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Daily Activities of the Giant Pill-Millipede *Zephronia* cf. *viridescens* Attems, 1936 (Diplopoda: Sphaerotheriida: Zephroniidae) in a Deciduous Forest in Northern Thailand

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Nattarin Wongthamwanich, Somsak Panha, Duangkhae Sitthicharoenchai, Art-ong Pradatsundarasar, Tosak Seelanan, Henrik Enghoff, and Kumthorn Thirakhupt (2012) Daily activities of the giant pill-millipede *Zephronia* cf. *viridescens* Attems, 1936 (Diplopoda: Sphaerotheriida: Zephroniidae) in a deciduous forest in northern Thailand. *Zoological Studies* **51**(7): 913-926. For the 1st time in the order Sphaerotheriida, daily activities of the giant pill-millipede *Zephronia* cf. *viridescens* Attems, 1936 (family Zephroniidae) were studied. In 2009 and 2010, an investigation was conducted during the rainy season (May-Sept.), the period when millipedes are most active, in a deciduous forest at Wiang Sa District, Nan Province, Thailand. From a total of 20 observation periods of 1 d each, 16 males and 23 females were marked with acrylic paint on the anal shield, and each was optically observed in its natural habitat every 30 min for 24 h. Key visually discernible activities of each individual, such as feeding, walking, mating, and resting, were recorded. The majority of millipedes fed throughout the day under the leaf litter. Walking activity was significantly higher in males than females throughout the day. Compared to males, females rested more during the night and fed more during the day. Average daily distances moved were significantly higher in males than females. It was concluded that females tend to accumulate energy throughout the day, probably for reproduction, while males tend to spend more time walking, probably for the purpose of finding mates. http://zoolstud.sinica.edu.tw/Journals/51.7/913.pdf

Key words: Giant pill-millipede, Daily movement, Behavior, Reproduction, Survival.

The number of described millipede species that has been reported varies from 7753 (Shear 2011) to 12,000 with an estimated 80,000 extant species in the world (Hoffman 1979, Sierwald and Bond 2007), including approximately 325 described species of giant pill-millipedes (in the order Sphaerotheriida) (Wesener et al. 2010). Giant pill-millipedes occur in discontinuous geographical areas (Jeekel 1974, Hoffman 1982, Shelley 1999, Wesener and VandenSpiegel 2009), and are separated into 4 families: the Sphaerotheriidae in South Africa, the Procyliosomatidae in Australia and New Zealand, the Arthrosphaeridae in southern India and Madagascar, and the Zephroniidae in southern China, Southeast Asia, and the Sunda Islands (Wesener and VandenSpiegel 2009).

Activity patterns in most animals, including feeding and reproduction, are influenced by environmental factors, such as temperature changes, rainfall, day length, and food availability. For example, the peak activity of the cylindrical millipede *Ommatoiulus moreletii* (in the order

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Julida) in South Australia occurs during autumn to early winter when adults actively search for food, mates, and oviposition sites (Baker 1979). Activities of cylindrical millipedes (in the superorder Juliformia) in Zimbabwe were found to rapidly increase after emergence from the soil at the beginning of the rainy season and then to decline a couple of weeks later (Dangerfield and Telford 1991). In southern India, the abundance and biomass of the giant pill-millipede *Arthrosphaera magna* were positively correlated with rainfall during the monsoon season (Ashwini and Sridhar 2006).

Knowledge of the daily activities of any organism is important in order to be able to evaluate their home-range sizes and daily distances travelled by individuals in any location, and from this to be able to design appropriate sampling procedures to evaluate their population dynamics and population genetics, and develop an understanding of their ecology, such as habitat use, energy requirements and allocation, and intra- and interspecific behaviors. Such information is essential for any realistic habitat management and conservation strategy. However, this basic information is lacking for giant pill-millipedes, many of which have very limited distributions and are critically threatened (Wesener 2009).

Previous studies did not directly monitor activities of millipedes throughout the day in their habitats, but rather were either conducted in the laboratory or in the field and used indirect observation methods, such as pitfall traps or quadrat sampling (Cloudsley-Thompson 1951, Banerjee 1967, Bano and Krishnamoorthy 1979, Boccardo and Penteado 1995, Koilraj et al. 1999 2000, Tuf et al. 2006, Kadamannaya and Sridhar 2009). To date, observations of the ecology of millipedes in the family Zephroniidae have not been reported, although it is the largest family of giant pill-millipedes. The present study focused on daily activities, daily movements, and some other aspects of behavior of a zephroniid millipede species in a deciduous forest in northern Thailand, which is a part of the Indo-Burmese biodiversity hotspot (Myers et al. 2000).

Observations were made in the rainy season as this is the period of activity for millipedes, which require relatively high humidity levels in addition to suitable vegetation matter for food. Accordingly, the temperature and relative humidity (RH) were measured throughout the observation periods to correlate with the observed activities, since it is expected that these factors would influence their activities (Perttunen 1953, Banerjee 1967, Tuf et al. 2006). In addition, across diverse animal species, a sex-biased polymorphism in behavior is often observed. For example, females are often more sessile to allow provision of more resources to eggs and reduce predation risks, while males show higher energy allocation to movement for mate seeking and territory defense (Andelt and Gipson 1979, Thompson et al. 1999). The basic biology of millipedes does not exclude this possibility (Rowe 2010), and so this study evaluated the daily activities of males and females separately to test for any such gender-specific behavioral traits and the effects of climatic conditions upon these activities, since if 1 gender is more active it may be influenced more by temperature and humidity effects.

