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Preliminary life history observations of the pseudoscorpion *Megachernes ryugadensis* (Pseudoscorpiones: Chernetidae) phoretic on wood mice in Japan

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Abstract. Pseudoscorpions are predators of arthropods and primarily inhabit soil litter and tree bark in forests, although some species have been collected from animal nests, suggesting close associations with mammals and birds. We made preliminary observations on the life cycle and life history traits of *Megachernes ryugadensis* Morikawa, 1954, phoretic on the wood mice *Apodemus speciosus* and *A. argenteus*, by sampling wild specimens in the field and rearing these specimens in a laboratory. The main phoretic host at the study site was *A. speciosus*; we observed an average of 1–1.7 pseudoscorpions on 5–36% of mice within the 2-year study period. The observed phoretic stages of *M. ryugadensis* were adults and tritonymphs; the phoretic ratio on *A. speciosus* was relatively stable for 2 years. The duration of full development from egg to adult in *M. ryugadensis* was unclear, probably due to unsuitable rearing conditions; however, individuals survived as adults for over one year. Typical maternal care was confirmed in pseudoscorpions and egg hatching was synchronized to within ca. 8 h. Further study, including close examination of mouse nests, is required to elucidate the symbiotic relationship between the pseudoscorpion and host rodents.

Keywords: Life cycle, phoresy, symbiosis

Arthropods are relatively small organisms that contribute significantly to the sustainability of ecosystems by their abundance, omnipresence, and broad ecosystem functionality (Southwood et al. 1982; Altieri 1999; Siemann et al. 1999). Some ecosystem functions and services, such as pest control in agriculture and forestry, have been quantitatively assessed for commercialized biological control agents, while other elements of their ecology, such as predation in a natural ecosystem have been much less quantified (Wilby & Thomas 2008; Letourneau et al. 2009). To fully comprehend these natural ecosystems within the context of the food web, it is necessary to accumulate more data, specifically life history traits of predacious and parasitic organisms.

Pseudoscorpions are a group of predacious arthropods belonging to the class Arachnida and order Pseudoscorpiones (Harvey 2013). Although more than 3,000 species have been described worldwide, from every continent except Antarctica, our understanding of the biology and ecology of these organisms is still fragmented (Murienne et al. 2008; Harvey et al. 2012; Harms & Dunlop 2017). Many live in soil litter or under the bark of trees in forests, but some have also been collected from animal nests, suggesting a close association with mammals and birds, though evidence is scant (Levi 1953; Weygoldt 1969; Zeh & Zeh 1992; Francke & Villegas-Guzmán 2006; Tizo-Pedroso & Del-Claro 2007). Significant natural predation of many small arthropods by pseudoscorpions is expected in phoretic host habitats (Okabe et al. 2018), though life history traits of most predacious species, including impacts on prey and host populations, are largely unknown.

Megachernes ryugadensis Morikawa, 1954, first collected from bat guano in a cave in Kochi, Japan, is one of the largest pseudoscorpions in Japan (Morikawa 1954). Thus far, it has been divided into the following three subspecies based on differences in pedipalpal morphologies and habitats (Morikawa 1960): *M. r. ryugadensis*, *M. r. naikaiensis* Morikawa, 1957, and *M. r. myophilus* Morikawa, 1960. The subspecies *M. r. ryugadensis* was originally described as *M. ryugadensis* from the specimen collected in bat guano in a cave in Kochi Prefecture, *M. r. naikaiensis* was recorded in caves in western Japan, and the subspecies *M. r. myophilus* was collected from small mammals, *Rattus norvegicus* (Berkenhout, 1769) (Muridae) and *Mogera wogura* (Temminck, 1842) (Talpidae), and from nests of bumblebees. Although researchers of wild rodents have noticed phoresy and the use of other animals as a means of transportation by *M. ryugadensis* (Shimada, unpublished data), details of life history traits are unclear for any subspecies.

