

# First Characterization of the Behavioral Repertory in a Ricinuleid: *Cryptocellus narino* Platnick & Paz 1979 (Arachnida, Ricinulei, Ricinoididae)

L. F. García<sup>1,5</sup> · E. Torrado-León<sup>2</sup> · G. Talarico<sup>3</sup> · A. V. Peretti<sup>4</sup>

Revised: 14 July 2015 / Accepted: 21 July 2015 /  
Published online: 1 August 2015  
© Springer Science+Business Media New York 2015

**Abstract** Ricinuleids are considered one of the most enigmatic and neglected arachnid orders. The low diversity and poor local abundance of several species, makes the study of most aspects related to biology and behavior of this group very difficult. Most of the current knowledge related to ricinuleid biology relies on anecdotal observations. So far, no published studies exist that describe in detail ricinuleid behavior. Here we present the behavioral repertory of a ricinuleid, the Neotropical species *Cryptocellus narino*. Eighteen individuals (six males, six females and six immatures) were examined under laboratory conditions to describe and quantify their behavioral repertory and its variation along the day. The behavioral repertory in males exhibited a higher number of behavioral acts when compared to females and immatures. The most frequent

---

✉ L. F. García  
luizf.garciah@gmail.com

E. Torrado-León  
etorradol@unal.edu.co

G. Talarico  
giovanni.talarico@uni-greifswald.de

A. V. Peretti  
aperettibec@gmail.com

<sup>1</sup> Laboratorio de Ecología del Comportamiento, Instituto de Investigaciones Biológicas Clemente Estable, Avenida Italia, 3318 Montevideo, Uruguay

<sup>2</sup> Facultad de Agronomía, Universidad Nacional de Colombia, Carrera 30#35S-3, Bogotá, DC, Colombia

<sup>3</sup> Department of Forensic Toxicology, Institute of Legal Medicine, University of Greifswald, Kuhstrasse 30, 17489 Greifswald, Germany

<sup>4</sup> Instituto de Diversidad y Ecología Animal (CONICET-UNC) & Laboratorio de Biología Reproductiva & Evolución, Universidad Nacional de Córdoba, Av. Velez Sarsifeld 299, Córdoba, Argentina

<sup>5</sup> Present address: Centro Universitario Regional Este, Universidad de la República, Simón del Pino 1132, Treinta y Tres, Uruguay

behavioral categories were “resting”, “exploring” and “feeding”. “Resting” was the most common behavior during the photophase, while “feeding” and “exploring” were the most common during scotophase, suggesting this species is predominantly nocturnal. This study also provides behaviors previously not known for this group as well as a description of the daily schedule. We expect this work will become a baseline study for further research on ricinuleid ethology.

**Keywords** Ethogram · daily activity · neotropical · hooded tickspiders

## Introduction

Arachnids of the order Ricinulei (hooded tickspiders) are a very peculiar group. They exhibit unique morphological modifications such as the hood-like cucullus covering the mouthparts dorsally as well as the sexually dimorphic third pair of legs in males which is modified for sperm transfer (e.g., Platnick 2002). Most studies about this group, including the most recent publications, have mainly focused on its taxonomy (e.g., Botero-Trujillo 2014; Valdez-Mondragón and Francke 2011; Tourinho and Saturnino 2010; Tourinho et al. 2014), ultrastructure (e.g., Talarico et al. 2006, 2008, 2011), biogeography (e.g., Muriene et al. 2013) and ecology (e.g., Barreiros et al. 2005), while other aspects remain unknown. Indeed, the behavior of ricinuleids relies mostly on occasional observations without detailed analyses of the behavioral patterns.

The main studies about the behavior of ricinuleids have focused on general characterization of feeding and mating behaviors (Pollock 1967; Cooke 1967). Ricinuleids prey on a wide variety of invertebrates such as dipteran larvae, enchytraeid annelids, nematodes, spiders and termites (Platnick and Pass 1982). Although some species reject dead items, others include carrion and feces in their diet (Mitchell 1970). Similarly, the observations about mating behavior are scarce and focused mainly on the functional aspects of ricinuleid genitalia. Ricinuleid mating occurs after the male encircles the female using its leg and grasps it in a position similar to the “amplexus” of amphibians (Pollock 1966; Legg 1977). This position enables the male to insert one of its copulatory organs (modified metatarsus and proximal two tarsomeres of the third legs) for the purpose of sperm transfer into the genital opening on the ventral side of the female. Descriptions about the defensive behaviors of ricinuleids include the display of thanatosis and the production of anal secretions by a rectal gland (Pollock 1967; Legg 1977; Talarico et al. 2011).

The behavioral catalogues or ethograms are important tools for biologists and behavioral ecologists, since they allow standardizing the description and nomenclature for a given set of behaviors of a particular species. Indeed, ethograms work as a starting point for species-oriented behavioral research, (e.g., Lehner 1996; MacNulty et al. 2007; Fagen and Goldman 1977). The use of behavioral catalogues has allowed unveiling some complex behaviors such as the division of labor in social insects (e.g., Santos et al. 2005).