MATERIALS AND METHODS

Identity of the studied species

Giant pill-millipedes of Thailand are very poorly known. Although several species obviously exist, only 1 species of the genus *Zephronia* has previously been recorded, viz., *Zephronia siamensis* Hirst, 1907, from Si Chang I. in the Gulf of Thailand, Chonburi Province and in Chantaburi Province (Enghoff 2005). According to the original description (Hirst 1907) and after comparison with newly collected topotypical material of *Z. siamensis*, we concluded that the species studied here is not that species. Instead, it is very similar to *Z. viridescens* Attems, 1936, described from a specimen from Dawei, southeastern Myanmar (Attems 1936, Jeekel 2001). However, because of some differences, we refer to the studied species as *Zephronia* cf. *viridescens*. Voucher specimens were preserved in 70% (v/v) ethanol and are stored at Chulalongkorn Univ. Museum of Zoology, Bangkok, Thailand (CUMZ 2010.20-9) and at the Field Museum of Natural History, Chicago, Illinois, USA (FMNH-INS 072671, 072672, 072675, and 072676) for future identification.

Study area

Daily activities of *Z.* cf. *viridescens* were investigated during the rainy season in July-Sept. 2009 and May-Sept. 2010 at the Chulalongkorn Univ. Forestry and Research Station (18°34'5"N, 100°47'43"E). The area covers 300 ha and is located in the Nam Wa sub-watershed, Lai-Nan

Sub-district, Wiang Sa District, Nan Province, Thailand. The elevation ranges 200-260 m. This area is covered by secondary deciduous dipterocarp forest and mixed deciduous forest dominated by *Dipterocarpus obtusifolius*, *D. tuberculatus*, *Shorea obtusa*, *S. siamensis*, *Pterocarpus macrocarpus* (Dumrongrojwatthana et al. 2009), and bamboo (*Gigantochloa albociliata*). The forest floor is covered by saplings and seedlings, including leaf litter of up to 3 cm deep throughout the year.

Laboratory-based millipede marker evaluation

Giant pill-millipedes were collected and were marked on the anal shield in the laboratory by one of several waterproof markers, including nail varnish (paint), liquid paper, a permanent marker pen, and pink acrylic paint. After application, millipedes were returned to their tank and observed for any adverse reaction for 5-10 min. They were then maintained for up to a week with daily checking of the applied marker for its visibility, followed by the ability to remove the marker. From this preliminary experiment, the marker for use in the field studies (24-h application) was selected based on having less-visible adverse effects on application, ease of visibility over time, and the ability to remove it afterwards. Note that although marked millipedes were kept in standard tanks with soil and leaf strata, they were kept alone during this post-marking observation period and so potential interactions with other millipedes were not evaluated.

From the preliminary study in the laboratory to select a suitable waterproof marker for field observations, the application of nail paint and liquid paper was found to adversely affect the millipedes in that they rolled and un-rolled several times within a few minutes. In contrast, application of the permanent marker pen or acrylic paint caused no such observed changes in their behavior. Since the acrylic paint could be easily removed from the millipedes after investigation, in contrast to the permanent marker pen, and the pink color was easily visible in the habitat, making the detection of the marked millipede easier, especially at night, it was selected for use over the permanent marker pen.

Observation of activities

In total, 16 males and 23 females of *Z.* cf. *viridescens* were observed over a 24-h period. Each collected millipede was sexed and weighed, and its length, width, and height were measured while it was rolled up into a ball shape (Wongthamwanich et al. 2012). Then it was individually marked with a different symbol using pink acrylic paint (PMK-B; Sakura Color Products, Osaka, Japan) on the anal shield and released back into its original habitat. After marking and releasing, its actions were observed and recorded every 30 min during the 24-h observation period. Whether the millipede was feeding, walking, mating, or resting was recorded, and any other types of observed behavior, including interactions with other millipedes, were recorded. The position of the millipede at each 30-min sampling time was marked by a small flag. A small stick was used to open the leaf litter during each observation when the millipede was under the cover so as to locate the position of the millipede without unduly disturbing it. A flashlight covered with red cellophane was used for nighttime observations in order to minimize disturbance. The number of changed positions observed at each 30-min recording time over a single 24-h period was counted to evaluate the frequency of movement. At the end of the 24-h observation period, the acrylic paint was removed by scraping it off with the observer’s fingernail, and then the millipede was released. The total minimum distance moved each day was evaluated from the total distance between each of the mapped positions of the millipede's location every 30 min, assuming a direct route between points. The daily displacement was determined as the direct distance on the ground between the start and finish positions.

In any given 24-h observation period, only 1 millipede was typically observed, but in some cases where 2 or 3 millipedes were located close to each other, they were marked and observed in the same 24-h period. Thus, up to 3 individual *Z.* cf. *viridescens* millipedes were followed during any given 24-h period (Table 1). Observations of the activity of any unmarked *Z.* cf. *viridescens* encountered during these observation periods were recorded but were not analyzed here.

