BEHAVIORAL REPERTORY OF THE NEOTROPICAL HARVESTMAN *ILHAIA CUSPIDATA* (OPILIONES, GONYLEPTIDAE)

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ABSTRACT. In this study, we provide an ethogram for the harvestman *Ilhaia cuspidata* and describe the daily activity pattern of captive individuals. We also provide a comparison between the behavioral repertory of this species with that of the syntopic *Discocyrtus oliverioi*. Five females and four males of *I. cuspidata* were maintained in the same terrarium from November 1999–November 2000 for qualitative and quantitative observations. Twenty behavioral acts were recorded, classified in seven categories and the relative frequency of each was determined: exploration (69.8%), resting (16.7%), feeding (6.3%), grooming (4.4%), social interactions (2.6%), reproduction (0.1%) and others (0.3%). There was a marked difference in the frequency of the behavioral categories between sexes: females fed more frequently than males and males were involved in social interactions more frequently than females. During most of the daylight hours, individuals remained inside shelters and became active from 19:00–09:00 h. Although *I. cuspidata* and *D. oliverioi* showed almost the same behavioral acts, there were quantitative differences in their repertories: the relative frequency of behavioral categories ‘‘resting’’ and ‘‘social interactions’’ were higher for *I. cuspidata* whereas ‘‘reproduction’’ and ‘‘grooming’’ were higher for *D. oliverioi*. The main qualitative difference between these two species was related to the forms of parental care: females of *D. oliverioi* guard their eggs and first instar juveniles, whereas females of *I. cuspidata* scatter their eggs in time and space and do not actively protect their offspring. Since both species share the same habitats (sometimes in multi-species aggregations), the behavioral differences between them may be explained by particular morphological and physiological characteristics of the species, as well as by phylogenetic constraints.

Keywords: Activity pattern, defensive behavior, *Discocyrtus*, ethogram, gregariousness, parental care

The Opiliones constitutes a highly diversified order in terms of morphology and habits, and includes approximately 5000 species widespread throughout the world (Adis & Harvey 2000). Harvestmen are particularly suitable for behavioral studies because individuals of many species are abundant and easy to observe, both in the field and laboratory. Selected species may be good model organisms for experimental manipulations since they allow researchers to test hypotheses about the ecological meaning of certain behavioral patterns (e.g. Mora 1990; Machado & Oliveira 1998; Machado et al. 2002). Representatives of the suborder Laniatores may be maintained in captivity, where they behave in a similar way to that observed in the field (e.g. Capocasale & Bruno-Trezza 1964; Elpino-Campos et al. 2001; Willemart 2001), facilitating quantitative and qualitative comparisons between species.

An ethogram is a set of comprehensive descriptions of the behavioral repertory of a species (Brown 1975). Allied with field observations, ethograms are important starting points for any ethological research and for understanding the biology and ecology of a wide range of animals (Lehner 1940). *Discocyrtus oliverioi* H. Soares 1945 (Gonyleptidae, Pachylinae) was the first harvestman to have its behavioral repertory studied and is so far the only species available for comparison (El-

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pino-Campos et al. 2001). This harvestman species showed 25 behavioral acts that were divided into six major categories: exploration, resting, foraging, social interactions, self-grooming, and reproduction. The individuals were inactive during the day and foraged and interacted with other individuals at night. Females reproduced in captivity and showed maternal care toward the eggs and newly hatched offspring (Elpino-Campos et al. 2001).

Discocyrtus oliverioi is very abundant in urban areas of Uberlândia, state of Minas Gerais, Brazil, where it occurs syntopically with two other harvestmen, *Discocyrtus* sp. and *Ilhaia cuspidata* Roewer 1913 (Elpino-Campos et al. 2001). In this paper, we provide a detailed ethogram for *I. cuspidata* (Gonyleptidae, Gonyleptinae) and describe the daily activity pattern of captive individuals. Some comments on the foraging, defense, gregariousness, and reproduction of this harvestman are also presented for the first time. In addition, we have made qualitative and quantitative comparisons between the behavioral repertories of *I. cuspidata* and *D. oliverioi*.