Among arachnids, behavioral repertoires have been widely used in order to describe the basic behavior of some poorly known groups. These include scorpions (Mineo et al. 2003), schizomids (Alves de Oliveira and Lopes Ferreira 2014), harvestmen (Osses et al. 2008; Pereira et al. 2004) and pseudoscorpions (Tizo-Pedroso and Del-Claro 2011). The description of their basic behaviors turned out

to be useful as background for further studies related to parental (e.g., Nazareth and Machado 2009) and social behavior (e.g., Tizo-Pedroso and Del-Claro 2011), systematics (e.g., Caetano and Machado 2013), as well as sexual selection (e.g., Willemart et al. 2009). Nevertheless, the current knowledge about the behavior of many arachnid orders is still scarce and in many cases only based upon anecdotal observations about specific behaviors.

Due to the evident lack of information related to the biology and behavior of the ricinuleids, the aim of the present study is to describe the behavioral repertory of this order. We carried out this work using the species *Cryptocellus narino* Platnick and Paz 1979, an epigeal Neotropical species that is widely distributed in Colombia (Platnick and García 2008). We used individuals of different sex and age. Additionally, we describe the activity schedule of *C. narino* based on the variation of the behavioral repertory along the day.

## Material and Methods

### Field Capture and Rearing

Individuals of *C. narino* were collected between June and July of 2007, in a secondary forest found in the urban zone in the city of Ibagué, Colombia (4° 25' 52"N, 75° 11' 19" W). Eighteen individuals (six males, six females and six tritonymphs) were used. Individuals of other nymphal stages were not used because of their low local abundance on the collecting sites. Most individuals ( $n=12$ ) were found associated to termite mounds. The remaining individuals were found under logs and rocks. We used small sample sizes for the behavioral observations because most ricinuleid species are considered uncommon and only few species have been reported to be locally abundant (e.g., Tourinho et al. 2014).

After collection, individuals were placed together inside a terrarium (20 cm width × 30 cm length × 20 cm height) since *C. narino* has gregarious habits in nature, and it is found in groups which include up to 26 specimens (García 2007). The terrarium was filled with previously sterilized soil, logs and rocks collected from the sampling locality. Temperature ( $25\pm 3$  °C) and humidity ( $70\pm 10$  %) were held constant during the study. Photoperiod was kept for a 12 h:12 h light:dark cycle. During the night, we observed individuals under red light, since it is known that several arthropod species are not able to perceive this light spectrum (Fleissner and Fleissner 2001). In order to distinguish each specimen, individuals were marked on legs and abdomen using water paint, following methods used by Hagler and Jackson (2001).

We performed preliminary trials to test prey consumption before starting the behavioral records. On these previous essays, several individuals of different arthropod groups found in association to ricinuleids, namely collembolans (Collembola: Symphypleona), termites (Isoptera: Termitidae) and thysanurans (Thysanura: Nicoletiidae) were offered as food items. Termites were the only food item readily accepted by all individuals, so we used them as prey in all further behavioral observations. Voucher specimens were deposited in the biological collection from the Centro de Biosistemas, Universidad Jorge Tadeo Lozano.

## Analyses of Behavioral Repertory

To characterize the behavioral acts and units of ricinuleids we performed initially 60 h of ad libitum observations (Stamp Dawkins 2007) using all available individuals at different times of the day. After we had characterized the behavioral repertory, we evaluated behavioral completeness. To do this, we randomly chose an individual and observed it during one hour following the “all occurrences focal animal recording” method (Martin and Bateson 2007). We repeated this procedure 15 times per each group (males, females and tritonymphs) totalizing 15 h of records per group and 45 observations.

All individuals were recorded at least once and we observed them on different time periods, namely photophase (10:00–12:00), transition photophase/scotophase (17:00–19:00) and scotophase (22:00–0:00). Night observations were recorded using a Sony DCR-TRV480 video camcorder in nightshot mode to improve visibility under logs and other hidden places in the terrarium. To elicit feeding behavior, we placed 18 termites inside the terrarium 10 min before each observation, and subsequently recorded all the activity related to feeding.

Behavioral completeness was evaluated using the method suggested by Dias et al. (2009) where new behaviors are recorded as a function of the observation period. This method is particularly useful to describe the relationship between the sampling effort and the behavioral observations, since the probability of adding new acts decreases with the number of recorded behaviors, graphically the behavioral completeness can be visualized by using asymptotic curves (Lehner 1996). The recorded proportion of the behavioral repertoire is estimated as the ratio between the total number of observed behaviors and the predicted number of behavioral acts, the latter parameter can be obtained by using a non-linear regression on the data, which is fitted to the Clench equation (Dias et al. 2009). Non-linear curve fitting and parameter estimation were performed with the R statistical software version 3.1.1 (R Core Team 2014).

## Behavioral Quantification

In order to quantify the behavioral repertory, we used the method suggested by Osses et al. (2008), where the behaviors of specimens are recorded on different time points. To register the individuals, one hour is chosen (between 0:00 and 23:00) and divided into 60 intervals of one minute. For each minute, an individual is randomly observed and the behavioral act displayed is recorded using the “fixed-interval time point sampling” method (Martin and Bateson 2007). This method allowed us to evaluate the change in the different behavioral categories along the day and the incidence of each evaluated group on behavioral categories. This approach also reduces the pseudoreplication, by registering randomly one individual at a time. All observations including those related to mating, were carried out with all the individuals together.

We left a period of 24 h between two successive observations. At the end of each observation period, 60 records were obtained. This procedure was repeated twice per each day hour, so at the end of the study we had recorded the individuals for 48 h. Data were analyzed using a generalized linear mixed model with a Poisson error structure and a log-link function (Zuur et al. 2009), because individuals were recorded repeatedly. We used the behavioral category, group (male, female, immature) and day phase

(photophase, scotophase) as explanatory variables and the number of behavioral records as response variable. We evaluated the incidence of each explanatory variable as well as all the possible interactions. Data were analyzed using R statistical software version 3.11 (R Core Team 2014).