The relative humidity, air temperature at 130 cm above the ground in the shade, and soil temperature at a 5-cm depth were respectively recorded using a wet-dry hygrometer, a mercury thermometer, and Chaney soil thermometer. The 24-h observation period was subdivided, based on these physical factors (Fig. 1). The proportions of time feeding, walking, and resting were plotted against time. Differences between activities of males and females were compared in relation to daytime versus nighttime periods and to physical factors, using a Chi-squared test. Differences in daily movements between males and females were compared using the Mann-Whitney *U*-test.

RESULTS

Daily activities

Total numbers of *Zephronia* cf. *viridescens* millipedes observed in each time period are summarized in table 1. Although locating millipedes when they were undercover required the use of a stick to carefully lift the leaf litter, no evidence of disturbance (such as coiling up or changing their current activity) was observed, and in all 24-h observation periods, there was never a 30-min period when the respective millipede under observation was not located. The 3 key daily activities of these 39 specimens (16 males and 23 females) are shown as the percentage of individuals in figures 2 and 3. Physical factors in the rainy season such as soil temperature and RH fluctuated only slightly (Fig. 1). Overall, over the 24-h observation period, the millipedes spent an average of 57.4% of their time feeding, followed by resting, with walking the lowest of the 3 activities at 12.1% (Fig. 2). Mating activity was not found in any of the 39 marked millipedes during the survey period, even though it was observed in a few unmarked individuals in the study area. Indeed, the almost balanced opposite behavior patterns between males and females with respect to their diurnal and nocturnal activities is such that if the data were analyzed without regard to gender, then there would be almost no diurnal differences in the 3 activities.

The percentage of individuals observed walking at any given 30-min time period during the 24-h observation periods is shown in figure 3A. A significantly higher proportion of males were found to be walking than females during the

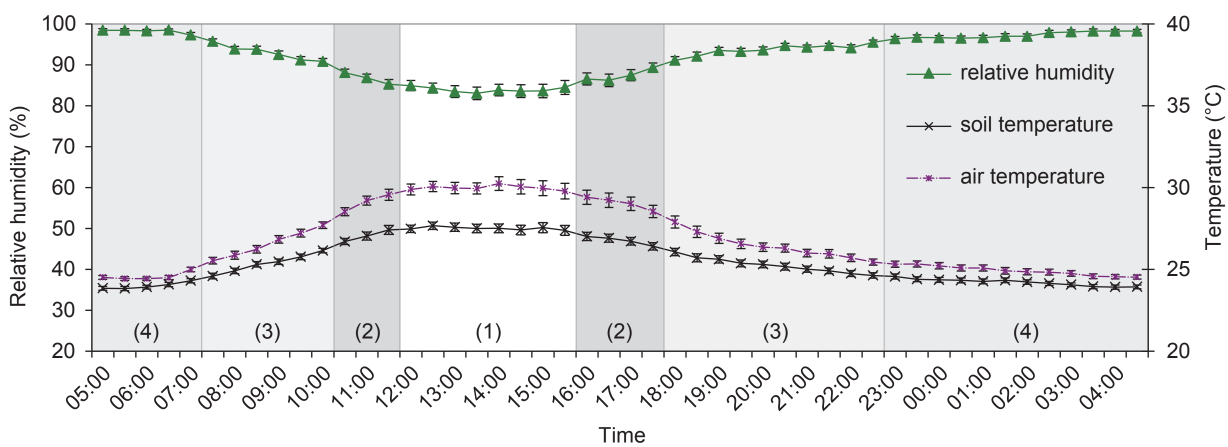

Fig. 1. Daily variations in physical factors (mean ± S.E.) within the study habitat during the study period. Shading indicates periods with similar environmental factors, where 1 = time at lowest humidity and highest temperature (LestH, HestT), 2 = time at low humidity and high temperature (LH, HT), 3 = time at high humidity and low temperature (HH, LT), and 4 = time at highest humidity and lowest temperature (HestH, LestT).

Table 1. Numbers of marked *Zephronia* cf. *viridescens* specimens observed in the rainy season of 2009 and 2010 at Lai-Nan forest, Nam Wa sub-watershed, Lai-Nan Sub-district, Wiang Sa District, Nan, Thailand

Sex	July 2009	Aug. 2009	Sept. 2009	May 2010	June 2010	July 2010	Aug. 2010	Sept. 2010	Total number observed
Male	3	3	3	0	2	4	1	0	16
Female	3	3	3	4	4	0	1	5	23
Total	6 (3)	6 (3)	6 (2)	4 (2)	6 (3)	4 (2)	2 (2)	5 (3)	39 (20)

The number of separate 24-h observation days in each month is shown in parenthesis in the "Total" line. This might not equal the total number of observed individuals since sometimes 2 or 3 millipedes were observed in the same 24-h period.