METHODS

Collection of harvestmen and maintenance in the laboratory.—Individuals of *I. cuspidata* were collected in the Experimental Garden of the Universidade Federal de Uberlândia (18° 53′S, 48° 15′W; 863 m ele.), an urban area in the state of Minas Gerais, southeastern Brazil. The behavioral observations were based on nine individuals (5 females and 4 males) maintained in the same terrarium (20.5 × 44.5 cm × 27.5 cm high) containing soil, leaves and two pieces of tree fern trunk (8 × 10 cm each) as shelters. The shelters had the shape of a gabled roof, so that the individuals could slip under them, finding protection against light. Temperature and moisture conditions in the laboratory were similar to those in the field (nearly 25 °C and 70–80% relative humidity). In addition, nine individuals of *D. oliverioi* and one of *Discocyrtus* sp. were also placed in the same terrarium. The harvestmen were fed live termite workers (Insecta, Isoptera), freshly chopped pieces of earthworms (Annelida, Oligochaeta), honey solution and an artificial diet for ants (Bhatkar & Whitcomb 1970). A light schedule of 14L: 10D was maintained in the laboratory, simulating the natural lighting at the time of the study.

Activity pattern.—The activity schedule of *I. cuspidata* was quantified by observing captive individuals at 1 h intervals during a 24 h period. Sampling at each interval consisted of counting the number of individuals accomplishing the different types of behavioral acts during a 5 min period. These observations were repeated on three non-consecutive days in January 1999 totaling 72 h of sampling. The main aim of these samplings was to determine the relative frequency of the major behavioral categories throughout the day. At this point, we were not interested in determining the biological rhythm of the species.

Behavioral repertory and ethogram.—In order to identify and describe the behavioral acts of *I. cuspidata*, six hours of field observations and another 6 h of observations in the laboratory (20 sessions of 36 min ad libitum sampling, sensu Altmann 1974) were done at night when the animals were most active (18:00–00:00 h) in January 1999. The description of all behavioral acts and their classification into behavioral categories were as described by Elpino-Campos et al. (2001). In addition quantitative data only on captive individuals were obtained in 30 sessions of observations from November 1999–November 2000. Each session consisted of scan samples of all individuals performed at 50 min intervals over 200 min. For each sampling all individuals were scanned twice. These observations were made between 19:00 and 03:00 h with a red lamp to avoid disturbing the animals (cf. Machado & Oliveira 1998; Elpino-Campos et al. 2001). Ten minutes before each behavioral sampling, 10 termite workers and three pieces of earthworm (1 cm each) were offered as food. The data recorded in these samplings were used to construct the ethogram. The absolute frequencies of the major behavioral categories were compared between sexes and between *I. cuspidata* and *D. oliverioi* using a G test (Sokal & Rohlf 1995). The null hypothesis was of no difference between sexes and between species. Some specific behavioral acts (see results) were also compared using a chi square test done on the raw data (Sokal & Rohlf 1995).

Voucher specimens of males and females of *I. cuspidata*, *D. oliverioi*, and *Discocyrtus* sp. were deposited in the Museu de Biodiversi-