During ecological studies of small mammals, mainly on wood mice *Apodemus speciosus* (Temminck, 1844) and *A. argenteus* (Temminck, 1844), in a forest in northern Japan, we noticed that many mice carried *M. ryugadensis* in their pelage. In this paper, we describe the phoretic ratio, or proportion of animals carrying pseudoscorpions, in the study forest. We also explore the seasonal changes in phoretic ratios for the main host over two years. Our research also documents the life cycle of *M. ryugadensis*, along with bionomic notes including feeding behavior and maternal care based on laboratory rearing experiments.

METHODS

Field sampling.—We censused small mammals, primarily targeting wood mice *A. speciosus* and *A. argenteus*, using Sherman-type live traps in the Takizawa Research Forest of Iwate University, Morioka, Iwate, Japan (39°47′N, 141°09′E, approximately 200 m a.s.l.) during alternate weeks between April and November in 2016 and 2017. The study site was a secondary deciduous forest in which *Quercus serrata* Murray, 1784 (Fagaceae) was the dominant tree species. For each census, 106 traps were set on the ground for three consecutive

Table 1.—Host preference and brooding status of *Megachernes ryugadenis* phoretic on mammals.

Mammal species	Total number of animals trapped*	Number of phoretic hosts	Animals with pseudoscorpions (%)	Brooding pseudoscorpions (%)
Apodemus speciosus	1982	373	18.8	74
A. argentius	188	7	3.7	0
Eothenomys andersoni	4	0	0	0
Urotrichus talpoides	15	1	6.7	0
Crocidura dsinezumi	2	0	0	0

* Including animals recaptured.

nights over the fixed study site (0.54 ha) and checked for the capture of small mammals. Captured animals were identified individually by toe-clipping. For 2016 censuses, when phoretic pseudoscorpions were found grasping hairs of host mammals with chela on the first two days of sampling, we recorded the host mammal's identification and the number of pseudoscorpions on each host. On the third and final day of sampling, we gently removed the pseudoscorpions from the hosts with forceps, placed them in small plastic bags, and brought them back to the laboratory. For the 2017 censuses, when phoretic pseudoscorpions were found, we recorded the host mammal's identification and the number of pseudoscorpions on each host, then removed them from hosts daily. We attempted to collect all phoretic pseudoscorpions, but sometimes failed due to escaping mice. Therefore, the number of pseudoscorpions found to be phoretic in the field differed from the number of those collected and brought back to the laboratory. The phoretic ratio, estimated only for *A. speciosus*, was defined as the number of individual mice found with attached pseudoscorpions at least once within each census relative to the number of individual mice captured in each census.

The censuses of mammals were conducted in compliance with a protocol reviewed by the Institutional Animal Care and Use Committee and approved by the Director General of the Forestry and Forest Products Research Institute (Permit Number: Animal Experiment H29 17A-8).

Identification of the pseudoscorpions.—The pseudoscorpions collected were identified as *Megachernes ryugadensis* based on adult characteristics using the key by Morikawa (1960). The length-to-width ratio of the palpal femur (female: 2.10–2.52; male:1.89–2.13; $n = 10$ each) of our samples was closer to the range of the subspecies *myophilus* in the key (2.1–2.6; sex not shown) than to the other two subspecies (3.1–3.2 in ssp. *ryugadensis*, 2.5–2.9 in ssp. *naikaiensis*). Only *M. r. myophilus* was recorded from the body of small mammals among the three subspecies descriptions noted above. However, the adult body colors of our samples, which varied from reddish or pale brown to dark brown as revealed by rearing, did not completely agree with the description of the subspecies *Megachernes r. myophilus* in the Morikawa (1960) key ("darkish brown species"). As the subspecies identification is unclear, we use *M. ryugadensis* to refer to our collective samples without referring to any particular subspecies.