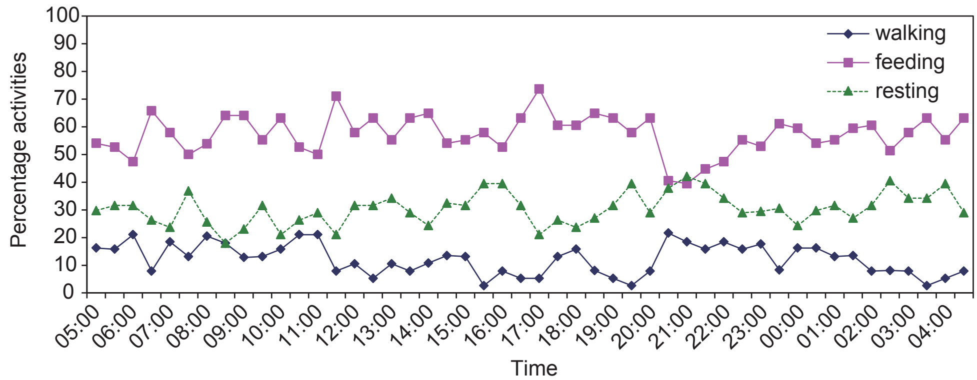

Fig. 2. Percentages of *Z.* cf. *viridescens* individuals engaged in each type of activity over a 24-h time interval. Data are from 39 individual millipedes (Table 1).

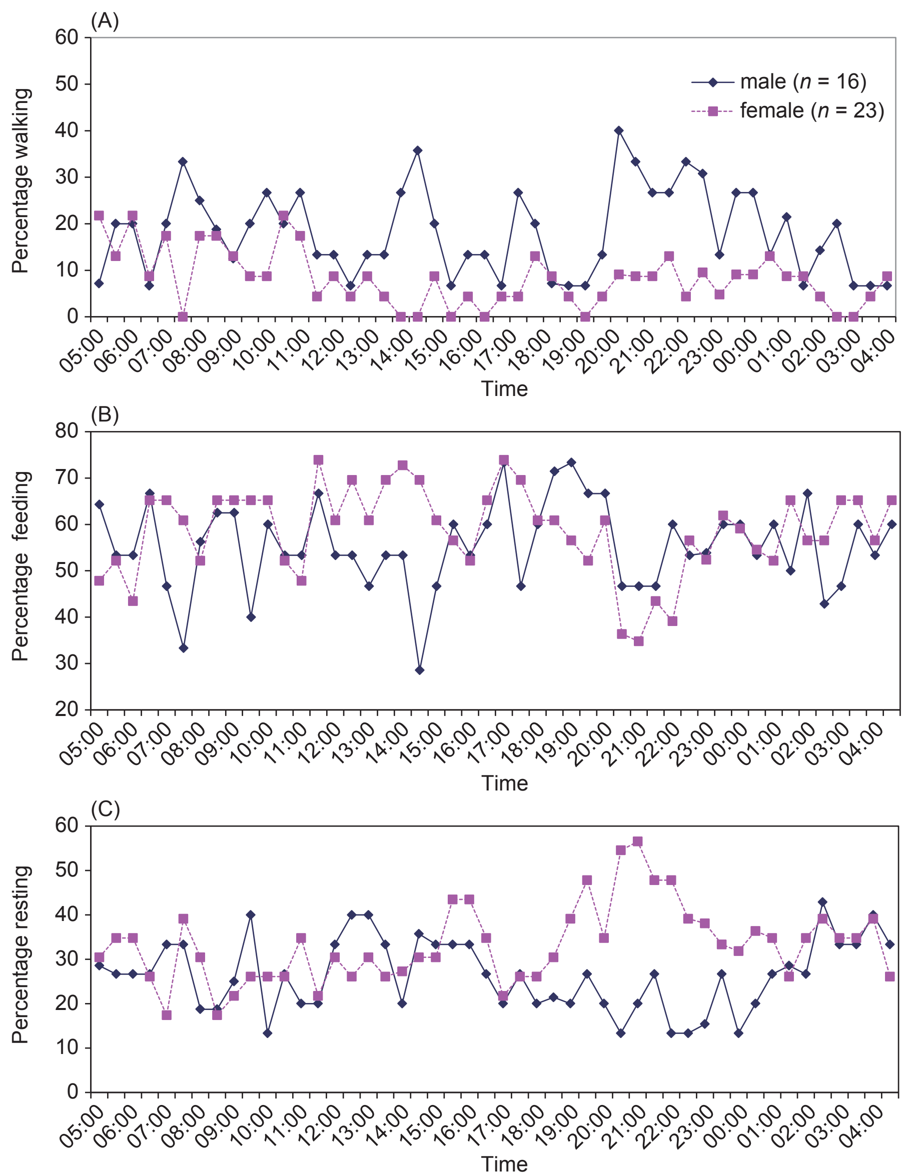

Fig. 3. Comparisons of percentages of individuals (A) walking, (B) feeding, and (C) resting between male and female *Z.* cf. *viridescens* over a 24-h period. Data were derived from 16 male and 23 female individuals (Table 1).