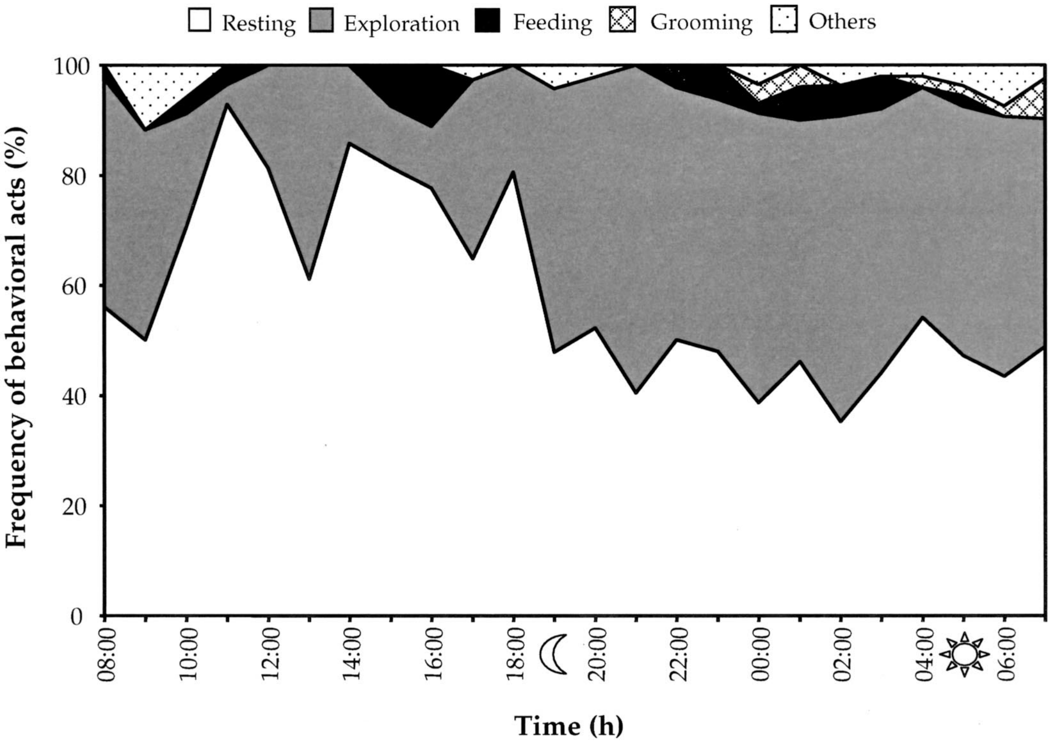

Figure 1.—Daily activity schedule of the harvestman *Ilhaia cuspidata*. The data are based on three different days of sampling and were obtained from nine captive individuals. The moon and the sun indicate dusk and dawn, respectively.

dade do Cerrado (MBC, Uberlândia, MG, Brazil) and at the Museu de Zoologia da Universidade de São Paulo (MZSP, São Paulo, SP, Brazil).

RESULTS

Activity pattern and foraging.—During most of the daylight hours, individuals of *Ilhaia cuspidata* were found hidden inside shelters (Fig. 1). Individuals became active with the onset of darkness (about 18:00 h), when they left the shelters to forage (Fig. 1). They accepted both live (termites) and dead (pieces of worm) animals, with the food item being grasped and taken to the shelter to be consumed. Fights for food and aggressive interactions were observed among conspecifics ($n = 7$) and with *Discocyrtus oliverioi* ($n = 3$) in the shelters. Sometimes, two or more conspecifics were seen feeding simultaneously on the same piece of food ($n = 3$). Most individuals of *I. cuspidata* became inactive at about 9:00 h, i.e., four hours after sunrise (Fig. 1). Notwithstanding, individuals were recorded outside the shelters sometimes during the day, drinking water or walking about (Fig. 1).

Behavioral repertory.—Twenty behavioral acts, classified into seven major groups of activities, were recorded for *I. cuspidata*: feeding, social interactions, resting, exploration, grooming, reproduction and others (Table 1). Exploration was the most common activity, followed by resting and feeding (Table 1). Although field observations indicated that *I. cuspidata* is a gregarious harvestman (see below), in captivity individuals rested alone more frequently than in groups (males and females combined; $\chi^2 = 8.33$; d.f. = 1; $P < 0.01$). Self-grooming activities, known as leg threading in harvestmen (cf. Edgar 1971), involved mainly legs II (males and females combined; $\chi^2 = 12.43$; d.f. = 3; $P < 0.001$) (Table 1). Grooming behavior occurred when the harvestmen were moving around the environment and, more frequently, after feeding (when both legs and pedipalps were cleaned).

There was a marked difference in the frequency of behavioral categories between

Table 1.—Behavioral repertory and frequency of each behavioral act for nine captive individuals of the harvestman *Ilhaia cuspidata*. n = number of individuals observed and, in parentheses, the number of behavioral acts observed for each sex.