Laboratory rearing.—The pseudoscorpions collected were identified by developmental stage before being reared in a laboratory in both 2016 and 2017. Additionally, in 2017, all adults were sexed based on the morphology of the genital area and size of the palpal tibia, which is shorter and wider in males (Sato 1999). All measurements were made under a stereomicroscope (Leica, S8APO). The pseudoscorpions were individually maintained in enclosed plastic containers 5 cm in diameter and 3.5 cm in height, with six small ventilation holes in the lid. The bottom of the containers contained wet coniferous chips to a depth of ca. 1 cm. Although humidity was not precisely controlled for each container, chips were kept damp with a small amount of moistened peat moss on top. Chips were replaced when degradation of any kind, e.g., molds, occurred. The sample containers were maintained in an incubation room at a temperature of 25°C (±1°C), relative humidity of 60% (±10%), and photoperiod of 16L:8D, although the containers were consistently covered with black cloths to avoid direct light. We maintained all protonymphs from the same adult female together in the same container, but when a silken chamber was made for molting, we transferred each individual into a small plastic Petri dish (diameter: 3.7 cm, height: 1.1 cm) with a small amount of moistened peat moss to maintain moisture levels. When a deutonymph emerged, we transferred it to another plastic container maintained under the same conditions described above for adults. We also released two to six adults in the same containers to observe interactions between them, but these specimens were not used to estimate species longevity.

We fed the pseudoscorpions with *Sancassania* spp. mites (Astigmata: Acaridae). Juvenile mites were fed to protonymphs every 1–3 days, and adult mites were fed to other developmental stages every 5–10 days. We also provided mites of *Sandrophela* spp. (Astigmata: Canestrinidae) to protonymphal pseudoscorpions to observe food preference and record feeding behavior. For the predation behavior of the pseudoscorpions on ticks (*Haemaphysalis* spp.), which are their preferred prey (Okabe et al. 2018), the behavior of the pseudoscorpions was observed and recorded *ad libitum* under a stereomicroscope equipped with a photosystem (Leica, MC170HD).

RESULTS

Phoresy on small mammals.—In 2016, 304 *M. ryugadensis* were detected from 205 *A. speciosus* and two *A. argenteus*. In 2017, 298 *M. ryugadensis* were detected from 168 *A. speciosus*, five *A. argenteus,* and one *Urotrichus talpoides* Temminck, 1984 (Talpidae) (Table 1). The main phoretic host was thus *A. speciosus*.

Phoretic pseudoscorpions grasped hosts' hairs with their chelae, primarily situating themselves on the posterior half of the host's body. Indeed, attachment on the anterior half of the body, head, or limbs of the hosts occurred very rarely. The maximum number of pseudoscorpions recorded on a single