daytime (Table 2; χ^2 = 15.8, *d.f.* = 1, $p \approx 0.000$) and nighttime (Table 2; χ^2 = 26.6, *d.f.* = 1, $p \approx 0.000$), and so also throughout the 24-h period (Table 2; χ^2 = 40.2, *d.f.* = 1, $p \approx 0.000$). The peak walking activity of male millipedes, in terms of the percentage of males observed at each time point, seemed to have 3 peaks per day (Fig. 3A), coinciding with high-humidity and low-temperature periods (07:30-08:00 and 20:30-23:00), and the lowest-humidity and highest-temperature period (14:30). In these periods, the walking activity of males was also significantly higher than females (Table 3; $\chi^2_{HH,LT}$ = 21.1, *d.f.* = 1, $p \approx 0.000$; $\chi^2_{LestH,HestT}$ = 13.3, *d.f.* = 1, $p \approx 0.000$). However, there were small peaks of female walking activity during the night, at dawn, at dusk, and during the daytime. Females' walking frequency tended to be higher during the daytime than at night, with a peak in the morning, broadly ranging 05:00-11:00 (but with no activity at 07:30). There were no significant differences in walking activity between daytime and nighttime in either sex (Table 2; χ^2_{male} = 0.2, *d.f.* = 1, p = 0.657; χ^2_{female} = 2.6, *d.f.* = 1, p = 0.108), but the mobility of females was low at night, while that of males peaked at this time. The high level of male walking activity tended to coincide with a low (80% RH) or high (100% RH) RH (Table 4; χ^2 = 10.6, *d.f.* = 4, p = 0.031).

The percentage of individuals observed feeding at each 30-min observation time point over the 24-h period (Fig. 3B) did not significantly differ between males and females (Table 2; χ^2 = 1.8, *d.f.* = 1, p = 0.175). However, it was significantly higher in females than in males during the daytime (Table 2; χ^2 = 4.9, *d.f.* = 1, p = 0.027), which was related to the lowest-humidity and highest-temperature period at 12:00-15:30 (Table 3; χ^2 = 7.1, *d.f.* = 1, p = 0.008). Feeding activity in males seemed to be high in the evening (17:00 and 18:30-20:00), with smaller peaks of activity in the morning (06:30 and 09:00-09:30). However, there was no significant difference in male feeding activity between daytime and nighttime (Table 2; χ^2 = 0.2, *d.f.* = 1, p = 0.660). Feeding activity of females tended to peak slightly at 06:30-07:30 and 08:30-10:00, with more-significant peaks at 11:30-12:30, 13:30-14:30, and 17:00 h, and to decrease during 20:30-22:00. Indeed, females mainly fed during the daytime (Table 2; χ^2 = 5.5, *d.f.* = 1, p = 0.019). There were no significant sexual differences in feeding in relation to environmental factors; although females tended to feed more when the humidity was low (Table 4; χ^2 = 9.1, *d.f.* = 4, p = 0.059).

Resting was observed in addition to walking and feeding (Fig. 3C). The proportion of individuals resting at each time point did not significantly differ between females and males during daytime (Table 2; χ^2 = 0.3, *d.f.* = 1, p = 0.605), but at night, females rested significantly more than males (Table 2; χ^2 = 16.2, *d.f.* = 1, $p \approx 0.000$), coinciding with the high-humidity and low-temperature period (Table 3; χ^2 = 15.5, *d.f.* = 1, $p \approx 0.000$). Females spent most of the time resting between 19:00 and 23:00, at which times, males rested the least. Resting in males was rather sporadic throughout the 24-h

Table 2. Activity levels (% of all observations) of *Z.* cf. *viridescens* over a 24-h period, and divided into daytime and nighttime periods, during the rainy season in 2009 and 2010 at Nam Wa Sub-watershed, Lai-Nan Sub-district, Wiang Sa District, Nan Province, Thailand. The number of observations is in parentheses

Analysis period	Sex		% Walking	% Feeding	% Resting
[a] Total 24 h	Male (716)		18.2 (130)	55.4 (397)	26.4 (189)
	Female (1096)		8.2 (90)	58.7 (643)	33.1 (363)
		χ^2	40.2***	1.8	9.2**
[b] Daytime	Male (420)		17.6 (74)	54.8 (230)	27.6 (116)
	Female (643)		9.3 (60)	61.6 (396)	29.1 (187)
		χ^2	15.8***	4.9*	0.3
[c] Nighttime	Male (296)		18.9 (56)	56.4 (167)	24.7 (73)
	Female (453)		6.6 (30)	54.5 (247)	38.9 (176)
		χ^2	26.6***	0.3	16.2***
[d] Daytime-nighttime	Male	χ^2	0.2	0.2	0.8
	Female	χ^2	2.6	5.5*	11.5***

[a-c]Comparison of activity levels (% of all observations) between males and females for the [a]24-h period, and divided into the [b]daytime (05:00-18:30) and [c]nighttime (19:00-04:30) periods. [d]Comparison of activity levels between daytime and nighttime. Levels of statistical significance at * $p \le 0.05$, ** $p \le 0.01$, and *** $p \le 0.001$.

