘‘Whip spiders are not social animals, in fact they are not even gregarious. On the contrary, they avoid each other or react aggressively when encountering a congener.’’ Other researchers have also concluded that adult amblypygids are solitary animals both in the field and laboratory (Gray & Robinson 1986; Alexander 1962). Alexander (1962) observed only aggressive and threatening behavior between adult conspecifics of both sexes in *Damon variegatus* (Perty 1834; from central and southern Africa) and *Phrynus barbadensis* (called *Admetus barbadensis*) (Pocock 1894; from Barbados). She concludes that much of the intraspecific behavior that does not lead up to courtship ‘‘consists of threatening contests in which the delicate feelers [whips] are used as ‘weapons’.’’ Other accounts describe similar adult male-male conflicts (Weygoldt & Hoffman 1995; Weygoldt 2000).

In contrast, Weygoldt (1977) found that *Heterophrynus longicornis* Butler 1873 (Family Heterophrynidae) from the Brazilian Amazon were especially tolerant of one another. Individuals were often found in male-female pairs, along with a variable number of immature individuals, up until the fourth or fifth instar. In one case seven adults were found inhabiting a large log. Quintero (1981) notes that ‘‘Within favorable habitats, [*Phrynus asperatipes* Wood 1983, from Mexico] individuals tend to aggregate, and numerous specimens could be collected from a single cave.’’ It is common in outhouses or slit latrines throughout the neotropics, to find multiple amblypygids in proximity to one another, probably to take advantage of the abundant insect prey at such sites (Rayor pers. obs.). In Florida, *P. marginemaculatus* are frequently associated with lightning downed trees with active termite colonies where a number of amblypygids may be found approximately 30 cm apart at regular intervals along the termite trails (T. Gearheart pers. comm).

Female amblypygids lay eggs and carry them in a brood pouch underneath their abdomen and the newly emerged young climb onto their mother’s abdomen for the duration of their first instar (first incomplete juvenile or pullius, Canard & Stockmann 1993; praenymphae, Weygoldt 2000). Alexander (1962), Weygoldt (2000), and we have observed that if one of the immobile, helpless young falls from the mother’s back during the first instar, and cannot get back on, the mother will do nothing to help, and may even eat this individual. From observations of this behavior, Alexander (1962) concludes ‘‘that there is no maternal behavior towards young [amblypygids] that leave their perches on the back of the mother’’ (Alexander 1962). However, Mahsberg (2001) describes similar cannibal-

Table 1.—Extended. 22 = Saito 1997; 23 = Schmidt 2003; 24 = Schneider 1995; 25 = Shivashankar 1994; 26 = Tizo-Pedroso & Del-Claro 2005; 27 = Weygoldt 1969; 28 = Weygoldt 2000; 29 = Whitehouse & Lubin 2005; 30 = Zeh & Zeh 1990. Note: There is extensive confusion over the different developmental patterns and terminology related to arachnid development (Canard & Stockmann 1993). In the arachnids, after emergence from the egg, in most there is a first instar (incomplete juvenile) that does not feed independently and is essentially immobile, while the second instar is capable of feeding independently and is mobile. For each order, we have consistently referenced the patterns of behavior from the first mobile, independent instar as defined by Canard & Stockmann (1993).

Arachind order				
Opiliones	Solifugae	Pseudoscorpiones	Scorpiones	Acari
	C: 18	T: 26, 27		
			T: 17	
R: 12				R: 15, 22
		27	T: 17	
R: 12			17	R: 15, 22
T: 12	T: 4, 18			
R: 12	R: 4	T: 2, 26, 27, 30	T: 14, 17	R: 22

ism of first instars that have fallen from the mother's abdomen among the social emperor scorpions, *Pandinus imperator* Koch 1841, and suggests that maternal cannibalism at this stage weeds out deformed individuals in order to allocate energy towards other young with superior reproductive value. We consider Alexander's (1962) conclusions about the limits of maternal behavior based solely on damaged individuals during the first instar that cannot survive independently to be flawed.

Alexander (1962) concluded that after leaving their mother's back, young amblypygids were ''clearly independent'' of their mother. Gray & Robinson (1986) describe laboratory observations of a small Australian species, *Charinus pescotti* Dunn, 1949, that also disperse from the mother after undergoing their first molt. Weygoldt (2000) states that after the young leave the mother's abdomen (in a laboratory setting) they ''begin their life without any further maternal care.'' However Weygoldt (2000) indicates that ''in most species the nymphal instars are not aggressive towards each other; moreover, the mother is not aggressive towards her offspring. Growing animals become increasingly aggressive shortly before reaching maturity but the adults are more tolerant of each other.''

In this paper, we expand upon Weygoldt's (2000) observations and describe in detail prolonged mother-offspring-sibling associations in two species of captive amblypygids, as well as associations between adults in one of these species. Our preliminary observations of *P. marginemaculatus* and *D. diadema* suggested that these animals not only tolerated one another, but consistently aggregated and interacted frequently with extensive whip contact. Here we document the tendency to aggregate, how social dynamics change with maturity, and the role of the whips in mediating social contact among amblypygids. In addition, we investigated the following three questions to evaluate possible costs and benefits that individuals may experience by aggregating. First, do individuals form aggregations merely to gain access to particularly favorable microclimates within our experimental cages? Second, given that amblypygids are obligate predators that potentially compete for prey (Weygoldt 2000), do differences in prey abundance effect individuals' tendency to aggregate? Third, since aggregation is often associated with reduced risk of predation (Alexander 1974), does the presence of a potential predator or a disturbance affect group size or proximity to other members of the group? Finally, we review the patterns of early parental care and more complex social behavior known for each of the non-Araneae arachnid orders, and make proposals about characterizing social behavior in these species.

METHODS

Study animals.—Two species of amblypygids were used in this study. Male, female, and

Table 2.—Patterns of association in the most social species known for each arachnid order. Citations are given as in Table 1. The numbers of species (*n*) known to display this type of association are listed for the non-Araneae arachnids. Spiders are represented by a few token species that represent particular features. The Acari are only represented by the seven tetranychid spider mites whose patterns of association

	Arachnid order			
Social trait	Araneae	Amblypygi	Uropygi	Schizomida
Association past 2nd instar, for 1–2 additional instars	8, 29			
Association part-way through development	3, 24			
Association up to sexual maturity	6	Dd, 21; $n = 1$		
Associate past sexual maturity-multiple adults	1, 29	Pm, 21; $n = 1$		

spermatophore stalk voucher specimens of *D. diadema* have been deposited in the Cornell University Insect Collection and at the Smithsonian National Museum of Natural History. Voucher specimens of *P. marginemaculatus* have been deposited in the Cornell University Insect Collection. Extensive video documentation of both species' social interactions and the exploratory response to lizards are available through the Cornell Laboratory of Ornithology, Macaulay Library. Video vouchers are archived in the Macaulay Library and can be found at: http://animalbehaviorarchive.org (or from the author). These videos can be located through an Advanced Search of the Notes for ''Rayor Amblypygid Sociality'' or ''Rayor amblypygid predator exploration'' or by species name, Rayor, & behavior.

P. marginemaculatus (Phrynidae) is a small species common in southern Florida, often found on houses, under boards, logs, trash, under the bark of dead trees, and limestone outcrops (Muma 1967, Hebets pers. comm.). All specimens used in this study were collected from pine and oak flatlands near Fort Myers, FL by Todd Gearheart between January 1998 and August 2000. Interactions between *P. marginemaculatus* mothers and offspring were observed in two clutches from emergence through eight months. Adult spatial interactions were observed in a captive colony of 29 unrelated adult and subadult *P. marginemaculatus*.

The second species, *D. diadema* (Phrynichidae), is found in coastal forests and caves in Tanzania and Kenya (Weygoldt 1999). Adult specimens were caught in southern Tanzania near the Usubara Mountain Range by local collectors and sold for export (Somma & Gearheart, pers. comm.), and all young were born in captivity. Body sizes of *D. diadema* closely match the allometric changes in body and palp width reported by Weygoldt (1999). Mother-offspring-sibling interactions in *D. diadema* were observed in five clutches produced by three adult females. Here we report spatial and behavioral changes that occurred during the first year until sexual maturity for the five groups, but most of the experimental data reported in this paper were collected from Group 4 (see Group details below). Spatial dynamics were observed in a group of ten unrelated adult *D. diadema*.

In total, nine amblypygid groups of different ages and housing conditions were observed. Initial clutch or group size is given for each group. All ages for immatures relate to the start of the second instar when the young descended from the mother's abdomen and were independently mobile and are referred to as the ''emergence date.'' The emergence date at the start of the second instar is comparable to the point when young, newly mobile uropygids and scorpions descend from their mother's back. The groups were: Group 1 (clutch size $n = 12$) and Group 2 ($n = 18$) each consisted of a single *P. marginemaculatus* mother and her offspring (emergence in late August 1998; observed September 1998–April 1999). Group 3 was a mixed colony of unrelated young, subadults and adults of *P. marginemaculatus* (group size $n = 29$: females = 13, males = 8, undetermined sex = 7; observed August 2000–May 2001). Group 4 consisted of one *D. diadema* mother and her offspring (clutch size $n = 18$; emergence November 1999; observed November 1999–March 2001). Groups 5–8 each consisted of *D. diadema* mothers housed with their offspring from May 2001 through October 2002. Group 5 ($n = 32$; emergence 24 April 2001) and Group 6 ($n = 38$; emergence 24 May

Table 2.—Extended. have been well studied, and omit species whose social interactions are anecdotal (Saito, pers. comm.). For the amblypygids, we have indicated the categories in which *Damon diadema* (Dd) and *Phrynus marginemaculus* (Pm) fit into the scheme based on the data in this paper.