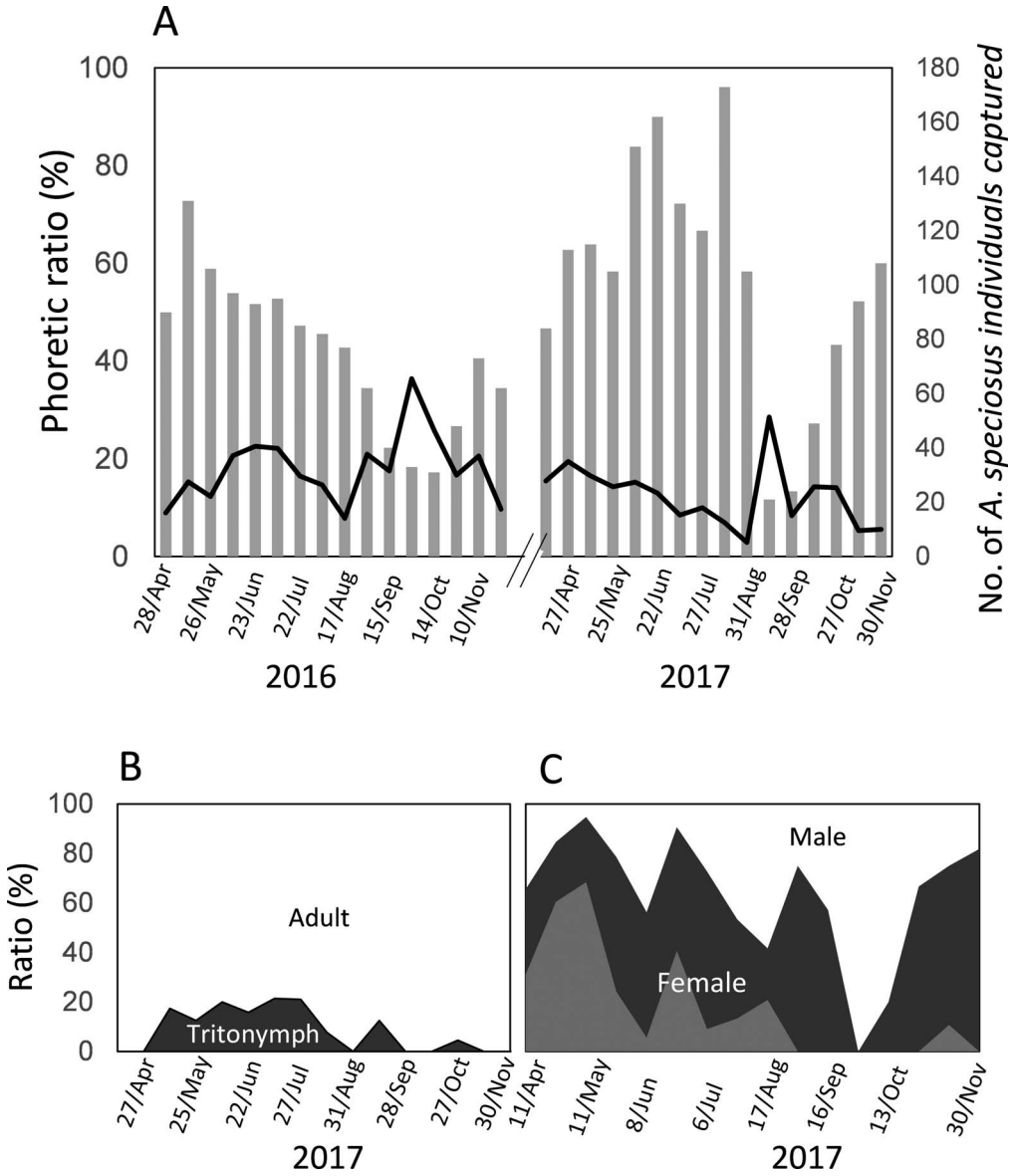

Figure 1.—*Megachernes ryugadensis* phoretic on *Apodemus speciosus* in a broad-leaved deciduous forest in Iwate, Japan. Phoretic stages and sexes were not checked in 2016 to avoid impacts on the wild *M. ryugadensis* population in the following year. A. Solid lines indicate the phoretic ratio (the number of *A. speciosus* individuals carrying *M. ryugadensis* / the total number of *A. speciosus* individuals captured), and bars indicate the total number of *Apodemus speciosus* captured. B. The ratio of tritonymph to adult *M. ryugadensis*. C. The male-to-female ratio of *M. ryugadensis*. The gray area within the black area indicates the proportion of females with a brood sac.

host was 12 over the 2-year sample period, with an annual average per host of 1.5±1.1 ($n = 207$) and 1.7±1.5 ($n = 174$) in 2016 and 2017, respectively. The phoretic ratio, or proportion of hosts (*A. speciosus*) with attached pseudoscorpions, fluctuated between 5.3 and 36.4% and peaked in late September (Fig. 1A). Although both adults and protonymphs were found to be phoretic, adults were dominant throughout the 2017 study period (Fig. 1B). Most of the adults sampled were females (Fig. 1C), some of which possessed a brood sac on the ventral surface of the abdomen. The percentage of females with a brood sac fluctuated but seemed to be synchronized with the male-to-female ratio in early 2017 (Fig. 1A, C). Although most mother pseudoscorpions had a large brood sac recognizable from the dorsal surface, some had much smaller ones that were recognized only from the venter. One female had newly hatched protonymphs attached to her body when she was collected from a mouse.