## Results

### Behavioral Completeness

After performing the ad libitum observations we found that the behavioral repertory was composed by 15 behavioral acts grouped into seven categories (Table 1). The highest number of behavioral acts was found in males ( $n=14$ ), followed by females ( $n=12$ ) and immatures ( $n=12$ ). Although some behaviors related to mating like the courtship behavior or reproduction like egg laying were not observed, the behavioral completeness percentage was high in all the evaluated groups being 90 % for immatures, 91 % for females and 92 % for males. In all the cases, the most representative fraction of the behavioral repertory was reached after 6 h of observation (Fig. 1). The most frequent behavioral categories are illustrated in Fig. 2. The total number of records for each behavioral act is shown in Fig. 3.

### Behavioral Quantification

We did not find a significant interaction between the group and behavioral category ( $\chi^2_2=2.79$ ,  $P=0.24$ ). Nevertheless, analyzing the grouped behavioral categories revealed significant differences between them ( $\chi^2_5=1617.97$ ,  $p<0.01$ ). The most frequent behavioral categories were “resting”, followed by “exploring”, “feeding”, “interacting” and “mating” (Fig. 2). The category “grooming” was excluded from the analysis because it had a very low frequency ( $<0.5$  %) when compared to other categories and occurred only in males, causing a bias in the data analysis. The frequency of each behavioral act per category is shown in Table 1. The individuals performing the three most frequent behavioral acts are illustrated in Fig. 4.

There was a significant interaction ( $\chi^2_5=625.57$ ,  $p<0.01$ ) between the frequency of behavioral categories and the time of the day (Fig. 5). Individuals of *C. narino*, were observed “resting” during most of the photophase, while other categories such as “exploring” and “feeding” were significantly more frequent during the scotophase, other categories such as “interacting” and “mating” did not show significant differences along the day. These results, confirm that *C. narino* is a species with a predominantly nocturnal activity. The daily activity schedule is displayed in Fig. 6.

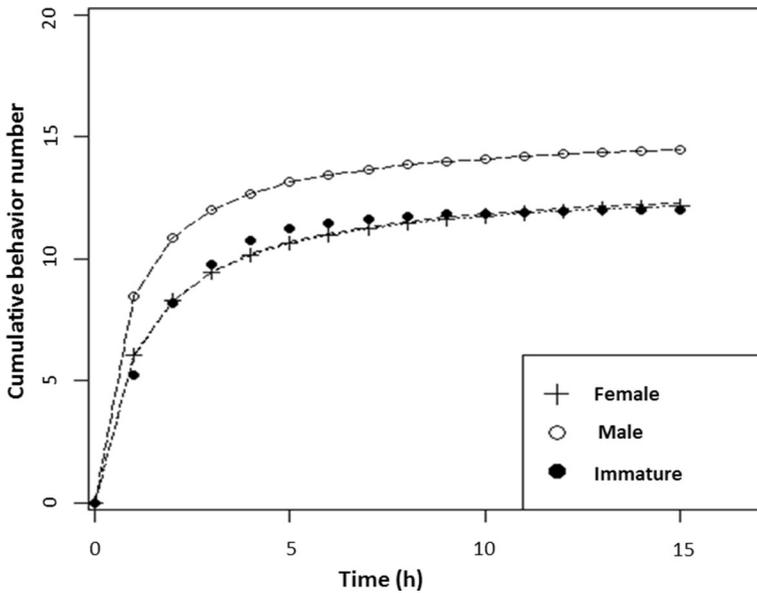
## Discussion

The repertory of the studied ricinuleid was smaller compared to other arachnid species. For example, the social pseudoscorpion *Paratemnoides nidificator* presents a very rich behavioral repertory composed by 95 behavioral acts (Tizo-Pedroso and Del-Claro 2011). Some solitary species such as the harvestmen species *Neosadocus maximus*, and

**Table 1** Behavioral categories of the ricinuleid *Cryptocellus narino* based on the observation of 6 adult males, 6 adult females and 6 immatures