Behavioral acts	Frequency of behavioral acts (%)		
	Males (n = 4) (881)	Females (n = 5) (1291)	Total (n = 9) (2172)
FEEDING	5.11	7.05	6.27
Feed on termites	1.82	1.94	1.89
Feed on pieces of worm	2.61	3.87	3.36
Feed on honey solution	0.23	0.31	0.28
Fight for food	0.45	0.93	0.74
SOCIAL INTERACTIONS	4.32	1.47	2.61
Touching conspecific with legs	1.70	0.70	1.10
Touching individual of *D. oliverioi* with legs	0.68	0.23	0.41
Attacking conspecific	1.14	0.54	0.78
Attacking individual of *D. oliverioi*	0.80	0	0.32
RESTING	17.59	16.11	16.72
Alone	10.33	9.14	9.62
In multi-species aggregation	7.26	6.97	7.10
EXPLORATION	68.10	70.73	69.65
Walkabout	18.50	19.60	19.15
Touching the substrate with first legs	16.80	17.82	17.40
Touching the substrate with second legs	32.80	33.31	33.10
SELF-GROOMING	4.54	4.26	4.37
Leg threading—first pair	1.02	0.93	0.97
Leg threading—second pair	1.70	1.63	1.66
Leg threading—third pair	0.68	0.93	0.83
Leg threading—fourth pair	0.80	0.54	0.64
Cleaning the pedipalps	0.34	0.23	0.27
REPRODUCTION	0	0.15	0.11
Oviposition	0	0.15	0.11
OTHER	0.34	0.23	0.27
Pressing the body against the substrate	0.34	0.23	0.27
TOTAL	100.0	100.0	100.0

males and females (G = 20.25; d.f. = 4; $P < 0.001$). Due to the low frequency of behavioral acts the categories ‘‘reproduction’’ and ‘‘others’’ were not included in this analysis. The frequency of feeding and exploration activities was higher in females than in males, whereas males were involved in social interactions more frequently than females (Table 1).

Notes on natural history.—When disturbed in the field, individuals of *I. cuspidata* remained motionless with the legs retracted over the body. In this position, the dark brown coloration of the animals was extremely cryptic against a dark background. Individuals also showed thanatosis in which the legs were fully extended laterally and the animal became rigid for up to 5 min. Even when persistently mechanically disturbed with forceps or manipulated, the harvestmen rarely released repugnant substances or attacked the aggressor with the pedipalps.

Oviposition of *I. cuspidata* was observed twice (January and February) in the laboratory. The females repeatedly touched a given point on the substrate with the first two pairs of legs before ovipositing. Subsequently, a single egg was laid and the female spent 5–10 s attaching debris and soil particles on the egg surface with the first two pairs of legs. Females abandoned the oviposition site, leaving the egg unprotected. Another four eggs (similar in size and color) were found unprotected in the terrarium and were probably laid by females of *I. cuspidata*. Two eggs were covered by debris, while the other two had no particles attached.