Arachnid order				
Opiliones	Solifugae	Pseudoscorpiones	Scorpiones	Acari
			14; $n = 8$	22
			14, 25; $n = 1$	15, 22; $n = 3$
			14, 16	22
		2, 26, 30; $n = 3$	16; $n = 2$	22; $n = 4$

2001; same mother as Group 4). Group 7 ($n = 50$; emergence 18 November 2001). Group 8 ($n = 20$; emergence 28 April 2002) born to the Group 5 female, and resided with their mother and subadult Group 5 siblings. Group 9 consisted of unrelated mature adults of *D. diadema* ($n = 9$: 6 females, 3 males; observed from August 2000–February 2001). When two females in a group oviposited, they were removed from the group cage.

Housing and Diet.—All animals were housed in clear plastic or glass aquarium cages with a substrate of vermiculite and potting soil to maintain humidity. Cage sizes for *P. marginemaculatus* were: Groups 1 and 2—10 × 10 × 18 cm; Group 3—50 × 25 × 30 cm. Cage sizes for *D. diadema* were: Groups 4 and 6—50 × 25 × 30 cm; Groups 5, 7, and 9—50 × 26 × 42 cm. Large sheets of cork bark were tilted along the vertical glass walls of each cage to provide a climbing surface with easy observer visibility. *P. marginemaculatus* were strongly thigmotactic and preferred to rest in the tight space between two vertical surfaces, in this case, the space between the glass walls of the cage and the surface of the cork bark. *D. diadema* were less thigmotactic but also favored the vertical surfaces between the glass walls and the cork bark. In all cases, the cages and sheets of bark were sufficiently large that all individuals could distribute themselves far apart from other individuals within the cage on suitable habitat. All animals were fed appropriate sized crickets (*Acheta domesticus*, *Gryllus bimaculata* or *G. oceanicus*) *ad lib* several times per week (except during periods of experimental manipulation of their diet). All cages were placed on turntables, so that they could be rotated and individuals in all positions in the cages could be viewed with minimal disruption. Because of the regular rotation of cages, all positions within the cages were presumed to have equal exposure to light or to human activities within the room. Behavioral and spatial observations were made at various times throughout the day and night, typically in the dark under red light. Additional behavioral observations were recorded in almost total darkness using a Sony digital camcorder (model DV-TRV9), with ‘‘nightshot’’ infrared lighting.

Amblypygid Whips.—The sensory and social lives of amblypygids are clearly centered on the first pair of legs (or whips), which are extensively used for odor discrimination (Hebets & Chapman 2000), spatial location, and tactile contact between individuals (personal observation). The whips are modified into thin antenniform sensory structures that can measure three to six times the length of the body. The whips are covered with sensitive chemosensory and mechanosensory setae (Foelix et al. 1975; Foelix & Hebets 2001; Foelix et al. 2002), and are capable of extremely delicate movements approximately 340° around the axis of their bodies (pers. obs.). Whip contact among individuals was a characteristic aspect of amblypygid behavior in aggregations. It was not always possible to discern whether the whips actually made contact or simply passed within millimeters of each other—both were considered to be contact. Social interactions appear to be mediated through whip contact. Unlike the extremely rapid, directed flicking motions with a vertical component that characterize whip movements in aggressive interactions, particularly in intrasexual conflicts (see Weygoldt 2000, 2002), the whip movements involved in amicable social interactions were typically long, comparatively slow repeated movements of one individual’s whips down the length of the others whip on a primarily horizontal plane. Throughout this research, we considered ‘‘within whip length’’

Table 3.—Characteristic traits of the social arachnid species. Citations are as in Table 1. The occurrence of features that have been used to characterize sociality are identified for the social species indicated in Table 2. For the amblypygids, we have indicated the categories in which *Damon diadema* (Dd) and *Phrynus marginemaculatus* (Pm) fit into the scheme based on the data in this paper.

Social trait	Arachnid order								
	Araneae	Amblypygi	Uropygi	Schizomida	Opiliones	Solifugae	Pseudoscorpiones	Scorpiones	Acari
Tolerance of group members	1, 3, 9	Dd, Pm, 21					2, 26, 30	14, 16, 25	15, 22
Tendency to aggregate	1, 3, 9	Dd, Pm, 21			5, 10, 13		2, 26, 30	14, 16, 25	15, 22
Overlapping generations of kin	1	Dd, Pm, 21					2, 26, 30	14, 16, 25	15, 22
Prey sharing	29						2, 26, 30	14, 16, 25	
Cooperative construction or use of retreat	1						26	14, 16, 25	15, 22
Non-agonistic communicative behavior		Dd, Pm, 21					2, 26, 30	14, 16, 25	15, 22
Cooperative defense							2, 30	14, 16	15, 22
Temporary aggregations of adults and subadults	29				5, 10, 13		27	16	

to be an appropriate variable for evaluating whether the individuals were close enough to make contact with one another, and essentially, as a measure of tolerance between neighbors. As illustrated by Figures 3–8, amblypygids within whip length of one another were often far closer together and touching more body parts than simply their whips. ‘‘Whip length’’ was defined as the length of a single whip fully extended. Whips were measured from living animals through the glass sides of their cages as they extended their whips using dial calipers or retroactively measured from exuviae from marked individuals. Both methods produced comparable measures.

Mother-Offspring-Sibling Interactions.— To determine if mother-offspring and sibling spatial dynamics in *P. marginemaculatus* (Groups 1 and 2) and *D. diadema* (Groups 4–8) changed over developmental time, we recorded the locations of all individuals in the groups relative to one another in a scan sample taken no more than once daily at a randomly chosen point in time. At each scan sampling, we recorded how many young were found in mother-offspring groups, sibling groups, or solitarily. Individuals were considered to be within a mother-offspring group if they were within the mother’s whip length, in a sibling group if they were within whip length of one or more other individuals, or solitary if they were beyond whip length of another individual. In *P. marginemaculatus*, both clutches were observed once to three times a week from the time they emerged though 4 months old (Total sessions when spatial data collected: Group 1, $n = 14$; Group 2, $n = 27$), with casual observations until they were 8 months old. In *D. diadema*, we also recorded each individual’s location and nearest neighbor distance several times a week from emergence throughout the observation periods for Groups 4–7 (Total sessions when spatial data collected: Group 4, $n = 68$; Group 5, $n = 41$; Group 6, $n = 42$; Group 7, $n = 26$). Comparable spatial data were collected for adult *D. diadema* in Group 9 (Total sessions when spatial data collected: $n = 32$).

As preliminary observations suggested that young *P. marginemaculatus* oriented their bodies toward the mother, the angle of orientation of the young was calculated relative to the mother. During each scan sample to assess spatial dynamics, the spatial orientation of the individuals toward one another was sketched at one randomly chosen time. Orientation was determined by measuring the vector angle between the direction of the young (the orientation of the midsagittal plane extended anteriorly through the longitudinal body axis toward the palps) and a line drawn toward the closest part of the mother's body using a protractor. The mean vector angle of orientation towards each adult female was calculated using the Rayleigh test (Batschelet 1981).

Whip contact among individuals was a characteristic aspect of amblypygid behavior in aggregations. If social interactions are mediated by whip contact, we would expect individuals to position themselves closer than one extended whip-distance apart. To evaluate this, we compared mean whip length for amblypygids of a given age with mean nearest neighbor distance at that age for *D. diadema* using *t*-tests. Whip lengths were measured directly with dial calipers and nearest neighbor distances were measured with a ruler through the glass walls of the observation cage, or distances were calculated from x-y coordinates.

In addition to the spatial data collected, extensive behavioral observations were made throughout their lives. Observations and records were made through direct observation and by video, in order to gain a better understanding of general behavior patterns of the amblypygids. These qualitative descriptions are reported where relevant.

Adult Dynamics.—Spatial data, including group association, nearest neighbor distances, whip length, and whether the animals were courting, were collected over time on the unrelated *D. diadema* adults in Group 9 for comparison with immature individuals.

Evidence of Aggregation in Immatures.—To determine whether there was evidence of aggregation by *D. diadema* (Group 4 at 10 months old), we recorded the locations of individuals on the cork bark within the cages once daily at one randomly chosen point in time for 19 days. We predicted that if individuals were evenly spaced throughout the cage or distributed at random, the number of individuals found on each piece of bark at a given time should be proportional to the area of that piece of bark. Since thigmotactic individuals preferred to rest in the vertical space between the bark and the glass walls of the cage, we used only the area on this side of the bark in our calculations. Amblypygids do not have scopula and were unable to climb on the sides of the glass or plastic cages, so this area was not considered to be part of the potential usable space. We calculated the expected number of individuals for each piece of bark, based on the size following the logic above, and then used chi-square goodness of fit tests to evaluate whether the amblypygids were randomly or evenly distributed on the bark or whether there was evidence of aggregation.