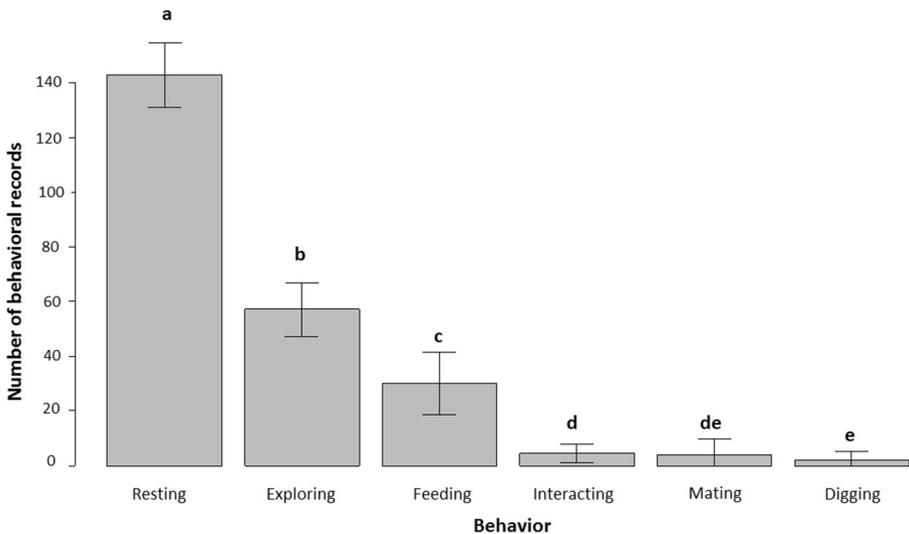
Behavioral act	Description
1. Exploring	
Roaming	The individual touches the substrate using the two first pairs of legs and the pedipalps while moving.
Substrate exploration	The individual touches the substrate using the two first legs and the pedipalps without walking.
Substrate manipulation	The ricinuleid grabs small rocks with cucullus and pedipalps without walking.
2. Interacting	
Conspecific contact	The individual touches conspecifics using the pedipalps and the two first pairs of legs.
Fighting for food	Two or more individuals grab the same prey and each tries to push back the rivals using the second pair of legs and pedipalps.
Food sharing	Two or more individuals feed simultaneously on the same prey item, without pushing back conspecifics.
3. Cleaning	
Grooming	The individual puts the distal parts of the pedipalps or the legs inside the preoral cavity and removes soil particles from the surfaces with its mouthparts until the tips of the appendages are reached.
4. Feeding	
Walking with food	The individual walks while carrying one prey item with chelicerae, cucullus and pedipalps
Feeding on the same place	The ricinuleid manipulates the prey using the cucullus, chelicerae and pedipalps without walking
Overfeeding	The ricinuleid feeds simultaneously on two prey items while avoiding contact with other individuals.
5. Mating	
Male mount	The male ricinuleid displays an “amplexus” position, placing over the female while inserting the modified tarsomeres of a third leg into the female genital opening
Mount allowing	The female ricinulei remains motionless while the male mounts her in an “amplexus” position and inserts the modified tarsomeres of a third leg into the female genital opening
6. Resting	
Resting alone	The individual remains motionless, with the legs folded against the body, more than one body length in distance to the closest conspecific
Resting aggregated	The individual remains motionless with the legs folded against the body, lesser than one body length distance to the closest conspecific
7. Digging	
Soil removal	The ricinuleid moves soil particles using the cucullus and mouthparts

*Ilhaia cuspidata* have a catalogue composed of 32 and 20 acts respectively (Osse et al. 2008; Pereira et al. 2004). Arachnids with smaller behavioral repertoires include the

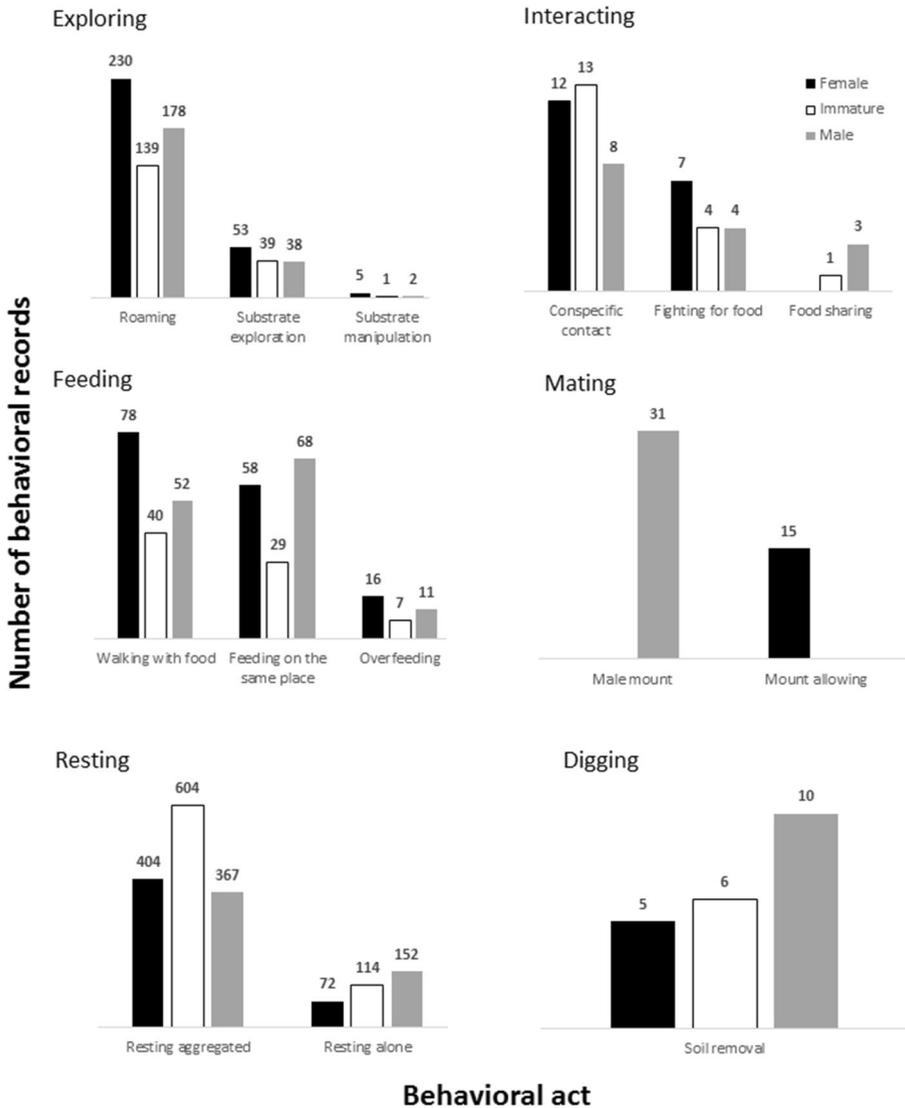


**Fig. 1** Cumulative number of behaviors of adult males ( $n=6$ ), adult females ( $n=6$ ) and immatures ( $n=6$ ) of *Cryptocellus narino* after 15 h of ad libitum sampling