In the field, five multi-species aggregations

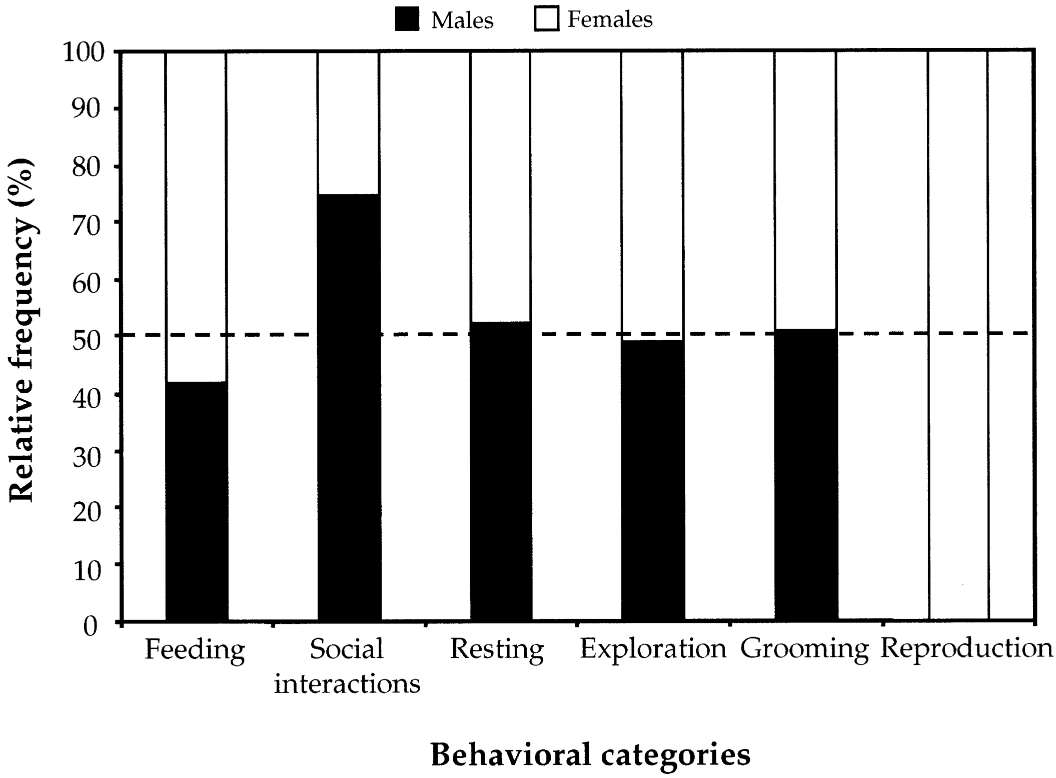

Figure 2.—Comparison of the relative frequency of the behavioral categories observed for males and females of the harvestmen *Ilhaia cuspidata* in captivity.

were found under fallen tree trunks (Fig. 3). The mean number of individuals was 21.6 ± 20.5 for *I. cuspidata*, 5.0 ± 2.2 for *D. oliverioi*, and 2.8 ± 1.8 for *Discocyrtus* sp. Females were always most frequent within the aggregations, and accounted for 55.6%–76.9% of the aggregated individuals of *I. cuspidata*.

Comparisons with *Discocyrtus oliverioi*.—There were both qualitative and quantitative differences between the behavioral repertories of *I. cuspidata* and *D. oliverioi* (Fig. 4). These two harvestmen species showed the same behavioral acts in the categories feeding, social interactions, resting, exploration, and self-grooming (Table 1; Elpino-Campos et al. 2001). In the category reproduction, however, *D. oliverioi* showed a more diversified repertory, including seven acts, whereas *I. cuspitada* showed only one (Table 1; Elpino-Campos et al. 2001). In contrast to *D. oliverioi*, whose females laid a batch of eggs and remained over the eggs, protecting them for about 22 days (Elpino Campos et al. 2001), females of *I. cuspidata* scattered their eggs in time and space and did not actively protect their offspring. The relative frequency of the major behavioral categories differed statistically between the two species ($G = 86.29$; d.f. $= 6$; $P < 0.001$). Individuals of *I. cuspidata* rested and interacted with other individuals more frequently than *D. oliverioi* (Fig. 4). In turn, the frequency of reproductive and cleaning activities were higher in *D. oliverioi* than in *I. cuspidata* (Fig. 4).

DISCUSSION

Although the subfamily Gonyleptinae is one of the largest among the Gonyleptidae (Pinto-da-Rocha 1999), there are few studies describing the ecology and behavior of its representatives (but see Machado & Pizo 2000; Machado & Vidal 2001). Some behavioral patterns of *Ilhaia cuspidata* are very similar to other gonyleptids, especially those of the subfamily Pachylinae (see Acosta et al. 1993, 1995; Capocasale & Bruno-Trezza 1964; Elpino-Campos et al. 2001). Individuals of *I. cuspidata* are mainly nocturnal, generalist