Life cycle.—Collections of the pseudoscorpions occurred between April and November. In 2016, 106 adults and 12 tritonymphs were collected, and in 2017, 254 adults and 23 tritonymphs were collected. These specimens were then reared in the laboratory. The brood sacs carried by a female contained 22.8 ± 1.2 ($n = 13$) embryos. Although the time from the formation of the brood sac to hatching was not clear, under laboratory conditions, very small brood sacs barely visible at the genital area between the coxae of the fourth pair of legs resulted in eggs hatching within 29 days ($n = 76$). We videotaped the hatching of protonymphs from the brood sac

and found that all protonymphs hatched within ca. 8 hr (Supplementary Material S1, online at http://dx.doi.org/10.1636/JoA-S-19-079.s1). Protonymph hatching was assumed to occur primarily at night; 13 brood sacs that were still unhatched on the previous evening had produced protonymphs by the next morning, although the exact period was not recorded, except in a single case, when the hatching period was from 18:30 to about 2:00 (the recorded period was 18:43–6:16). Newly hatched protonymphs stayed on the mother in the brooding nest for approximately one day and left the nest when their outer skins became reddish (Fig 2).

The protonymphal period, from hatching to the emergence of the deutonymph out of the protonymphal molting chamber, was 61.7 ± 11.8 d (33–73 d, $n = 16$). Protonymphs spun a silken chamber (molting nest) with silken threads, sometimes including several small wood chips, and remained inside to molt for approximately a week. The survival ratio of protonymphs during the protonymphal period under the laboratory rearing conditions was ~10%, based on 16 protonymphs produced from six different females. All deutonymphs died before becoming tritonymphs in the laboratory. The longest survival period of a deutonymph was 147 d. The cause of death was unclear.

When they survived, phoretic tritonymphs collected from the mice molted to adults within 98 days. The sole exception was one tritonymph that survived without molting for more than a year after sampling. The accurate duration of the tritonymphal period was undeterminable because we were unable to obtain newly molted tritonymphs. The survival periods of newly molted adults were 7, 77, and 245 d, including both sexes. The median survival period in phoretic adults was 82 d (18–404 d; $n = 135$), including both sexes. Specimens that died within a week of collection were excluded.

The body color of adults potentially changes during their lifetime. New adults were lighter in color compared to those found phoretic on hosts. In newly molted adults, the pedipalps and scutum were brighter reddish-brown, and the dorsal opisthosoma was pale brown, whereas in phoretic adults these were dark brown and brown, respectively (Fig 2). On November 18, 2018, we found mature embryos in a brood sac on a female that had been isolated under laboratory conditions after collection in the field on May 16, 2017. The eggs hatched, though all juveniles died before the tritonymphal stage.

Mating behavior was not observed. Although we maintained a female and a male together in the container for a month in spring and fall, no evidence of sperm transfer was observed. Other behavioral observations included a male preying on another male under the mass rearing, and a different male preying on a female during the transportation from the field to the laboratory.

Feeding behavior.—The protonymphal instar *M. ryugadensis* was an aggressive hunter. When *Sandrophela* mites that were smaller than the protonymphal pseudoscorpion in body size were released in a rearing container, several protonymphs immediately approached and seized the prey with a chela. Other stages of pseudoscorpions have tended to ambush prey (Okabe et al. 2018). A protonymph attempted to prey on an adult *Sancassania* mite that was larger than itself (ca. 700 μm

Figure 2.—Color differences in *Megachernes ryugadensis*. A. A young female within a week of emergence. Appendages are reddish and the rest of the body is pale. B. Likely mature male collected in the field. The entire body surface is darker compared to that of the young adult.

in idiosoma and oval shape), but the protonymph was unsuccessful.