schizomid *Rowlandius portiguar* (19 behavioral acts [Alves de Oliveira and Lopes Ferreira 2014]) and the scorpion *Tityus serrulatus* (17 behavioral acts [Mineo et al. 2003]). The smaller size of the behavioral repertory of *C. narino* could be explained by the fact that ricinuleids display fewer behavioral acts in some categories such as “mating” and “feeding”, in comparison to other arachnid species. Nevertheless, a



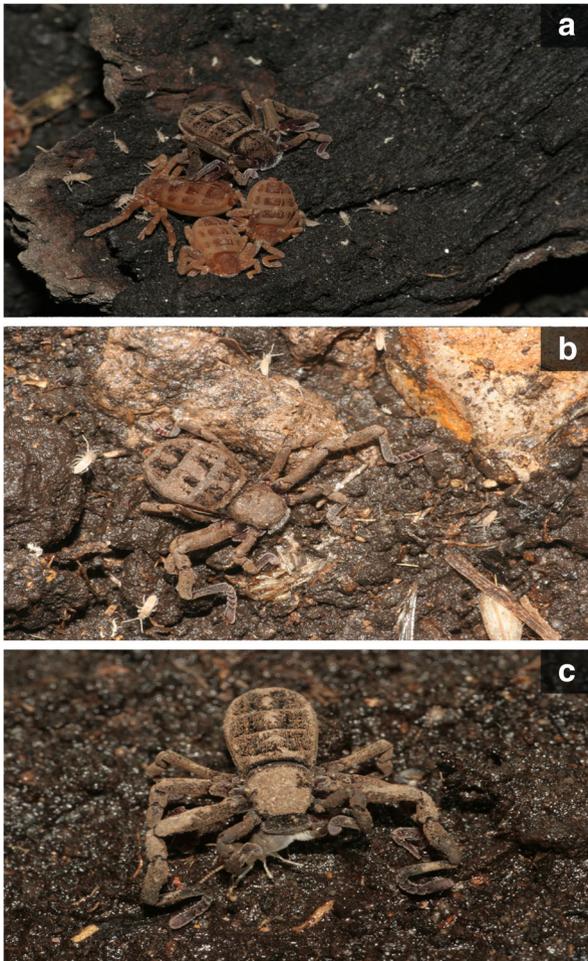
**Fig. 2** Number of records for each behavioral category of adult males ( $n=6$ ), adult females ( $n=6$ ) and immatures ( $n=6$ ) of *Cryptocellus narino*. The category “Cleaning” was not included because it presented a very low frequency. Bars which do not share the same letter are significantly different ( $p < 0.05$ ). Bars represent means; whiskers represent 95 % confidence intervals



**Fig. 3** Total number of behavioral acts discriminated for each behavioral category in the ricinuleid *Cryptocellus narino*. The category “Cleaning” was not included because it had a very low number of behavioral records ( $n=4$ ) and it was observed only in males

sampling coverage higher than 90 % indicates that most of the repertory for all the evaluated groups was completed (Lehner 1996).

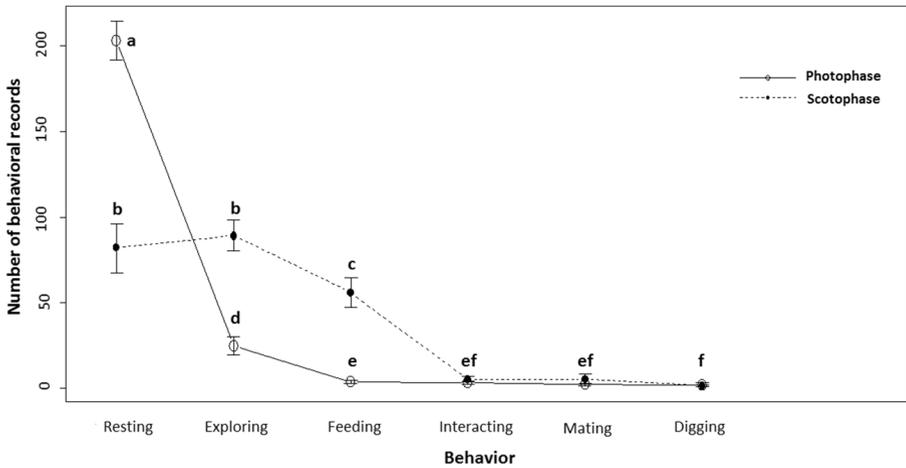
The high frequency for the category “resting”, exhibited a similar tendency with other arachnid orders such as scorpions and harvestmen (Mineo et al. 2003; Pereira et al. 2004). The emphasized frequency of this category during daylight hours and its gradual replacement by other categories (such as exploration, feeding, etc.) during the scotophase suggests that *C. narino* is nocturnal. With regard to other arachnids, our data of *C. narino* resemble previous observations about the daily activity rhythm of