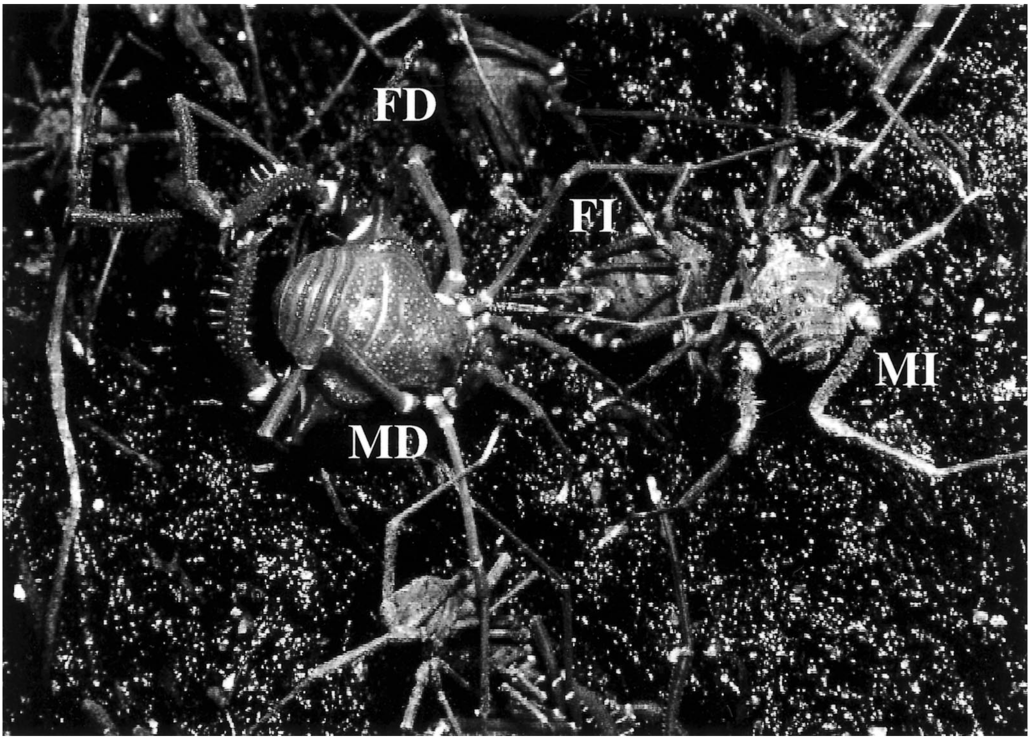

Figure 3.—Multi-species aggregation of harvestmen under a fallen trunk in the Experimental Garden of the Universidade Federal de Uberlândia, in the state of Minas Gerais, southeastern Brazil. MD = male of *Discocyrtus oliverioi*; FD = female of *D. oliverioi*; MI = male of *Ilhaia cuspidata*; FI = female of *I. cuspidata*.

predators that carry their food to shelter before feeding, and may be found in small aggregations during the day, like many gonyleptids (see Capocasale & Bruno-Trezza 1964; Acosta et al. 1993, 1995; Gnaspini 1996; Hoenen & Gnaspini 1999; Machado et al. 2000; Elpino-Campos et al. 2001; Santos & Gnaspini 2002). The defensive behavior, however, is more similar to that of cosmetids (Eisner et al. 1978), manaosbiids (Cokendolpher 1987), and trogulids (Hillyard & Sankey 1989), which also feign death and rarely emit gland secretions.

The most frequent behavioral act for the captive individuals of *I. cuspidata* was to touch the substrate with the second pair of legs. In harvestmen these legs possess numerous sense organs and are used to touch the substrate, food, and other organisms (Edgar 1963). During such activities, offensive organisms and debris come into contact with the sense organs. Thus, the main functions of leg threading probably are to remove pathogenic fungi or other free-loading organisms before they have time to penetrate the cuticle, and to restore sensory receptors to their full sensing status (Edgar 1971).

Males and females of *I. cuspidata* differed in the relative frequency of the behavioral categories, with females feeding more frequently than males. It is known that the respiratory rate of female harvestmen increases when they are producing and maturing eggs (Phillipson 1962, 1963). This physiological change during egg development probably accounts for the higher requirement for food (Phillipson 1962, 1963; Gnaspini 1996). Indeed, in the cavernicolous harvestman *Goniosoma spelaeum* (Mello-Leitão 1923), females bearing eggs leave the cave to forage more frequently than other adult individuals in the population (Gnaspini 1996). The month in which the quantitative observations were conducted in our study (January) coincided with the period when females of *I. cuspidata* were laying eggs in the laboratory. Thus, the higher frequency