Costs and Benefits of Aggregation.—*Manipulation of Spatial and Textural Uniformity:* To determine whether individuals aggregated to gain access to the most favorable or protected locations in the cages, we created an environment in which all surfaces were presumed to be texturally and spatially uniform by manipulating bark texture and unifying the position of the bark relative to the glass sides of the cages. Both *P. marginemaculatus* (Group 3) and *D. diadema* (Group 4 at 14 months old) were tested in ''uniform'' environments. The original cork bark was removed and replaced with uniform rectangular pieces of plywood (5 mm thick) approximately the same size as the four walls of the cage. The plywood was placed 2 cm from and parallel to the walls, so that every position in the cage was equally favorable in terms of texture, distance from the cage wall, and relative light levels. With the ''uniform'' plywood setup, location and distance between individuals were recorded. To evaluate the animals' spatial distribution, the total area of the plywood was visually divided into rectangular areas of comparable size. If the animals were distributed at random, the expected number of individuals found in each of these areas of the plywood would be proportional to the size of that area. In Group 3 (*P. marginemaculatus*), the total area of the plywood was divided into 12 sections of equal area. In Group 4 (*D. diadema*), where the individuals were significantly larger and typically formed larger aggregations, the total area was divided into six sections of equal area. Chi-square goodness of fit tests were used to determine if individuals were randomly or evenly distributed or if there was evidence of aggregation.

Manipulation of Food Abundance: To determine if aggregation might increase the competition for food, we manipulated food abundance for the adult *P. marginemaculatus*.

For this experiment, Group 3 ($n = 29$) was divided up into two equivalent groups, and housed in separate 3.8-l glass cages. From 15 September through 22 October 2000, Group 3A ($n = 15$) was fed daily so that there were always at least ten live uneaten crickets in the cage at any given time. Group 3B ($n = 14$) was deprived of food during this time: only two small crickets were put into the cage at the beginning of each week of this period. From 25 October through 20 November, the feeding schedules were reversed so that Group 3A was food deprived and Group 3B was well fed. Observations were made several times per week ($n = 20$ observations) and both location and distances between individuals were recorded. For each individual, the linear distance to the nearest neighbor was determined on each observation day. The mean nearest-neighbor distance was then calculated for each individual during each experimental period and a paired *t*-test was used to compare these variables during the food deprived and the food surplus phases of the experiment.

Response to Disturbance and to a Potential Predator: Since reduced predation risk is one of the predicted benefits of sociality for most animals (Alexander 1974; Krause & Ruxton 2002), we predicted that young amblypygids would benefit by the presence of their mother or other amblypygids through active defense, earlier warning, or through aggregation. To determine the response of amblypygids to potentially dangerous disturbances or predators, we conducted two experiments. In the first experiment, we examined the response of a mother and her offspring to a disturbance in which the experimental cage was gently rattled for approximately 15 seconds. We recorded the siblings nearest neighbor distances and group size for two clutches of *D. diadema* (Groups 5 and 6) 5 minutes before the disturbance and then again 2 minutes after it. Disturbance trial replicates were done one or more days apart between. Data were collected for Group 6 at 1.5 and 8 months ($n = 4$ replicates at each age), and Group 5 at 2 months ($n = 4$ replicates). The data were analyzed using a mixed model with age group (3 age levels) and treatment (before and after the disturbance) as fixed effects and replicate for each group as a random effect, followed by a multiple comparison analysis using the Tukey-Kramer adjustment.

Little is known about the predators of amblypygids (Weygoldt 2000; Hebets 2002). As a first attempt to see if there is a reaction to an animal that could potentially be a predator, we introduced a generalist insectivorous, semi-arboreal, male lizard (*Anolis carolinensis*) as a potential predator into the cages of Groups 3, 4, and 7 in a second experiment. The interactions between the lizard and amblypygids were observed and videotaped for 1 hour in each cage before the lizard was removed. This lizard species is sympatric with *Phrynus*, and similar in size to insectivorous chameleons, gekkos, skinks, or agamid lizards which may prey on *D. diadema* in Tanzania (where our adult specimens were collected) (Conant & Collins 1998; Spawls 2002). The lizard measured 16.1 cm from nose to tip of tail, while the amblypygids ranged in size from the smallest specimens of *P. marginemaculatus* (body length = 6 mm) to the largest adult specimens of *D. diadema* (body length = 42 mm). Although the lizard may have had difficulty in killing the largest of the *D. diadema* adults, its size would have been sufficient for it to easily attack juvenile *D. diadema* or any of the *P. marginemaculatus*.

RESULTS

Mother-Offspring-Sibling Interactions.—From emergence through four months, more young *P. marginemaculatus* were found aggregated near their mother or in several groups of closely associated siblings than were found solitarily (Figs. 1–4). Patterns of association changed little during those first four months.

Young *P. marginemaculatus* in proximity to their mothers oriented their bodies towards her body significantly more than expected (Rayleigh test: Group 1: $r = 0.5704$, angle = 58.5, $P < 0.001$, $n = 67$; Group 2: $r = 0.3672$, angle = 49.6°, $P < 0.003$, $n = 69$). Such orientation indicates that the young are attentive to the presence of their mother. Similar directed orientation is seen in courting adults (Weygoldt 2000).

Our observation of these clutches of *P. marginemaculatus* young did not extend until they reached sexual maturity due to mass mortality from mites at nine months. We believe that *P. marginemaculatus* reach sexual maturity at between 12 to 18 months old. We have casual, unquantified observations of two ad-

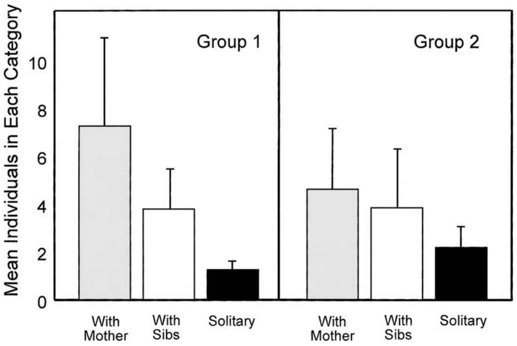


Figure 1.—Mean number (+SD) of *Phrynus marginemaculatus* young in Groups 1 and 2 found in association with their mother, in sibling groups, or solitarily. Data from Group 1 (n = 14 observations) and Group 2 (n = 26 observations) were collected on an approximately weekly basis from age 1 month to 4 months.

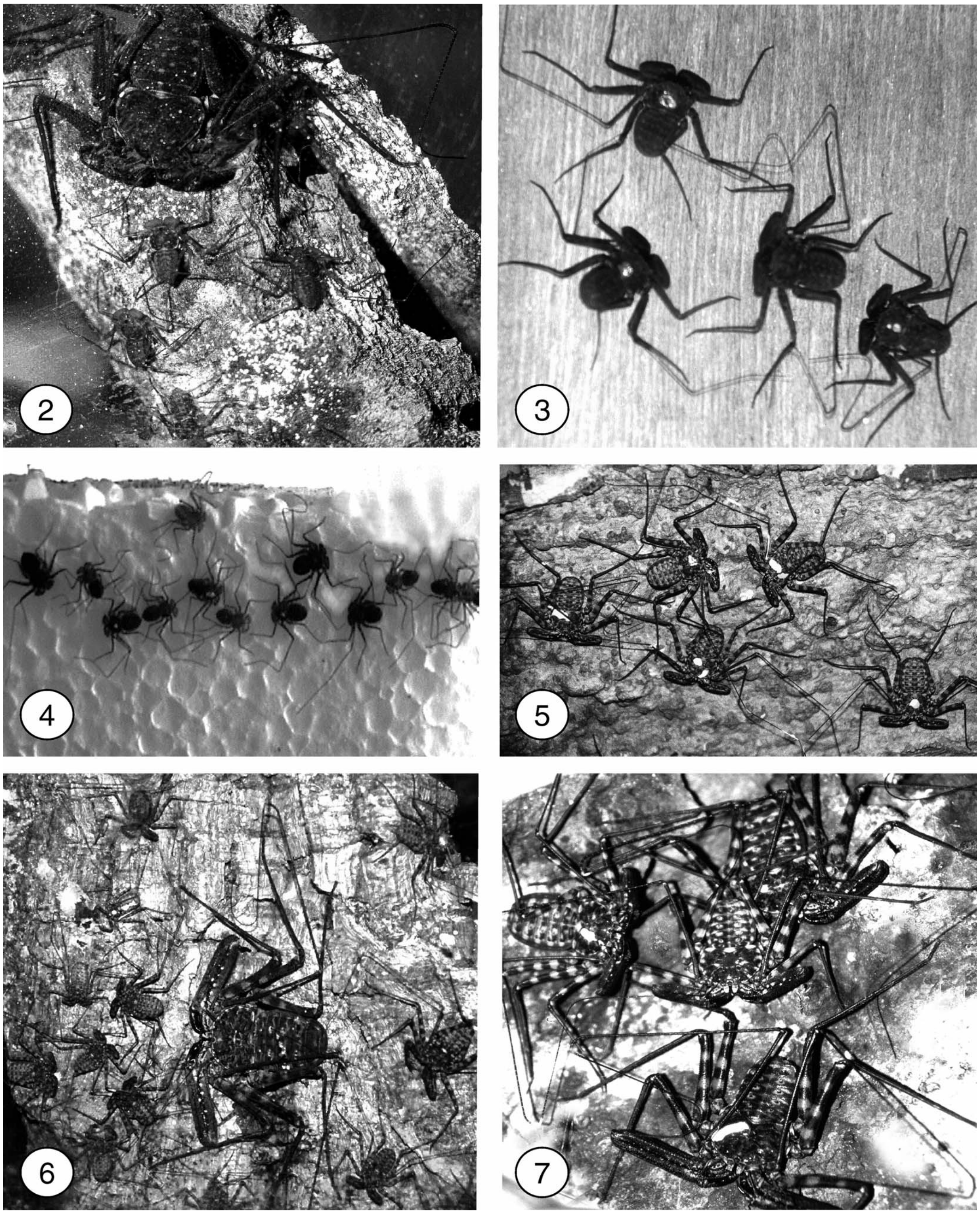
ditional clutches suggesting that when young are born into group colonies with multiple adults present, the young were not harmed and readily interacted with other adults. However, in both colonies mother-offspring groups were more labile than in the solo cages. Soon after the young emerged, the mother moved away from her offspring, while the young dispersed from the natal site in small groups to associate with older individuals throughout the colony.