**Fig. 4** Macro photographs of the most frequent behavioral acts displayed by the ricinuleid *Cryptocellus narino*. **a** Adult and immatures resting in aggregation. **b** Adult male exploring the substrate. **c** Adult male feeding on a termite. Body lengths of immatures rank between 5 and 6 mm, the length of adult males ranks between 8 and 9 mm

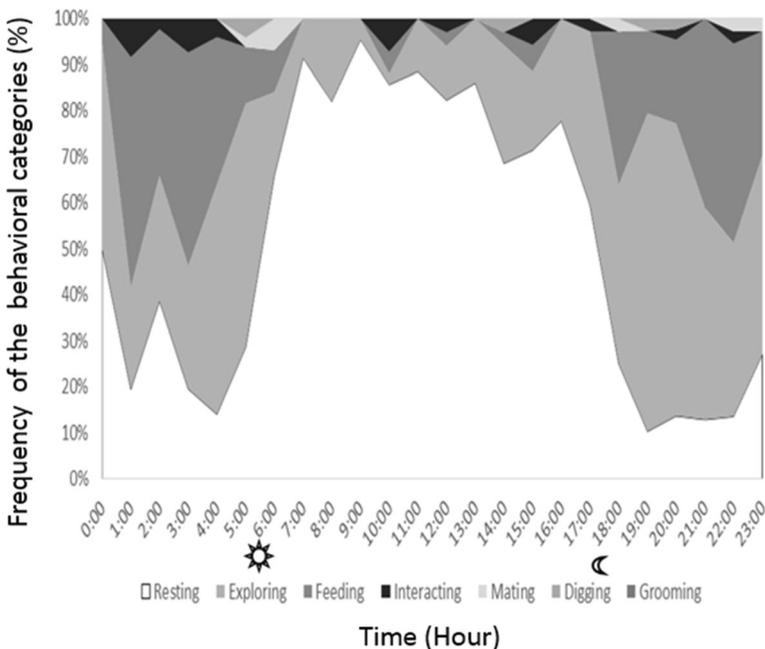
other orders such as harvestmen (Osses et al. 2008), scorpions (Mineo et al. 2003), schizomids (Alves de Oliveira and Lopes Ferreira 2014) and some spiders (Schmitt et al. 1990). Like in some of the above mentioned groups, the nocturnal activity preference could aid ricinuleids as a behavioral strategy to avoid dehydration, since they are susceptible to water loss (Pollock 1967). The higher activity peaks during darkness periods in *C. narino* indicates that light is apparently the main Zeitgeber synchronizing the activity rhythm in this species, a fact previously observed in some scorpions (Fleissner and Fleissner 2001) and harvestmen as well (Osses et al. 2008).

The exploratory behavior in *C. narino* is very similar to other species of ricinuleids, such as *Pseudocellus pearsei* (personal observation by G. Talarico) and *Ricinoides afzelli* (Pollock 1967), where the elongated second pair of legs is commonly used as a sensory device, mostly while the animal walks, confirming its importance for ricinuleid



**Fig. 5** Interaction plot between the daytime and behavioral category of adult males ( $n=6$ ), adult females ( $n=6$ ) and immatures ( $n=6$ ) of *Cryptocellus narino*. Means which do not share the same letter are significantly different ( $p < 0.05$ ). Points represent means; whiskers represent 95 % confidence intervals

orientation (see also Platnick and Pass 1982). We also found that the first pair of legs and both pedipalps are used by *C. narino* to explore the substrate, especially when the animal is not walking. These results confirm previous observations and morphological studies that showed that the first two pairs of legs, as well as the pedipalps and the chelicerae are equipped with numerous chemo-, mechano-, thermo- and hygroreceptors which act as the main sensing devices in these animals (e.g., Pittard and Mitchell 1972;



**Fig. 6** Daily activity schedule of the ricinuleid *Cryptocellus narino*. The sun- and moon-symbols indicate the starting times of photophase and scotophase respectively

Talarico et al. 2005, 2006, 2008). The continuous exploratory behavior exhibited by this species also suggests that *C. narino* are active foragers, which roam around in their environment and search for their food items. Our results on ricinuleid feeding behavior also confirmed previous observations, where the forelegs, chelicerae and pedipalps were used as the main organs employed during prey capture (Cooke 1967; Pollock 1967; Platnick and Pass 1982).

The mating behavior in *C. narino* is very similar to other ricinuleid species, where the male inserts the modified tarsomeres of a third leg into the female genital opening without any previous elaborate courtship, suggesting this might be a common pattern in the order (Legg 1977). In contrast, we described for the first time the interactions between individuals. The observed individual interactions were mainly related to food and included sharing or fighting. Individuals of *C. narino* were observed sharing food or fighting for it; nevertheless, the aggressive interactions never produced injuries or the death of the rivaling animals. Among arachnids, similar behaviors are reported in some groups that exhibit social or gregarious habits such as harvestmen, pseudoscorpions and spiders (Viera et al. 2005; Pereira et al. 2004; Osses et al. 2008). Since previous records suggest that *C. narino* is a gregarious species (García 2007), some interactions like those linked to feeding behavior might be predominant in this and other gregarious ricinuleids such as *Pseudocellus paradoxus* (Teruel and Cala 2007). Nevertheless, the incidence of these behaviors might vary under natural conditions, influenced by the density of individuals and the abundance and availability of food.