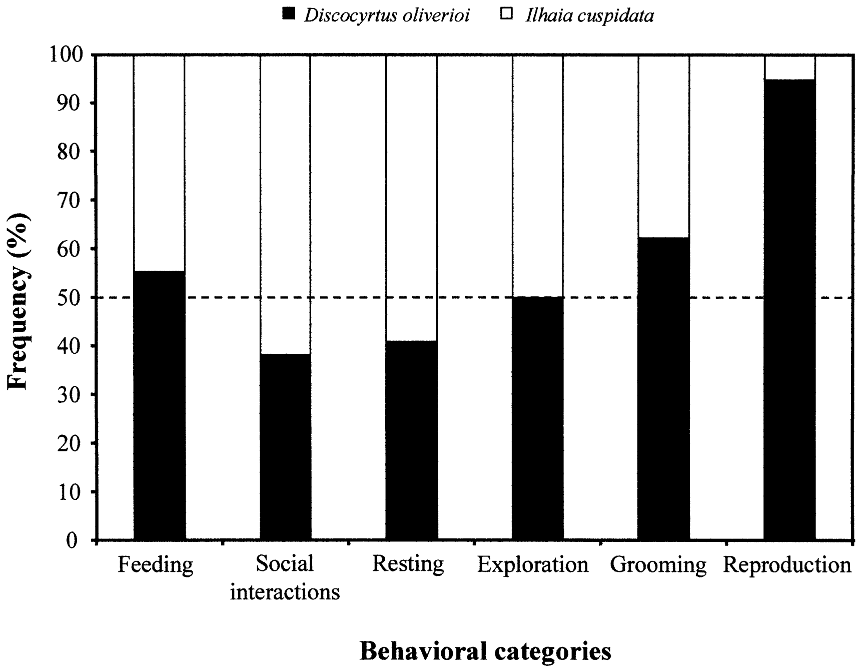

Figure 4.—Comparison of the relative frequency of the behavioral categories observed for the harvestmen *Ilhaia cuspidata* and *Discocyrtus oliverioi* in captivity.

of feeding activities in females compared to males may be related to the accumulation of energy for egg production and maturation.

Males of *I. cuspidata* interacted aggressively with conspecifics at a higher frequency than females. Possible explanations for this behavioral pattern include intolerance among males, competition for females, and territorial fights (see Macías-Ordóñez 1997). More details of the natural history of this species in the field are needed to assess the causes of aggressive behavior in males. The aggressiveness among males, however, may explain why females account for most of the aggregated individuals.

Under natural conditions, *I. cuspidata* and *D. oliverioi* live in the same habitat, use the same microhabitats to forage, take shelter and reproduce, and show a considerable overlap in their periods of activity (see also Elpino Campos et al. 2001). Our results, however, showed that, at least in captivity, these species differ in their allocation of time and energy to the behavioral categories studied. Individuals of *I. cuspidata* rest more and seem to be more aggressive than *D. oliverioi*, which may explain why individuals of the former species tended to rest alone more frequently than in groups in the laboratory.

The main qualitative difference between these two harvestmen species was related to the forms of parental care: females of *D. oliverioi* guarded their eggs and first instar juveniles, whereas females of *I. cuspidata* scattered their eggs in the substrate and did not show any additional interaction with the offspring. Since eggs of *I. cuspidata* and *D. oliverioi* are laid in the same environment and supposedly face similar selective pressures (such as abiotic factors and predators), how can we explain the differences in the forms of parental care?

The evolution of the different forms of parental care is a complex function of many interacting factors including morphology, defensive behavior, and phylogenetic constraints (see Tallamy & Wood, 1986). Harvestmen with a short ovipositor, like all Laniatores, are unable to hide their eggs in deep cavities where they are inaccessible to most predators. In these cases, the physiology of egg production, life span, and defensive strategies may offer a partial explanation on when subsocial behavior may evolve (review in Machado & Raimundo 2001). Maternal care is a viable strategy only when females lay eggs aggregated in the time and space, live long enough to benefit one or more batches, and have defensive strategies that enable them to protect the offspring against predators. Species in which females do not fit these features (or are constrained by phylogenetic inertia) present alternative forms of parental care including egg hiding and/or egg covering. This is probably the case of *I. cuspidata* that, despite living more than one year as adult, may be physiologically constrained to iteroparity and relies mainly on evasive strategies of defense.

Egg hiding by females is probably the most common form of parental investment among harvestmen of the suborder Laniatores (Machado & Raimundo 2001). Generally, nonsubsocial harvestmen hide their eggs inside small natural crevices or cover them with debris and leave the offspring without additional care (Canals 1936; Cokendolpher & Jones 1991; Juberthie 1965, 1972; Willemart 2001). Laying eggs in several batches or scattering single or few eggs over a very wide area may be advantageous and confer protection to the offspring because detection by natural enemies would be reduced (Edmunds 1974; Willemart 2001).

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