Mothers of both species studied interacted frequently with their offspring; often the mother would sit in the middle of a group of her offspring and stroke their bodies with her whips. The following is a typical observation of *P. marginemaculatus* with three-week-old young: Initially the adult female stood alone on a section of vertical bark. She made a directed walk into a group of ten closely associated offspring and gently stroked them with her whips. The young moved to surround and orient to her, and stroked her in return, touching her whip, pedipalps, and legs. Of these ten young, the mother made individual contact with seven of them over ~4 minutes. Although the young initially had been sitting close together, slowly waving their whips, once the adult female joined the group the youngsters' whip movements quickened so that most of the young contacted one another as well as the female. Then the mother walked directly to a separate group of two youngsters five body lengths away, engaged in mutual stroking for ~30 seconds. Next she walked directly to a third group of five young on the opposite side of the cage and repeated the interaction for several minutes, before returning to sit in the middle of the first group. In each case, the young oriented towards the mother and were tactilely interactive. The interactions were deliberately initiated and appeared to be affiliative behavior between the mother and her offspring.

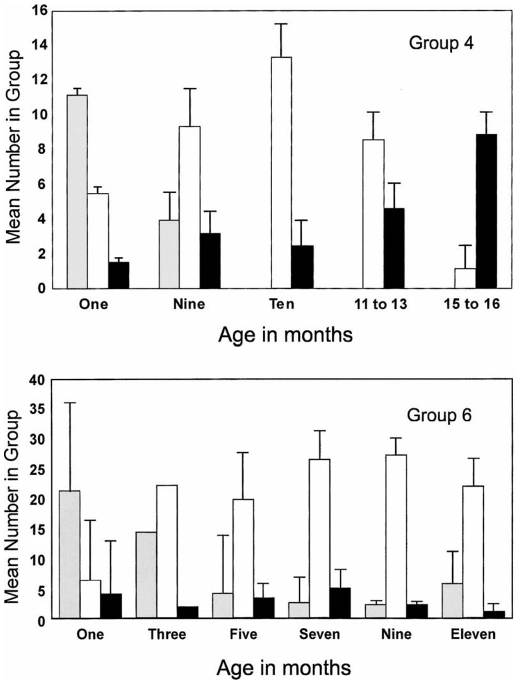
Immature *D. diadema* (Groups 4–8) remained closely associated and interactive with their siblings until they reached sexual maturity between 13 to 15 months old (Fig. 5–9). For the first few weeks to a month after descending from the mother's dorsum the young clustered tightly around their mother (see Figs. 17, 18). The young surrounded their mother, sat beneath her, or hid in small cracks on the cork bark nearby. As they matured, the young distributed themselves more widely through the space available in the cage but continued to aggregate in sibling groups or in groups near the mother, with only a few individuals found solitarily until reaching sexual maturity (Figs. 8, 9).

The mother's physiological state affected the duration and amicability of the mother-offspring association. Based on our observations, for several weeks prior to molting some of the mature females actively moved away from her offspring, reduced interaction rates, and in Group 4 became agonistic. In the wild, premolt behavior could be a time when the female permanently leaves the young. In captivity, the females reinitiated ''amicable'' (tolerant, nonaggressive) interactions with offspring and returned to rest in the middle of young soon after molting.

Constant whip contact among immature amblypygids characterized aggregations. For immature *D. diadema*, the average nearest neighbor distance was significantly less than the extended length of the whips, indicating that individuals positioned themselves close enough for tactile interactions with their neighbors (Figs. 10, 11). Nearest neighbor distances among individuals in groups were consistently small relative to the size of the animals. Although nearest neighbor distances increase with the increasing size of the animals, the tendency to aggregate and the size of groups remained fairly constant (Figs. 10, 11).



Figures 2–7.—Photographs of typical amblypygid associations at different ages. Note the extent of whip contact among individuals and the closed, non-aggressive positions of the palps. 2. Three *Phrynus marginemaculatus* young (Group 2) oriented to and interacting with their mother at age 2 months. Two additional individuals are under the adult female's left legs. 3. *P. marginemaculatus* adults (Group 3) on uniform plywood bark. 4. Amicable interactions among 9-month old *P. marginemaculatus* from Groups 1 and 2 (distinguished by the presence or absence of a white dot on the carapace) that had been combined 2 days previously. 5. *Damon diadema* young (Group 5) at age 6 months. 6. Adult female *D. diadema* and 13 of her 10-month old offspring (Group 6). Note that the group was not limited to the small space shown, but had 4,446 cm^2 of suitable bark throughout the cage. 7. *Damon diadema* offspring at age 13 months (Group 4). The male on the left (wider, thinner palps) molted to sexual maturity before his three sisters.



Figures 8-9.—Mean number (+SD) of *Damon diadema* young found in association with their mother (grey bars), siblings only (white), or found solitarily (black) at different ages. Group 4 was composed of 18 siblings and their mother until they were 10 months old, when two subadults died of natural causes. The adult female was removed when the offspring were 11 months old, due to her increasingly aggressive interactions with her offspring. Between age 13 and 15 months, the amblypygids reached sexual maturity. By the time the siblings were 15 months old, 7 siblings died after losing appendages during aggressive interactions or starved while evading their more aggressive siblings, resulting in $n = 10$ adults. Mean numbers per group were based on 8–15 observations per month. Group 6 was composed of 38 siblings and their mother. All siblings were present until age 11 months when eight subadults died. The mother remained with her offspring throughout these observations. Mean number of animals in each category per month was based on 3 or more observations (range $n = 3$–10 observations/month), except for when the animals were 3 months old (observation $n = 1$).

In both *D. diadema* and *P. marginemaculatus* we observed frequent whip contact and few aggressive interactions among immature siblings until sexual maturity. Familiar individuals were almost always approached directly, rather than avoided, and were greeted with repeated stroking of the whips. In both species, agonistic interactions were mild and infrequent *prior to* sexual maturity. Aggression was rarely observed among immature siblings and their mothers, and among familiar adult *P. marginemaculatus*. Often when an animal entered a tight aggregation of other individuals, others briefly opened their palps in a mild threat display. However, within a few seconds, they would close their palps and stroke the individual with their whips. The animal would rapidly settle into the group without any further evidence of aggression. We found no evidence of cannibalism or missing appendages attributable to aggressive interactions in immatures.

Sexual maturity in *D. diadema*, starting at age 12–13 months, was characterized by distinct morphological and behavioral changes. Within a clutch, molting to maturity varied by as much as two months. Although they were slightly smaller than older adults when they molted to sexual maturity, it is at this molt that males acquire the characteristically elongate, thin palps of adult males. In contrast, adult female palps remain short and wide at sexual maturity. Upon sexual maturity, aggregation patterns changed dramatically as individuals spread out widely and were more likely to be solitary (Fig. 8–11). Although we rarely observed siblings fighting during the day, only at the onset of sexual maturity were animals found with injured legs or whips. Smaller individuals starved as they attempted to avoid aggressive males by remaining on the ''ceiling.'' Males persistently courted their sisters and threatened their brothers. Members of some groups were separated soon after maturity to minimize mortality.

Adult Dynamics.—Unrelated adults of *D. diadema* (Group 9) were solitary and widely distributed in the cage, except when male-female pairs were courting (Fig. 12). Non-courting individuals stayed far apart from one another, with an average nearest neighbor distance of 22.0 cm. In contrast, courting male-female pairs were on average only 6.75 cm apart, closer than the average adult whip length of 11.56 cm. Courting pairs were within ready whip contact with each other, while non-courting adults positioned themselves far enough apart that they were not in contact with one another except during infrequent interactions.

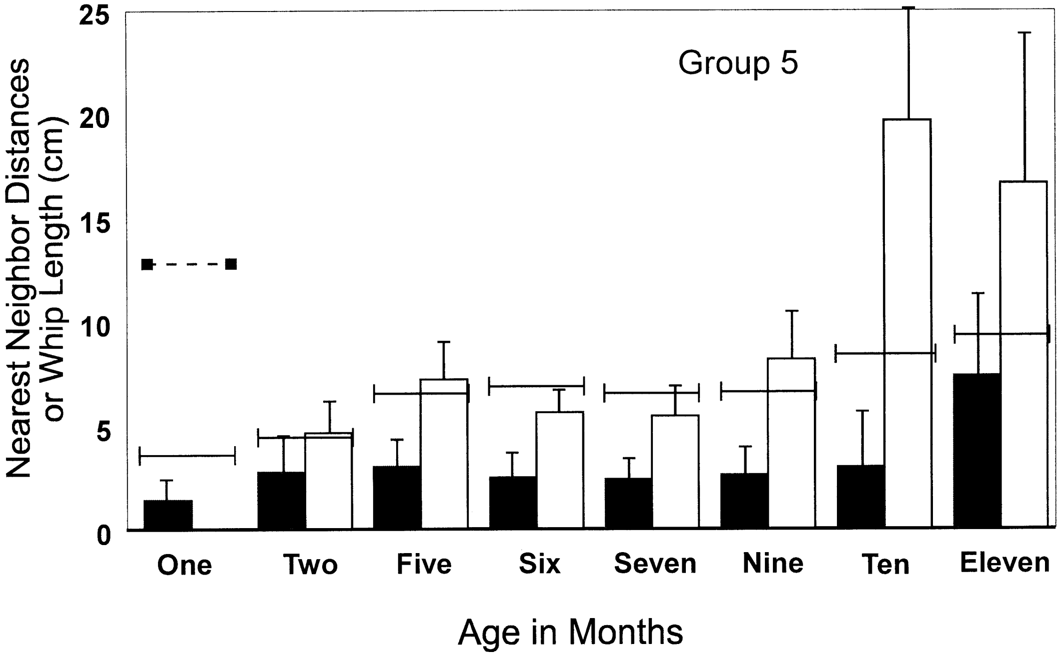


Figure 10.—Nearest neighbor distances among *Damon diadema* in Group 5 relative to whip length for individuals in sibling groups (black bars) and solitary individuals (white) at different ages. Mean whip length of the young (l——l) and their mother (l– – –l) is indicated. Individuals in groups of siblings sit significantly closer together than necessary to make whip contact with one another.