The “digging” behavior was also recorded for *C. narino*. Platnick and Pass (1982) had suggested this behavior might occur among ricinuleids, based on preliminary observations in *Pseudocellus seacus* which used its chelicerae on plasticine and tree bark. In *C. narino*, the digging behavior might allow the animals to hide within the substrate/soil in cases of adverse conditions (e.g., occasional events of flooding or exceeding aridity). Anyway, some morphological characteristics of *C. narino*, such as the navicular setae on its body surface, might support the assumption of a temporal substrate-/soil-dwelling lifestyle of this species. The ricinuleid *Cryptocellus adisi* is known to inhabit the organic and upper mineral soil layers of Central Amazonian upland forests (Adis et al. 1999). Its hydrophobic surface sculpture, including navicular setae, is thought to enable facultative plastron respiration due to a retaining thin layer of air around the body surface of temporarily submerged animals. In our experiments, the chosen substrate type as well as the constant humidity level might have caused the low occurrence of digging behavior in *C. narino*.

Although the results obtained in this study still need to be compared with other Ricinulei, the new insights provide information about previously unknown aspects of the behavioral biology of ricinuleids. This is particularly applicable to the newly described interactions between the individuals, which should be explored deeper in further studies. Intraspecific interactions (e.g., mate choice, brood care, avoidance of aggression, etc.) could be important regarding the observed aggregation of different sexes and instars within this species. Given the gregary habits of these animals and the newly observed interactions, further studies should explore if, like other arachnids, ricinuleids have developed a particular social lifestyle.

It has been shown that the occurrence and frequency of some behavioral acts may vary along the year in some harvestmen species (Osses et al. 2008), therefore the behavioral repertory of *C. narino* might also be influenced by this parameter. In spite of

this, the description of other aspects like the daily activity rhythm is particularly important for further studies as it provides a timeframe for planning additional experiments and observations to investigate behavioral patterns of these animals. Considering the limited information about the biology of this amazing and beautiful group of arthropods, we expect this study will promote new research on its biology.

**Acknowledgments** We are indebted to Hno. Antidio Bolívar and Hno. Eduardo Bartolomé for providing permits in their locality to sample the ricinuleids. Tim Meehan, Stano Pekár and Fernando Casanoves significantly improved the statistical analysis. Diana Rojas provided us great help with R programming. We also thank to Alexánder Sabogal, Carmen Viera, Glauco Machado and Patricia Torres for previous discussions and suggestions about this research. Two anonymous reviewers provided very useful comments to improve the manuscript. We want to dedicate this research to the memory of Luís O. Hernández for all his great support and contributions during this study.

**Conflict of Interest** The authors declare that they have no conflict of interest.

## References

- Adis J, Messner B, Platnick N (1999) Morphological structures and vertical distribution in the soil indicate facultative plastron respiration in *Cryptocellus adisi* (Arachnida, Ricinulei) from Central Amazonia. *Stud Neotropical Fauna Environ* 34:1–9
- Alves de Oliveira MP, Lopes Ferreira R (2014) Aspects of the behavior and activity rhythms of *Rowlandius potiguar* (Schizomida: Hubbardiidae). *PLoS One* 9, e91913
- Barreiros JAP, Pinto-da-Rocha R, Bonaldo AB (2005) Abundância de *Cryptocellus simonis* Hansen and Sorensen. *Biota Neotrop* 5:1–9
- Botero-Trujillo R (2014) A new Colombian species of *Cryptocellus* (Arachnida, Ricinulei), with notes on the taxonomy of the genus. *Zootaxa* 3814:121–132
- Caetano DS, Machado G (2013) The ecological tale of Gonyleptidae (Arachnida, Opiliones) evolution: phylogeny of a Neotropical lineage of armoured harvestmen using ecological, behavioural and chemical characters. *Cladistics* 29:589–609
- Cooke JAL (1967) Observations on the biology of two Ricinulei (Arachnida) with descriptions of two new species of *Cryptocellus*. *J Zool* 151:31–42
- Core Team R (2014) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Dias PAD, Rangel-Negril A, Coyohua-Fuentes A, Canales-Espinosa D (2009) Behavior accumulation curves: a method to study the completeness of behavioral repertoires. *Anim Behav* 77:1551–1553
- Fagen RM, Goldman RN (1977) Behavioral catalogue analysis methods. *Anim Behav* 25:261–274
- Fleissner G, Fleissner G (2001) The scorpion's clock. In: Brownell P, Polis G (eds) *Scorpion biology and research*. Oxford University Press, Oxford, pp 139–158
- García LF (2007) Primera observación del comportamiento de gregarismo en el ricinuleido *Cryptocellus narino* Platnick & Paz 1979 (Arachnida: Ricinulei: Ricinoididae). *Bol Soc Entomol Aragon* 41:458
- Hagler JR, Jackson CG (2001) Methods for marking insects: current techniques and future prospects. *Annu Rev Entomol* 46:11–43
- Legg G (1977) Sperm transfer and mating in *Ricinoides hanseni* (Ricinulei: Arachnida). *J Zool* 182:51–61
- Lehner P (1996) *Handbook of ethological methods*, 2nd edn. Cambridge University Press, Cambridge
- MacNulty DR, Mech LD, Smith DW (2007) A proposed ethogram of large-carnivore predatory behavior, exemplified by the wolf. *J Mammal* 88:595–605
- Martin PM, Bateson P (2007) *Measuring behavior: an introductory guide*, 3rd edn. Cambridge University Press, Cambridge
- Mineo MF, Franco-Assis GA, Del-Claro K (2003) Repertório comportamental do escorpião amarelo *Tityus serrulatus* Lutz and Mello 1922 (Scorpiones, Buthidae) em cativeiro. *Rev Bras Zool* 5:7–21
- Mitchell RW (1970) Population size and dispersion and species associations of a Mexican cavernicole ricinuleid (Arachnida). *Ciencia, Mexico* 27:63–74