Table 3. Activity levels (% of all observations) of *Z.* cf. *viridescens* over a 24-h period, specified according to environmental factors during the rainy season in 2009 and 2010 at Nam Wa Sub-watershed, Lai-Nan Sub-district, Wiang Sa District, Nan Province, Thailand. The number of observations is in parentheses

Analysis period	Sex	% Walking	% Feeding	% Resting
[a]Highest humidity (HestH),	Male (250)	15.6 (39)	56.0 (140)	28.4 (71)
lowest temperature (LestT)	Female (385)	9.6 (37)	57.9 (223)	32.5 (125)
	χ^2	5.2*	0.2	1.2
[b]High humidity (HH),	Male (242)	21.9 (53)	56.6 (137)	21.5 (52)
low temperature (LT)	Female (367)	8.7 (32)	54.8 (201)	36.5 (134)
	χ^2	21.1***	0.2	15.5***
[c]Low humidity (LH),	Male (105)	17.1 (18)	58.1 (61)	24.8 (26)
high temperature (HT)	Female (161)	8.1 (13)	62.1 (100)	29.8 (48)
	χ^2	5.1*	0.4	0.8
[d]Lowest humidity (LestH),	Male (119)	16.8 (20)	49.6 (59)	33.6 (40)
highest temperature (HestT)	Female (183)	4.4 (8)	65.0 (119)	30.6 (56)
	χ^2	13.3***	7.1**	0.3

[a-d]Comparison of activity levels (% of all observations) between males and females for the time periods with [a]the highest humidity and lowest temperature (23:00-07:00), [b]high humidity and low temperature (07:30-10:00 and 18:00-22:30), [c]low humidity and high temperature (10:30-11:30 and 16:00-17:30), and [d]the lowest humidity and highest temperature (12:00-15:30). Levels of statistical significance at * $p \le 0.05$, ** $p \le 0.01$, and *** $p \le 0.001$.

Table 4. Activity levels (% of all observations) of *Z.* cf. *viridescens*, specified according to environmental factors, with the number of observations in parentheses, during the rainy season in 2009 and 2010 at Nam Wa Sub-watershed, Lai-Nan Sub-district, Wiang Sa District, Nan Province, Thailand

Analysis factor		% Walking		% Feeding		% Resting	
		Male	Female	Male	Female	Male	Female
T_{air} (°C)	24	17.7 (17)	12.5 (21)	54.2 (52)	58.3 (98)	28.1 (27)	29.2 (49)
	25	21.7 (39)	11.3 (23)	58.3 (105)	54.2 (110)	20.0 (36)	34.5 (70)
	26	25.4 (30)	7.8 (9)	53.4 (63)	56.9 (66)	21.2 (25)	35.3 (41)
	27	12.2 (10)	6.5 (10)	54.9 (45)	54.2 (84)	32.9 (27)	39.4 (61)
	28	10.5 (6)	7.9 (6)	56.1 (32)	57.9 (44)	33.3 (19)	34.2 (26)
	29	9.8 (4)	7.8 (7)	53.7 (22)	63.3 (57)	36.6 (15)	28.9 (26)
	30	17.9 (7)	8.8 (5)	46.2 (18)	70.2 (40)	35.9 (14)	21.1 (12)
	χ^2	11.7	5.3	2.3	6.7	12.7*	8.9
T_{soil} (°C)	23	9.7 (3)	9.8 (8)	48.4 (15)	62.2 (51)	41.9 (13)	28.0 (23)
	24	21.3 (43)	10.3 (25)	59.4 (120)	55.0 (133)	19.9 (39)	34.7 (84)
	25	22.6 (37)	12.9 (22)	57.3 (94)	57.1 (97)	20.1 (33)	30.0 (51)
	26	15.0 (17)	5.1 (10)	50.4 (57)	57.9 (114)	34.5 (39)	37.1 (73)
	27	13.1 (11)	9.2 (13)	52.4 (44)	59.2 (84)	34.5 (29)	31.7 (45)
	28	10.5 (2)	9.4 (3)	36.8 (7)	62.5 (20)	52.6 (10)	28.1 (9)
	χ^2	7.8	7.1	6.2	1.9	25.7***	3.8
% RH	80	25.0 (2)	12.5 (1)	50.0 (4)	75.0 (6)	25.0 (2)	12.5 (1)
	85	11.3 (6)	6.8 (8)	50.9 (27)	63.6 (75)	37.7 (20)	29.7 (35)
	90	7.5 (3)	7.8 (6)	70.0 (28)	66.2 (51)	22.5 (9)	26.0 (20)
	95	14.0 (20)	7.7 (15)	53.8 (77)	50.5 (99)	32.2 (46)	41.8 (82)
	100	22.2 (82)	10.9 (51)	54.5 (201)	57.5 (268)	23.3 (86)	31.5 (147)
	χ^2	10.6*	3.3	4.2	9.1	8.0	11.2*

Levels of statistical significance at * $p \le 0.05$ and *** $p \le 0.001$. RH, relative humidity.

period, with no significant difference between nighttime and daytime (Table 2; χ^2 = 0.8, *d.f.* = 1, *p* = 0.337), while in females, it was significantly higher at night (Table 2; χ^2 = 11.5, *d.f.* = 1, *p* = 0.001). The high level of resting in females tended to coincide with a high humidity of 95% RH (Table 4; χ^2 = 11.2, *d.f.* = 4, *p* = 0.024), while that in males tended to coincide with a high air temperature (Table 4; χ^2 = 12.7, *d.f.* = 6, *p* = 0.048) and low (23°C) or high (28°C) soil temperatures (Table 4; χ^2 = 25.7, *d.f.* = 5, *p* ≈ 0.000).