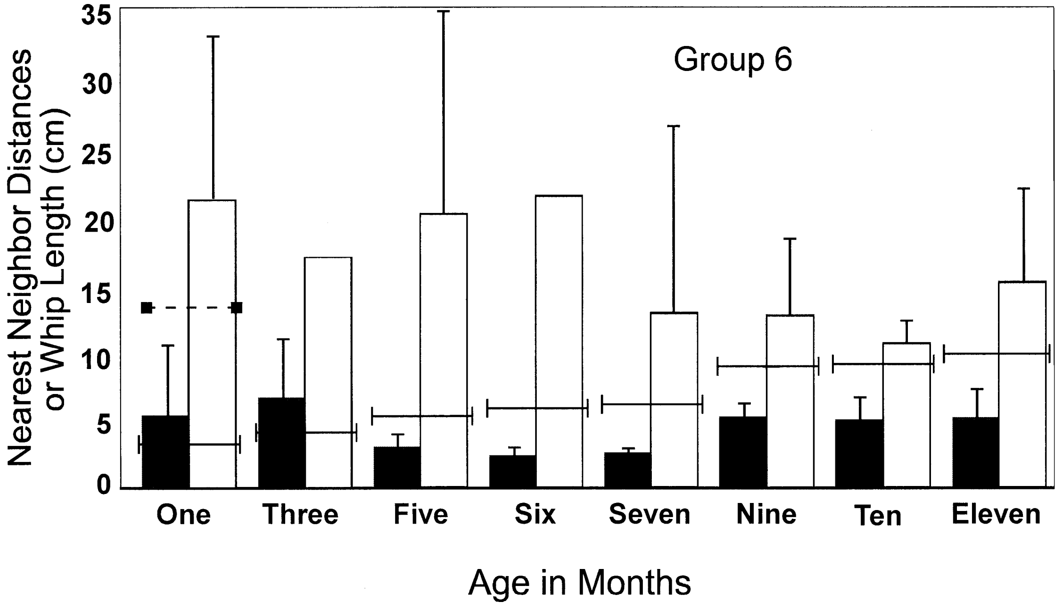


Figure 11.—Nearest neighbor distances among *Damon diadema* in Group 6 relative to whip length for solitary individuals and individuals in sibling groups at different ages. See Fig. 10 for explanation of symbols.

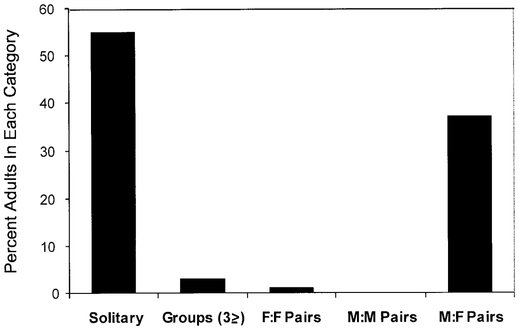


Figure 12.—Percent of the nine adult *Damon diadema* (Group 9) found solitarily or with other individuals during observations (n = 27) from September 2000 to February 2001.

When same sexed adults of either species were newly introduced into the same cage when establishing the colonies or due to temporary removals, fights invariably occurred similar to those described by Alexander (1962), Weygoldt & Hoffmann (1995), and Weygoldt (2000). Fighting among adult *D. diadema* was rarely observed, but adults were twice cannibalized and injuries occurred occasionally. Conflicts among adult *P. marginemaculatus* were short-lived and rarely led to injury.

Evidence of Aggregation in Immatures.—Ten-month old *D. diadema* (Group 4) did not distribute themselves evenly or randomly on the available bark surface (Fig. 13). Rather, individuals aggregated in higher densities than expected in some areas, while others had lower densities than expected from a random distribution. The mean observed spatial distribution within the cage, based on observations over 19 days, differed significantly from the expected random distribution (Fig. 13, $\chi^2 = 23.5$, $df = 5$, $P < 0.01$). Moreover, analysis of individual daily distributions demonstrate that aggregations did not just occur in certain 'prime' locations that attracted many individuals, but that the site of aggregations varied daily indicating preferences for being in a group rather than for specific favorable locations.

Costs and Benefits of Aggregation.—*Manipulation of Spatial and Textural Uniformity:* Spatial and textural features of the cage mi-

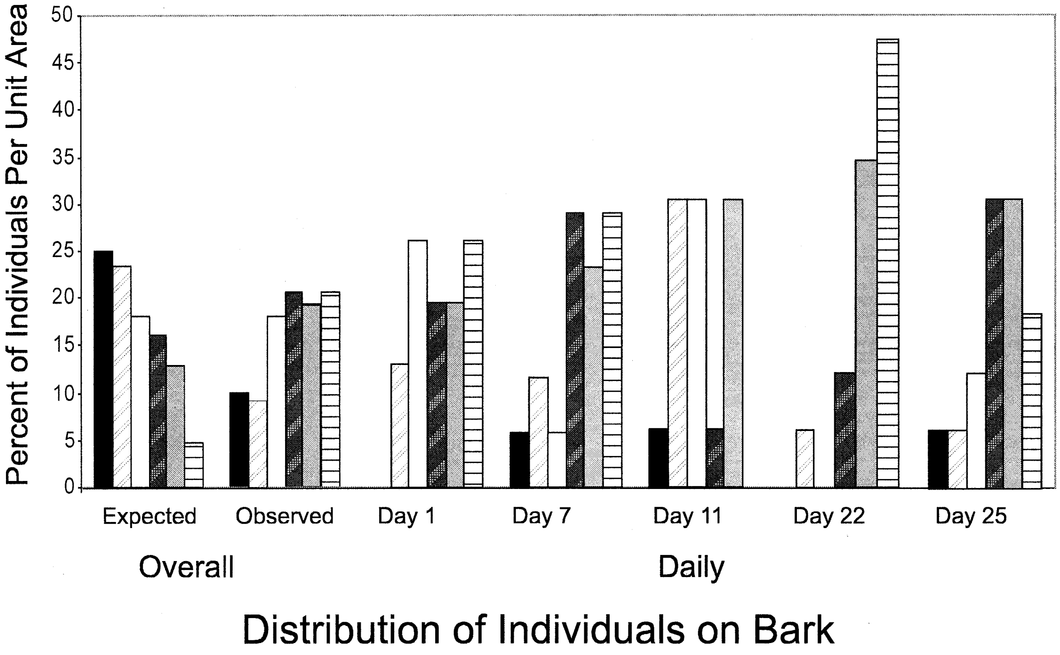


Figure 13.—Overall expected, observed, and five daily spatial distributions of *Damon diadema* (Group 4) on different sized pieces of cork bark in their cage. Expected values are based on the expected number of individuals per piece of bark unit area assuming a random distribution. Each bar represents the observed percentage of individuals on each piece of bark, with each bar pattern and location in the figure unique to a given piece of bark.

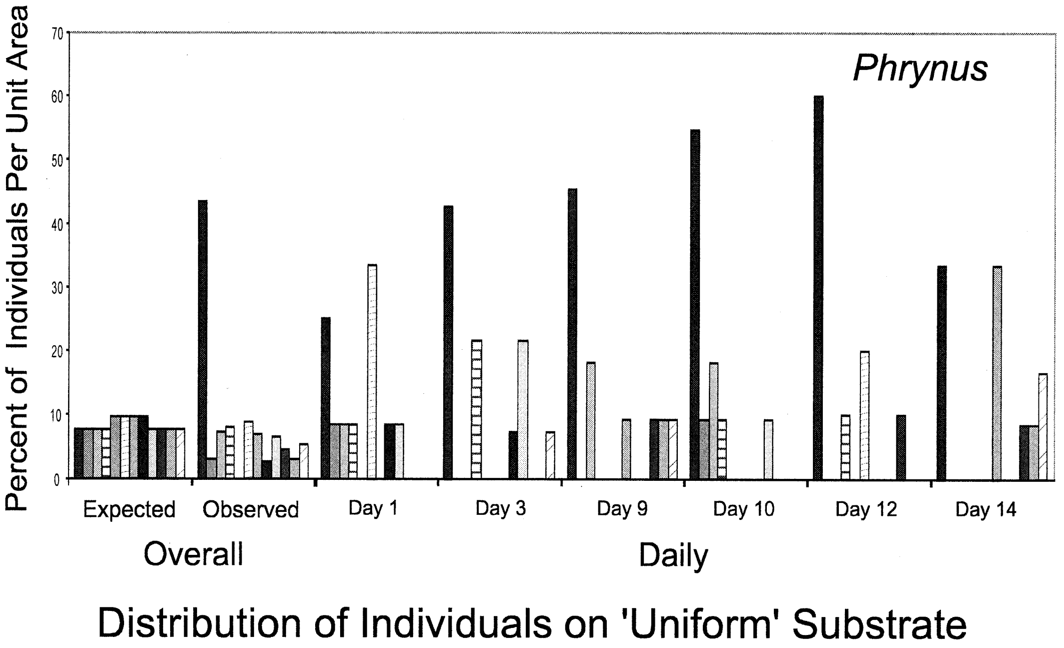


Figure 14.—Overall expected, observed, and daily spatial distributions of adult *Phrynus marginemaculatus* (Group 3) on texturally and spatially uniform plywood "bark". The amblypygids distributed themselves non-randomly relative to the space available on the bark, with more individuals in groups than expected on a daily basis. Each bar represents the observed percentage of individuals on each piece of bark, with each bar pattern and location in the figure unique to a given piece of bark.