- Muriene J, Benavides LR, Prendini L, Hormiga G, Giribet G (2013) Forest refugia in Western and Central Africa as 'museums' of Mesozoic biodiversity. *Biol Lett* 9:20120932
- Nazareth TM, Machado G (2009) Reproductive behavior of *Chavesincola inexpectabilis* (Opiliones, Gonyleptidae) with description of a new and independently evolved case of paternal care in harvestmen. *J Arachnol* 37:127–134
- Osses F, Nazareth TM, Machado G (2008) Activity pattern of the neotropical harvestman *Neosadocus maximus* (Opiliones: Gonyleptidae): sexual and temporal variations. *J Arachnol* 36:518–526
- Pereira W, Elpino-Campos A, Del-Claro K, Machado G (2004) Behavioral repertory of the neotropical harvestman *Ilhaia cuspidata* (Opiliones: Gonyleptidae). *J Arachnol* 32:22–30
- Pittard K, Mitchell RW (1972) Comparative morphology of the life stages of *Cryptocellus pelaezi* (Arachnida, Ricinulei). *Grad Stud Texas Tech Univ* 1:3–77
- Platnick NI (2002) Ricinulei. In: Adis J (ed) Amazonian arachnida and myriapoda: identification keys for all classes, orders, families, some genera, and list of known terrestrial species. Pensoft Publishers, Sofia, pp 381–386
- Platnick NI, García LF (2008) Taxonomic notes in Colombian *Cryptocellus* (Arachnida: Ricinulei). *J Arachnol* 36:145–149
- Platnick NI, Pass G (1982) On a new Guatemalan *Pseudocellus* (Arachnida, Ricinulei). *Am Mus Novit* 2733: 1–6
- Platnick NI, Paz N (1979) On the *Cryptocellus magnus* group (Arachnida, Ricinulei). *Am Mus Novit* 2677:1–9
- Pollock J (1966) Secret life of the Ricinuleid. *Animals* 8:402–405
- Pollock J (1967) Notes on the biology of Ricinulei (Arachnida). *J West Afr Sc Ass* 12:19–22
- Santos JC, Yamamoto M, Rodrigues Olivera F, Del-Claro K (2005) Behavioral repertory of the weaver ant *Camponotus (Myrmobrachys) senex* (Hymenoptera: Formicidae). *Sociobiology* 45:1–11
- Schmitt A, Schuster M, Barth FG (1990) Daily locomotor activity patterns in three species of *Cupiennius* (Araneae, Ctenidae): the males are the wandering spiders. *J Arachnol* 18:249–255
- Stamp Dawkins M (2007) Observing animal behavior. Oxford University Press, Oxford
- Talarico G, Palacios-Vargas JG, Alberti G (2005) First ultrastructural observations on the tarsal pore organ of *Pseudocellus pearsei* and *P. boneti* (Arachnida, Ricinulei). *J Arachnol* 33:604–612
- Talarico G, Palacios-Vargas JG, Fuentes Silva M, Alberti G (2006) Ultrastructure of tarsal sensilla and other integument structures of two *Pseudocellus* species (Ricinulei, Arachnida). *J Morphol* 267:441–463
- Talarico G, Palacios-Vargas JG, Alberti G (2008) The pedipalp of *Pseudocellus pearsei* (Ricinulei, Arachnida) ultrastructure of a multifunctional organ. *Arthropod Struct Dev* 37:511–521
- Talarico G, Lipke E, Alberti G (2011) Gross morphology, histology, and ultrastructure of the alimentary system of Ricinulei (Arachnida) with emphasis on functional and phylogenetic implications. *J Morphol* 272:89–117
- Teruel R, Cala F (2007) Un insólito caso de gregarismo en el ricinuleido *Pseudocellus paradoxus* (Cooke 1972) (Ricinulei: Ricinoididae). *Bol SEA* 40:496
- Tizo-Pedroso E, Del-Claro K (2011) Is there division of labor in cooperative pseudoscorpions? An analysis of the behavioral repertoire of a tropical species. *Ethology* 117:498–507
- Tourinho AL, Saturnino R (2010) On the *Cryptocellus peckorum* and *Cryptocellus adisi* groups, and description of a new species of *Cryptocellus* from Brazil (Arachnida: Ricinulei). *J Arachnol* 38:425–432
- Tourinho AL, Lo-Man-Hung NF, Salvatierra L (2014) A new Amazonian species of *Cryptocellus* (Arachnida, Ricinulei), with descriptions of its integumental structures and all free-living life stages. *Zootaxa* 3814: 81–95
- Valdez-Mondragón A, Francke OF (2011) Four new species of the genus *Pseudocellus* (Arachnida: Ricinulei: Ricinoididae) from Mexico. *J Arachnol* 39:365–377
- Viera C, Ghione S, Costa FG (2005) Regurgitation among penultimate juveniles in the subsocial spider *Anelosimus cf. studiosus* (Theridiidae): are males favored? *J Arachnol* 34:258–260
- Willemart RH, Osses F, Chelini MC, Macías-Ordóñez R, Machado G (2009) Sexually dimorphic legs in a neotropical harvestman (Arachnida, Opiliones): ornament or weapon? *Behav Process* 80:51–59
- Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer Science+Business Media, New York