Daily movements

Daily movements of millipedes, in terms of the minimum total distance moved per day and the net displacement distance per day, segregated by sex, are summarized in table 5. The minimum total daily distance moved by males was significantly higher than that by females (Mann-Whitney *U*-test: Z = -2.46, *p* = 0.014), while the longest minimum total daily distance movement in males (3690 cm) was some 3.3-fold greater than that in females (1121 cm). In addition, the daily displacement in male millipedes was significantly higher than that in females (Mann-Whitney *U*-test: Z = -2.11, *p* = 0.035), with the longest daily displacement in males (1014 cm) being 1.3-fold longer than that in females (768 cm). However, the frequency of movement, in terms of the number of different locations of the millipede between 30-min observation periods over the 24-h period, did not significantly differ between males and females (Mann-Whitney *U*-test: Z = -1.26, *p* = 0.208).

Notes on types of behavior

Walking (Fig. 4A): *Zephronia* cf. *viridescens* individuals were observed walking randomly using the sensorial cones on their antenna tips to touch objects above the ground surface as they moved from 1 position to another in search of resources, such as food and shelter. They were also observed walking from an open area exposed to the sunlight, with or without leaf litter, to a shaded area. Walking speed was observed to be faster in exposed areas than in shaded areas.

Feeding (Fig. 4B): Millipedes usually spent most of the time feeding under the leaf litter. They unrolled, curved themselves a little, and moved their anterior appendages to feed. Their feet were used to control the direction of the leaf litter. They could feed continuously for more than 1 h, and a few millipedes fed throughout the 24-h period. When they encountered a dry leaf with low moisture, they took a shorter time, < 5 min, for feeding and then continued searching for another food item. Their diets in the study area consisted of leaf litter and soil particles. Most of the leaf litter was from *Gigantochloa albociliata*, *Bauhinia* spp., and *Pterocarpus macrocapus*, with moisture contents of > 90% (weight/weight), as evaluated by a dry-weight analysis of collected samples.

Mating (Fig. 4C, D): Some unmarked male millipedes were observed to approach marked females. The walking routes of males were similar to those of females. Males used the sensorial cones on their antenna tips to search for food, and also to find mates. When a female did not allow a male to mate, the male then continuously followed

Table 5. Mass, size and daily movement of *Z.* cf. *viridescens* observed during the rainy season in 2009 and 2010 at Nam Wa Sub-watershed, Lai-Nan Sub-district, Wiang Sa District, Nan Province, Thailand

Parameter	Males (*n* = 16)	Females (*n* = 23)
	Mean ± SE	Mean ± S.E.
Mass (g)	2.3 ± 0.2	3.3 ± 0.2
Length in ball shape (mm)	17.9 ± 0.7	20.5 ± 0.5
Mean distance moved in a day (cm)	1080 ± 226	486 ± 59
Median distance moved in a day (cm)	898	475*
Range of distance moved in a day (cm)	193-3690	23-1121
Mean displacement in a day (cm)	403 ± 62	269 ± 32
Median displacement in a day (cm)	428	261*
Range of displacement in a day (cm)	120-1014	18-768
Mean frequency moved in a day (no. of times)	15 ± 3	10 ± 1
Median frequency moved in a day (no. of times)	13	10
Range of frequency moved in a day (no. of times)	2-34	1-23

*Significantly differed at *p* ≤ 0.05.

Fig. 4. *Zephronia* cf. *viridescens* behavior. Digital photographs of (A) walking, (B) feeding, (C, D) mating, (E, F) resting, and (G, H) guarding.

the same female throughout the night. Upon approaching a female, the male walked slowly backwards and turned his anal shield toward the female, extending his telopods to the female's anal shield as much as possible. When the female was unrolled, the male used his telopods to raise the posterior part of the female, which caused the female to turn over. Then the male walked rapidly backwards to the ventral side of the female. If the female rolled into a ball, the male tended to wait for her to unroll, which was sometimes more than 20 min, and then he followed her. Moreover, on 1 occasion, a male was observed to use his telopods to raise another male that was walking near the same female (Fig. 4G, H).

Resting (Fig. 4E, F): Giant pill-millipedes roll themselves into a ball when resting. This was mostly observed to occur after feeding on leaf litter in the same position between the soil surface and under the leaf litter or among litter strata (Fig. 4F). Two individuals were observed to have burrowed a few centimeters under the surface and so rested underneath the litter (Fig. 4E). Another 2 individuals were seen resting between litter strata at a bamboo clump throughout a cloudy day. In that case, the average soil surface temperature was 26.4°C and average RH was 87.9%.

Other activities: In addition to the above 3 behaviors, some other activities were observed, such as defecation and burrowing. After feeding, some millipedes were in a C-shape, and then rotated for a minute before defecating. However, most of the observed defecations occurred while feeding. During the late rainy season, in Sept. 2009, a male millipede was observed burrowing into the soil under a tree. Soil particles were subsequently moved from the anterior to the posterior feet and then to the ground surface. This millipede then rotated itself around in the soil and continued to burrow into a deep soil layer. Twenty-four hours later, the millipede was found at a 5-cm depth below the soil surface.