croclimate did not appear to be the only factor driving the formation of aggregations, since aggregations still occurred on uniform plywood surfaces. *P. marginemaculatus* (Group 3) and *D. diadema* (Group 4 at age 14 months) still formed aggregations when housed in cages with a uniform plywood habitat. The mean distribution of *P. marginemaculatus* over the entire experimental period differed significantly from the expected random distribution (Fig. 14, $\chi^2 = 22.3$, $df = 11$, $P < 0.05$). However, this was a result of a single "hot spot" in the cage where one aggregation consistently occurred. In other areas of the cage, distributions changed on a daily basis and on five of the six days observed, the distribution differed significantly from the expected random distribution. In contrast, the mean distribution for the immature *D. diadema* taken over the entire experimental period did not differ significantly from the expected random distribution (Fig. 15, $\chi^2 = 7.67$, $df = 5$, $P > 0.05$)), indicating that over the experimental period the animals used different locations of the wood surface equally. However, closer examination of daily distributions demonstrates that individuals were found in groups, but that the location of these aggregations was in constant flux.

Manipulation of Food Abundance: Manipulation of food abundance did not significantly affect the tendency of individual *P. marginemaculatus* to disperse or aggregate. There was not a significant difference in nearest neighbor distances between individuals in food-deprived and food-surplus situations ($t = 1.28$, $df = 15$, $P > 0.05$).

Unlike many social spiders (Whitehouse & Lubin 2005), no amblypygids were observed to engage in cooperative capture of large prey items throughout the entire study. Prey sharing was observed on rare occasions in both species (< 7 occasions for each species) in hundreds of hours of observation. Once, two 7-month old *D. diadema* shared prey for a ten-minute period before pulling it apart. In a *P. marginemaculatus* mother-offspring group kept by a student of LSR, three 12-month olds shared pieces from a large cricket that was being consumed by their mother (C. Fishel,

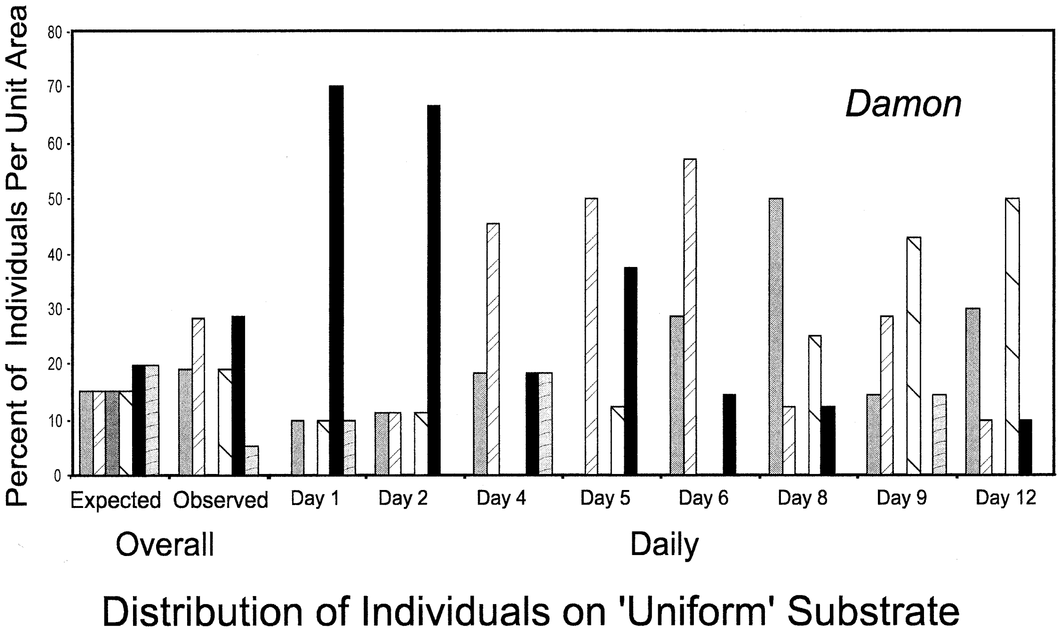


Figure 15.—Overall expected, observed, and daily spatial distributions of subadult, 14-month old *Damon diadema* (Group 4) on texturally and spatially uniform plywood "bark". Each bar represents the observed percentage of individuals on each piece of bark, with each bar pattern and location in the figure unique to a given piece of bark.

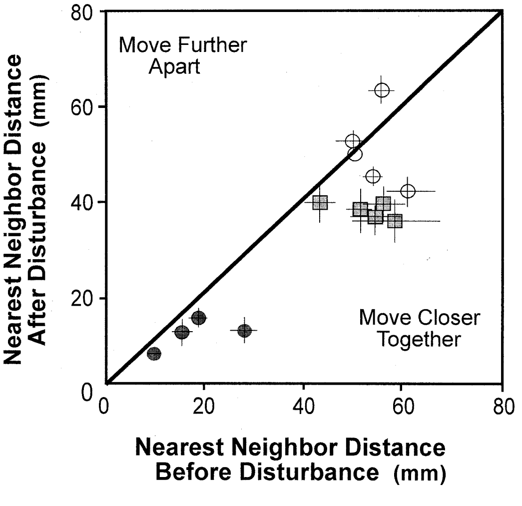
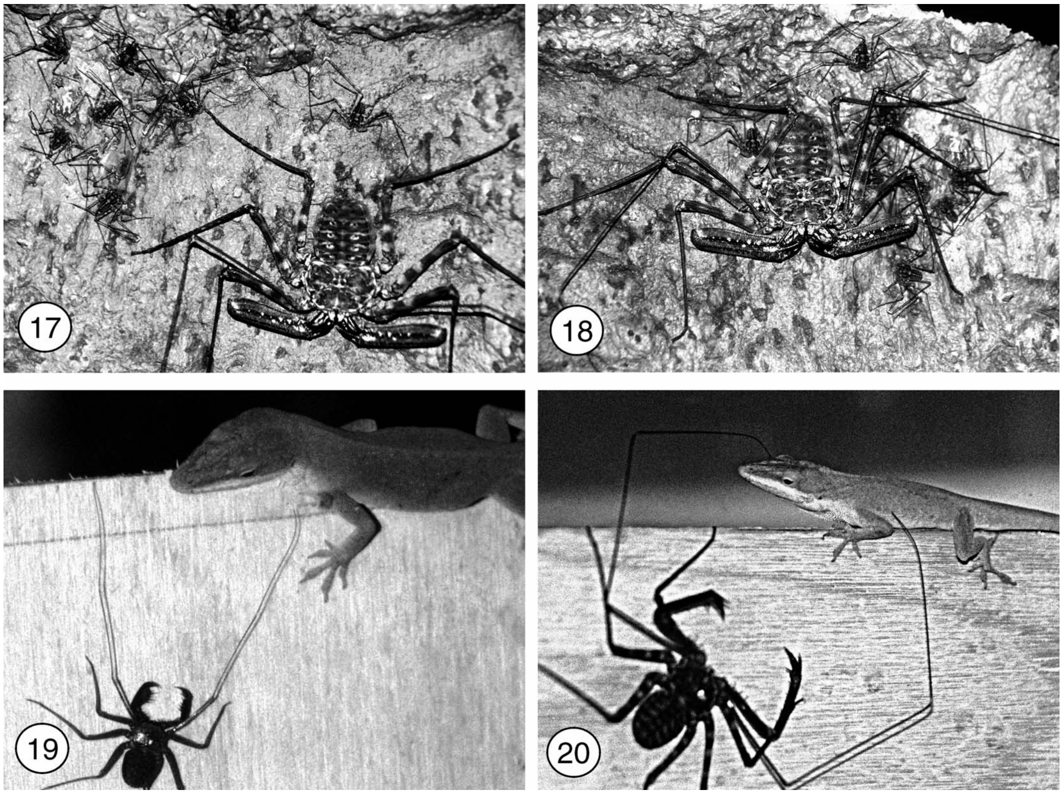


Figure 16.—In response to disturbance, *Damon diadema* (Groups 5 and 8) aggregated together significantly more than expected. Data show the ratio between the mean nearest neighbor distances immediately before and four minutes after a disturbance. Circles represent replicates of Group 5 at age 1.5 months (< 30 mm) and at 8 months (> 40 mm). Squares represent Group 8 at age 2months. Mean Standard Deviation for nearest neighbor distances before (vertical lines) and after (horizontal lines) are indicated in each datum.

pers. comm.). Although prey-stealing was uncommon when the animals were well-fed, immature *D. diadema* were observed stealing food from one another after being food deprived for only three days. On three occasions, individuals were observed successfully stealing a cricket from another individual. In each of these cases, the individual who stole the food returned to a tight aggregation of its siblings and, consequently, the food was stolen again by a third individual. Short feints toward siblings with prey occurred in both species occasionally, but longer chases were not observed.