Adult pseudoscorpions fed on mites similarly to protonymphs. They first caught a mite by extending a pedipalp and grasping it with a chela, after which, they always pulled the other pedipalp to the mouthpart and passed a finger through what appeared to be space between a chelicera and galea from the top of the finger to the bottom before eating; this appeared to be a chela cleaning procedure. Both while consuming prey and after a meal, the adults repeated the same behavior. Adult pseudoscorpions were never seen chasing prey, as similarly reported for protonymph feeding behavior in *Maxchernes iporangae* Mahnert & Andrade, 1998 (Andrade & Gnaspini 2002). Adult feeding behavior on ticks is described in detail in Okabe et al. (2018).

Maternal behavior.—A mother pseudoscorpion with a brood sac kept hatched protonymphs attached on her body for about the first 24 hr. The mother did not seem to consume food while hatching the protonymphs. Adult pseudoscorpions did not always hide under material in a container after a disturbance such as opening a lid or adding food. However, a mother pseudoscorpion with a brood sac tended to hide during similar disturbances. Particularly at later embryonic stages, she stayed in a nest-like web made of fine silken threads and interwoven with a few chips as if it were a tent. The structure was never stable and appeared to be a temporary shelter. Once it was disturbed, she abandoned it and never returned. Without disturbances, the mother pseudoscorpion left the nest soon after all protonymphs left.

The means by which mothers supplied nutrition to embryos was unclear, but very late-stage embryos in a brood sac (within 24 hr before egg hatch) were able to survive and hatch when separated from the mother (see Supplemental Material S1). Particularly during transportation between the field and laboratory, some mother pseudoscorpions dropped their brood sacs. In a few cases, we observed them immediately feed on the dropped brood sac.

When we maintained both a mother and hatched protonymphs together in the same container for weeks, no protonymphs developed into deutonymphs. We occasionally saw the mother feeding on protonymphs that had left her approximately a day prior.

DISCUSSION

The phoretic ratio of *M. ryugadensis* in the deciduous broad-leaved forest in Iwate appeared to be synchronized with either the reproductive season of *A. speciosus* (and maybe *A. argenteus*) or the numbers of trapped wood mice (Fig. 1). The reproductive season for both wood mouse species in this region peaks in spring (April to May) and fall (October to November), and consequently, the population density increased after these periods (Shimada, unpublished data). There are two possible scenarios: either the pseudoscorpion rides on the host constantly and the ratio was nearly zero due to low host numbers trapped, or the pseudoscorpion tends to be phoretic more often in spring and fall. If the latter is true, it may be because the pseudoscorpion intends to translocate to a host breeding nest that would likely be used for a few weeks until the mice brood left. As the ratio of *M. ryugadensis* with a brood sac was also similar to the trend of the phoretic ratio (Fig. 1), we argue that the latter is likely the case.

As observed in other *Megachernes* species associated with small mammals, the primary purpose of *M. ryugadensis* phoresis on small mammals in forests is dispersal (Harvey et al. 2012; Finlayson et al. 2015). In *Cordylochernes scorpioides* (Linnaeus, 1758), which is phoretic on the harlequin beetle *Acrocinus longimanus* (Linnaeus, 1758) (Cerambycidae), the male pseudoscorpion also exploits the occasion for interception and insemination of dispersing females (Zeh & Zeh 1992). Because the majority of phoretic females of *M. ryugadensis* observed already had brood sacs, except during late September, phoresy may bring pseudoscorpions to a new habitat and was not primarily for breeding. As found in *C. scorpioides* on *A. longimanus* (Zeh & Zeh 1992), *M. ryugadensis* may be able to find prey on a host (parasitic mites, for example), but it cannot feed on them while clinging to the host with pedipalps, as they are needed to capture prey. However, to test our hypothesis of phoresy, it was necessary to identify direct or indirect cues of embarkment or disembarkment from the host mouse. When we swung a paintbrush or a small part ($\sim 1 \times 1$ cm) of dead *A. speciosus* skin with fur in front of an adult *M. ryugadensis* during preliminary observations of their phoretic behaviors, it extended its pedipalps and pinched the brush or fur with its chelae. These observations suggest that pseudoscorpions respond to animals without host specificity. Generally, species specificity between rodents and pseudoscorpions is relatively low; typically, 5–10 spp. of pseudoscorpions are found associated with a rat species (Francke & Villegas-Guzmán 2006). Thus, the phoresy of *M. ryugadensis* on *A. speciosus* was common due to high population density of the wood mouse in this forest but may differ elsewhere.