Response to Disturbance and to a Potential Predator: Solitary amblypygids rapidly run away from threats in the field or in captivity (pers. obs.). Group dynamics when disturbed are striking. In response to their cages being rattled for fifteen seconds, young *D. diadema* significantly reduced their nearest neighbor distance to siblings (Fig. 16; Treatment effects $F_{1,22} = 15.81$, $P < 0.0006$). In response to the disturbance, many young amblypygids scuttled under their mother (Figs. 17, 18). Reductions in nearest neighbor distances among replicated disturbances within groups were not



Figures 17—20.—Responses of amblypygids to external factors. 17. *Damon diadema* (Group 5) at age 1.5 months prior to disturbance. 18. *D. diadema* (Group 5) immediately after disturbance. Note that some young moved beneath their mother. 19, 20. Investigation of lizard (*Anolis carolinensis*) by a subadult *Phrynus marginemaculatus* and an adult *D. diadema*, respectively.

significantly different from zero. There was a highly significant group (= age) effect detected as well, as the younger groups were more likely to move closer together than were older animals (Fig. 16, $F_{2,22} = 87.0$, $P < 0.0001$, $t = -12.31$, Tukey-Kramer adjustment $P < 0.0001$, $df = 22$). Mean group size increased in Group 5 at 2 months in response to disturbance (Paired *t*-test, $t = -4.34$: Before, x ± SD = 24.6 ± 6.8; After, 34.6 ± 2.5; $P < 0.012$). But group size did not significantly change with disturbance for Group 6 at either 1.5 months ($t = -2.03$: Before, 18.2 ± 6.2; After, 20.5 ± 6.1) or at 8 months ($t = -0.77$: Before, 32.7 ± 3.8; After, 34.7 ± 3.9). On several occasions during transfers between cages, an adult female with 7-month old offspring attempted to defend her young by an (effective) threat display and attack on the researchers (Walsh & Rayor pers. obs.). The female raised her body high above the substrate, opened her palps widely (~130° angle), and slowly stalked toward the offending hand(s). When we did not move back, she rapidly closed the palps and attempted to stab us with the stiletto-sharp terminal claw of her distitarsus.

Our attempts to elicit antipredatory behavior through the introduction of an insectivorous lizard were unsuccessful, as none of the amblypygids (of either species) were apparently threatened by the presence of the lizard. In contrast, the lizard evoked active exploration on the part of the amblypygids (Figs. 19, 20). Most individuals readily approached the lizard and repeatedly touched the entire length of the lizard's body and tail with their whips. In most cases, individuals extended their palps in what appeared to be a threatening behavior (similar to the behavior seen between two fighting individuals or similar to the hunting position prior to attack). Even a small year-old *P. marginemaculatus*, with a body length of 6 mm, walked directly up to the lizard and touched its whips along the entire length of the lizard's body for five minutes, and then walked away (Fig. 19). We were unable to determine if the amblypygids responded to the lizard as a potential, albeit very large, prey item or were simply curious about the novel creature in their cage.

DISCUSSION

Mother-Offspring-Sibling Interactions.— Our results demonstrate that, at least in captivity, young *P. marginemaculatus* and *D. diadema* remain closely associated and highly interactive with their mother and siblings for approximately one year. Interactions include both active aggregation and frequent amicable tactile interactions regardless of substrate features. Individuals aggregated on a variety of surface textures and locations that varied daily, rather than aggregating only on preferred microhabitats.

The social interactions observed among conspecifics of the two species were not identical. *P. marginemaculatus* were tolerant and interactive, and they readily formed multigenerational aggregations into adulthood. In contrast, *D. diadema* siblings were highly tolerant and interactive only until they reached sexual maturity at ~13 months old. After sexual maturity behavioral interactions were more agonistic, and individuals moved apart. Adults were essentially solitary, except during courtship, closely aligning with the description of adult amblypygids in the literature.

Should our observations on social behavior in amblypygids be considered an artifact of captivity? We do not think so. Although behavioral observations of immature amblypygids in the field are clearly necessary, these species are unlikely to be primarily solitary with only transient maternal care (see Table 1). The vast majority of solitary predaceous arachnids are cannibalistic, and keeping kin together to force sociality typically results in a group size of one. The behaviors of asocial animals that survive group situations are dominated by agonistic and territorial interactions. On the contrary, the two species of amblypygids displayed social tolerance, long-term associations, extensive tactile interactions, and an absence of cannibalism that more closely resemble the social dynamics of the better known subsocial and social species of spiders and other arachnids (Tables 2, 3). However, there is some evidence that these traits may be facultative, e.g., subsocial scorpions and spiders, where abundant food and limited dispersal options in captivity may delay dispersal and reduce conflict compared to the same species in the field (Gundermann et al 1993; Schneider 1995; Kim 2000; Mahsberg 2001; Mahsberg pers. comm.). Similar factors may have influenced the duration of tolerance and association among the amblypygids in this study but are unlikely to have structured the overall social pattern of interactions. Field studies that focus on the ontogeny of behavioral dynamics in immature amblypygids will clarify the duration of association and patterns of sociality in *P. marginemaculatus* and *D. diadema*.

As the amblypygids in this study are in distantly related families from different continents but still share aspects of their social interactions, similar patterns among mother-offspring-sibling groups of immature amblypygids may be predicted in other species. Other species of amblypygids that have been reported to be highly tolerant warrant further investigation, particularly *Heterophrynus longicornis* in Amazonia (Weygoldt 1977), and *Phrynus asperitipes* (Quintero 1981) and *Acanthophrynus coronatus* Butler 1873 both of Mesoamerica.

Costs and Benefits of Aggregation.—Benefits of living in social groups often include increased prey capture or a reduction in predation risk (Alexander 1974; Rayor & Uetz 1990, 1993). Whitehouse and Lubin (2005) suggest that benefits of sociality in the spiders can be broken down into either foraging or defensive advantages, but not reproductive advantages. The amblypygids did not hunt cooperatively or share prey, although they may benefit by advanced notice of the presence of prey by their neighbors' heightened whip activity. As food abundance increases tolerance in solitary spider species (see Uetz & Heiber 1997), we predicted that food-deprived individuals would be less tolerant and more spread out to reduce competition. On the contrary, manipulation of food availability did not alter aggregation levels of *P. marginemaculatus*, suggesting that the tendency to aggregate was not directly related to prey capture or hunger level. Because many arachnids can sustain long periods of time without food, it is possible that, had the food deprivation level been more extreme, we would have seen more dispersion or greater competition over prey. Regardless, foraging benefits are unlikely to be the primary explanation for social aggregation in these species.

Active defense of young and even cooperative defense is found in a number of the social arachnids (Buskirk 1981; Polis & Lourenco 1986; Mori & Saito 2005; Table 1). When frightened, young *D. diadema* moved significantly closer to their mother or siblings (Fig. 18), and mothers threatened or actively attacked human ''aggressors.'' Antipredator strategies in all amblypygids include nearly constant movement of the sensory whips providing acute awareness of their surroundings, rapid movements away from the threat, and dorso-ventrally flattened bodies which fit into extremely thin crevices (Weygoldt 2000). Field observations of predation are extremely rare: only Hebets (2002) reports observations of a single *Phrynus parvulus* Pocock 1902, being consumed by a scorpion and Adrian Barnett (pers. comm.) has observed a *Heterophrynus batesii* Butler 1873, captured by a neotropical primate, the golden-backed uacari (*Cacajao melanocephalus ouakary*). Whether a benefit of social grouping in amblypygids includes a reduction in predation risk will require manipulative field experiments, but advantages related to group defense are probable, especially in younger animals.

Our attempts to assess the social consequences of predation risk from a putative predatory lizard resulted in distinctive investigative behavior rather than evasive behavior in amblypygids of both species. A general tendency to investigate all aspects of their surroundings could help explain their continuous whip exploration of neighboring individuals.

In summary, our observations suggest that at least two species of amblypygids display social behaviors significantly more complex and prolonged than those characteristic of early maternal care.

A Reassessment of Social Patterns in Arachnids.—Parental care is defined as parents directly or indirectly investing in their offspring's fitness (Clutton-Brock 1991). ''Subsocial'' behavior in invertebrates is a subset of parental care provided to offspring that have emerged from the egg sac and which increases the survival of the offspring (Wilson 1971; Tallamy & Wood 1986). However ''subsocial'' has been used as a collective term to lump all associations from transient parent-offspring associations (''early parental care,'' Table 1) to much more complex social groups that include long-lasting mother-offspring-sibling associations extending until or even beyond sexual maturity of the offspring and the death of the mother (Table 2). ''Sociality'' has typically been defined as involving some level of cooperation, communication, and prolonged tolerance in groups of conspecifics (Kullmann 1972; Buskirk 1981; Costa & Fitzgerald 1996; Krause & Ruxton 2002). Unfortunately, there is often no clear division based on the complexity of the social behavioral repertoire, duration of associations, and social demographics, between the more advanced ''subsocial'' species and ''social'' arachnids. The use of ''subsocial'' terminology masks the social diversity among the arachnids that provides insights into the evolution of group-living. Over the last decade, there has been an increasing recognition that sociality occurs along a behavioral continuum, rather than in discrete categories, and that definitions of sociality need to be broadened to more accurately reflect the diversity of social dynamics in a broad range of animals (e.g., Sherman et al. 1995; Costa & Fitzgerald 1996; Choe & Crespi 1997; Crespi & Choe 1997; Whitehouse & Lubin 2005; Costa & Fitzgerald 2005). Wcislo (1997) suggests that in describing arthropod social organizations it has been too easy to use a terminology that *categorizes* the group, but does not actually describe the behaviors or traits that occur in these groups, such that natural variation within or between social species is missed. As Wilson (1971, p. 5) states ''[A society] is a group of individuals that belong to the same species and are organized in a cooperative manner. I believe the terms society and social must be defined quite broadly in order to prevent the arbitrary exclusion of many interesting phenomena. . . . Not only eusocial insect colonies but also most parasocial and subsocial groups should be designated as societies and their members as social in the most general sense.''

Here we propose that in describing and assessing social dynamics in ''subsocial'' arachnids, it is past time to take into account both the duration and patterns of association among mothers, offspring, and siblings. Key variables are the age of dispersal from the natal group, social demography, extent of cooperative behavior, and patterns of tolerance or amicable interactions within the social group. It is through incremental changes in these variables along the social continuum that higher sociality evolves. Because the term ''subsocial'' is so firmly entrenched in the literature as an evolutionary pathway from which cooperative spiders and eusocial insects have evolved, we feel it is impractical to suggest that it be eliminated. Instead, we propose that in future studies the terminology be modified to ''transient subsocial'' to describe transient parental care of eggs and young instars, such as seen in many arachnids and other arthropods (*sensu* Tallamy & Wood 1986). We propose that ''prolonged subsocial'' be used to describe species with complex and long-term associations between mothers and offspring or sibling groups that may extend up to or beyond sexual maturity, in which the associations do not last until there are multiple breeding adults within the group. We encourage the recognition that ''prolonged subsocial'' associations are, indeed, social groups in the broader use of the term (*sensu* Wilson 1971; Costa & Fitzgerald 1996, 2005). By this definition, both *D. diadema* and *P. marginemaculatus* live in prolonged subsocial groups.

We recognize that duration of association is a continuum and may vary with ecological factors, but general patterns of association are found in different taxa. Most arachnid orders have species that we characterize as ''transient subsocial.'' They exhibit early parental care with maternal (and in opilionids paternal) defense of eggs, as well as a brief association of newly emerged young (first and rarely second instar) with their mother prior to independent foraging and explosive dispersal from the natal nest (Table 1: Uropygi (Thelyphonida), Amblypygi, Schizomida, some Araneae, Pseudoscorpiones, Scorpiones, Acari, Solfugae, Opiliones). However, more prolonged associations between mothers and offspring, and siblings are rare among the arachnids and are only described in a few species per order (Table 2: Araneae, Amblypygi, Scorpiones, Pseudoscorpiones, Acari).

Of the approximately 39,000+ identified spider species less than 0.2% (55 colonial and cooperative species, 18 *Argyrodes* sp.) are social (Whitehouse & Lubin 2005; Platnick 2006). Perhaps another 0.06% (21 species) of spiders show social tendencies greater than transient early parental care (Whitehouse & Lubin 2005; Tables 2, 3). Among the approximately 45,200 Acari, there are ~13 (0.0001%) social species, primarily spider mites in the Family Tetranychidae (Saito 1997; Mori & Saito 2005). Of the ~10,525 species in the other arachnid orders (Coddington & Colwell 2002; Harvey 2003), there are approximately 0.15% (16 species) that show evidence of social traits beyond early parental care (Tables 2, 3). Some of the smaller arachnid groups, such as the 78 species of Palpigradi and 55 Ricinulei species, are so poorly known that no conclusions can be made about their social tendencies. Of the 23 social arachnid species (excluding the six non-tetranychid acarines for which little demographic data is available, Saito 1997, pers. comm.), 14 live in prolonged subsocial groups (amblypygids, scorpions, spider mites), while 9 are unquestionably ''social'' characterized by long-lasting groups with multiple breeding adults (pseudoscorpions, scorpions, spider mites). Thus, well over 99% of all arachnids are solitary, while perhaps as many as 0.05% exhibit social tendencies allowing largely predaceous creatures to live in groups for some extended period in their lives. As predators, the longer the parent(s) and siblings remain together, the greater the immatures' predatory capabilities and need for prey, and the more precarious the balance between the benefits of cooperation and costs of conflict inherent in all social groups (Krause & Ruxton 2002). Elucidating the selective factors that have enabled this tiny percentage of the arachnids to live in social groups is important to understanding the evolution of the arachnids, and the evolution of sociality generally.

Within the arachnids, there is a continuum between the prolonged subsocial and social species. The only obvious feature that separates these two groups is the presence or absence of multiple breeding females within the social group. The continuum ranges from relatively brief associations of mothers with their young offspring or within sibling groups (e.g., Schneider 1995; Kim 2000), associations that last for long developmental periods prior to sexual maturity (e.g., Polis & Lourenco 1986; Evans 1998; Mahsberg 2001; this study), long lasting groups with multiple breeding females (Brach 1978; Polis & Lourenco 1986; Zeh & Zeh 1990; Saito 1997; Mori & Saito 2005), and the complex sociality of the cooperative spiders (Aviles 1997; Whitehouse & Lubin 2005).

Patterns of social behavior among the spiders have been well documented (Buskirk 1981; Aviles 1997; Uetz & Heiber 1997; Whitehouse & Lubin 2005) and will not be repeated here except in comparison to the other social arachnids. Traits that are characteristic of colonial and cooperative social spiders include: (1) Prolonged association with conspecifics, (2) a high level of tolerance, (3) a strong tendency to aggregate, (4) overlapping generations of kin, (5) communicative behavior, (6), cooperation in prey capture, retreat construction, or defense, (7) a lack of colony identity (but see Rowell & Aviles 1996 for an exception), and (8) the presence of silk webs that facilitate cooperative prey capture and intraspecific communication (Kullmann 1972; Buskirk 1981; Aviles 1997). Many of these behavioral traits are present in the other social arachnid species (Table 3), but not in those species with only transient parental care (''transient subsociality''). The first three traits and communicative behavior are typical for the prolonged subsocial and social species. Prolonged subsocial species do not have overlapping generations of adults by definition, but offspring may overlap with their mother up until sexual maturity. The extent of cooperation varies among the groups, although the amblypgyids are notable in not overtly cooperating on anything. The lack of colony identity has not been examined in most of the social arachnids, although *D. diadema* demonstrates differential behavior toward kin and non-kin (Walsh & Rayor, unpub. data). Among the non-spider arachnids, shared silken retreats can only be produced by social spider mites and pseudoscorpions (Brach 1978; Mori & Saito 2005; Tizo-Pedroso & Del-Claro 2005). In both groups, the silk is used to construct retreats rather than prey capture webs.

We argue that sociality should not be characterized *strictly* based on traits that are typical of members of a few spider families at the high end of the social continuum. Rather, such definitions should reflect common variables such as the age of dispersal from the natal group, social demography, extent of cooperative behavior, and patterns of tolerance or amicable interactions within the social group. Studying the diversity and complexity of social behaviors in arachnids without applying the expectation that they will replicate *all* of the characteristics of the cooperative spiders (or eusocial insects, for that matter) will help elucidate general patterns in social evolution.

One form of ''social'' grouping in arachnids that we could not readily classify using this scheme were the temporary aggregations of (apparently) unrelated subadult and adult opilionids, pseudoscorpions, and scorpions (Weygoldt 1969; Polis & Lourenco 1986; Coddington et al. 1990; Machado & Vasconcelos 1998; Machado 2002) (Table 3). These aggregations are characterized by tolerance, preference for close contact with others, and cooperative defense from predators. Most occur in potentially limited habitats and may be associated with increased humidity or, in pseudoscorpions, opportunities for phoresy, but do not seem to be truly social groups by most definitions.

In summary, social behavior is rare among the arachnids. Rare behaviors provide the opportunity to pose ecological and evolutionary questions about the costs and benefits of group living. Here we have described two amblypygid species that clearly display some social behaviors characteristic of the other social arachnids, but are also not identical in all features. Further, we suggest that a broader terminology and clearer descriptions of the duration of association and the patterns of social behaviors will aide in our understanding of group-living among arachnids and the evolution of sociality.

ACKNOWLEDGMENTS

We would especially like to thank two undergraduates for their efforts on this project: Rachel Walsh was truly heroic in recording spatial and disturbance data for *D. diadema* Groups 5–7 in Spring 2002. Benjamin Larsen collected orientation and spatial data in *P. marginemaculatus* from 1998–1999. B. Larsen, Brenda Gonzalez, Leanne Cronin and Stephanie Johnson assisted with many observations before we discovered the social tendencies of the amblypygids. Cole Gilbert was a source of endless ideas and assistance, as well as explaining Rayleigh statistics. Input from Gail Stratton, Eileen Hebets, Peter Weygoldt, Jae Choe, Jim Costa, Mark Harvey, George Uetz, Dan Papaj, and Tom Seeley was invaluable. Chris Fishel, Todd Gearheart, Adrian Barnett, Yutaka Saito, Deiter Mahsberg, and Justin Schmidt graciously provided unpublished observations or clarifications. We appreciate the detailed suggestions on the manuscript by an anonymous reviewer and Gail Stratton. Frank Somma and T. Gearheart obtained the amblypygids, and provided extensive habitat information. We thank the Department of Entomology at Cornell University, Francoise Vermeylen of the Cornell Office of Statistical Consulting, Jonathon Coddington, Connie Rayor, and John & Marcia Taylor. This research was partially funded by the Cornell University Biology Honors Program to LT (who received high honors), and the Cornell Undergraduate Minority Research Fund (for B. Gonzalez).

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Manuscript received 3 May 2004, revised 30 June 2006.