The lifecycle and life history traits of most pseudoscorpions are poorly known, but the general lifecycle of this group of organisms has been summarized as follows: embryos are nursed in a mother's brood sac attached to her body surface; the protonymph, deutonymph, and tritonymph are active immature stages that mature as female and male adults (Weygoldt 1969). *Megachernes ryugadensis* followed this general lifecycle. The entirety of their lifecycle was not much longer than those of other species; they lived as adults for 2–4 years, similar to adults of *Pselaphochernes scorpioides* (Hermann, 1804) (Chernetidae) and *Chelifer cancroides* (Linnaeus, 1758) (Cheliferidae), or for a total lifetime of 4 years, similar to *Paratemnoides nidificator* (Balzan, 1888) (Atemnidae) (Levi 1953; Weygoldt 1969; Del-Claro & Tizo-Pedroso 2009). Our observations suggest that most protonymphs did not survive until the deutonymph stage when we reared them together due to cannibalism between sibling protonymphs or by their mother, as sometimes seen in other species such as *C. cancroides* (Levi 1948). The lack of molting in deutonymphs and tritonymphs was likely due to insufficient nutrition, as some of them lived long and died without a distinct cause. It may be that adults did not show mating behavior for the same reason.

For the first time in the Pseudoscorpiones, we found that eggs in the same brood sac hatched within a short period, over at most 8 hr. This may be to avoid cannibalism, often proposed as the function of synchronization of egg hatching in other organisms (Hahn 1981; Hopper et al. 1996; Kudo &

Nakahira 2004). The period during which protonymphs attached to their mother after hatching was also shorter than that of *Ephippiochthonius tetrachelatus* (Preyssler, 1790) (Chthoniidae), which takes 3–4 days to absorb the nutritive fluid remaining in the brood sac between hatching to leaving the brood pouch (Weygoldt 1969). We were not able to confirm that nutrition is provided by a mechanism that pumps food from the mother to the embryo, but such a supply mechanism is possible in *M. ryugadensis*, as very young embryos in a brood sac that were accidentally separated from a mother did not survive.

Morikawa (1954, 1957, 1960) described three subspecies of *M. ryugadensis* based on different combinations of habitats (a cave or others), body color (pale or dark brown), and ratio of length to width of the pedipalpal femur. However, our preliminary observations of *M. ryugadensis* showed that the body colors alone were not stable enough to differentiate subspecies. We found that newly emerged adults had paler colors on their appendages and dorsal surface compared to many adults found phoretic on the hosts in the field. We presume that the variations in color were due to age or environmental differences such as light intensity in habitats.

Although it has long been known that most species of the genus *Megachernes* are characteristically associated with mammals, especially rodents (see Harvey et al. 2012), their records are usually episodic and fragmented, leaving many aspects of their biology in the field unknown, including seasonal changes in the phoretic ratio on hosts. Our study is the first to show, based on regular trapping of their hosts, wild mice, that the phoretic ratio of *M. ryugadensis* changes. Further studies, particularly focusing on symbiosis with other nidicolous animals, are necessary to understand a sustainable forest ecosystem potentially mediated by species interactions between wood mice and associated pseudoscorpions.

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SUPPLEMENTARY MATERIALS

Video S1.—Synchronized egg hatching of *Megachernes ryugadensis* (mp4); online at http://dx.doi.org/10.1636/JoA-S-19-079.s1

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