DISCUSSION

Neutrality and reliability of the marker and detection

The use of marked animals in the field always raises the possibility of altered behavior due to observation-caused disturbance. Indeed, subsequent to this study, Drahokoupilová and Tuf (2011) reported that nail polish and bee marker affected the behavior of the pill-millipede, *Glomeris tetrasticha*. However, the acrylic color selected for this investigation showed no discernible effects on the millipedes' activities in the laboratory, and was removed in the field after the 24-h observation period to prevent any long-term problems, such as differential mortality. The observed types and general frequencies of behaviors of the marked millipedes were not noted to differ from those of unmarked ones incidentally observed during the field trials (although this cannot be statistically tested as the separate behaviors of unmarked individuals could not be ascribed to the same individual over time). Although mating was observed in unmarked but not in marked individuals, this was not observed frequently enough with respect to the total observation numbers to be significant, and unmarked males were observed to follow marked females along with a marked male, but no mating was observed. Thus, although potential effects were not formerly excluded, and are required to be, in this study, there is no strong reason to doubt the validity of the data. With respect to the reliability of tracking the millipedes, especially given that they spend a large amount of time under cover, it is worth noting that in all 24-h observation periods, there was never a 30-min period in which the millipede(s) under observation could not be located, nor was there any evidence of disturbance (change in activity or movement or curling once found) observed. Thus, with standard due care, we consider the data from the observations of the marked millipedes as likely to broadly represent that of unmarked and undisturbed ones, subject to the limitations of the sampling sizes.

Daily activities

The present study revealed that the 2 most frequently observed activities of *Zephronia* cf. *viridescens*, namely, feeding and walking, occurred throughout the day. However, earlier work reported that most millipedes in the tropical zone show a higher level of movement at dusk or nighttime (Cloudsley-Thompson 1951, Banerjee 1967, Bano and Krishnamoorthy 1979, Boccardo and Penteado 1995, Koilraj et al. 1999 2000, Tuf et al. 2006, Kadamannaya and Sridhar 2009). Although *Z.* cf. *viridescens* has ocelli for detecting light, it spends most of its time, including daytime, under leaf litter. Therefore, light might not be an important factor influencing its activity. The results of this study on *Z.* cf. *viridescens*, and those of most millipedes in the tropical zone, may vary due to different habitat types, because the transpiration rate of millipedes, and the temperature, humidity, and precipitation in various habitats also differ. This is supported by a previous report that the distribution of millipedes is closely correlated to their transpiration (Haacker 1968), while the nocturnal habits of tropical arthropods are presumed to be related to their high transpiration rates in the daytime, which in turn depends upon the moisture content in the atmosphere (Cloudsley-Thompson 1959). Webb and Telford (1995) explained that the transpiration rate was positively correlated with oxygen consumption levels in the juliform millipede, *Doratogonus bilobatus* (Schubart, 1966). Here, the resting behavior during the daytime could have decreased their metabolic rate, oxygen consumption, and transpiration rate. Moreover, a lower temperature during the nighttime was described as a trigger for activities (Cloudsley-Thompson 1951). For *Z.* cf. *viridescens*, the microclimate in their habitat (Fig. 1) changed a few degrees during the day with a high relative humidity (of > 80%) throughout the day. Thus, changes in the transpiration rate may not have been high enough to influence their daytime activities. Moreover, the millipedes could reduce their transpiration rate during the daytime by walking rapidly from sun-exposed to shady areas and spending more time feeding between the soil and leaf litter or litter strata.

The proportion (as a percentage of the number of individuals) of *Z.* cf. *viridescens* individuals feeding throughout the 24-h period did not significantly differ between sexes. Therefore, it is possible that males need broadly similar amounts of energy in their diet as females in the rainy season. The feeding of *Z.* cf. *viridescens* males tended to be high in the morning hours (06:30, 07:30-08:00) and at dusk (17:00-17:30 and 18:00-20:00), this being more consistent with a previous investigation of giant pill-millipedes in India (Kadamannaya and Sridhar 2009). In the afternoon (12:00-13:30), males of *Z.* cf. *viridescens* tended to rest when the temperature was the highest with the lowest RH, which is similar to observations made for *Arthrosphaera dalyi* and *A. davisoni* in a plantation in India (Kadamannaya and Sridhar 2009). Thus, temperature and humidity could influence millipede activity, in accordance with previous reports (Perttunen 1953, Banerjee 1967, Tuf et al. 2006). While females of *Z.* cf. *viridescens* spent a relatively high proportion of their time feeding from morning until dusk, they spent a short time resting after feeding (such as in the late afternoon) (Fig. 3C).

The amount of time spent walking, and more so for males than for females, was also similar to that reported for juliformian and flat-backed millipedes (Dangerfield et al. 1992, Rowe 2010). The percentage of time spent walking in *Z.* cf. *viridescens* males was highest at night (20:30-23:00), which could be explained by males using their energy and time to search for females. In contrast, the percentage of resting females was higher than that for males throughout the day and was highest at night (20:30-22:00). This would potentially serve to decrease the metabolic rate and so accumulating energy in the rainy season to invest in egg maturation. Therefore, based on movements of males and females, the mating behavior in *Z.* cf. *viridescens* may well occur more frequently at night than in the daytime.

Distance moved and displacement

No previous study has reported on daily movements of millipedes on the ground surface. In this study, the daily distance moved and daily displacement were higher in males than females of *Z.* cf. *viridescens*. According to traditional methods of determining monogamy in mating systems (Wu et al. 2012), *Z.* cf. *viridescens* might not be monogamous based upon the data of daily movements and observations of multiple males following individual females. However, this awaits further investigation, such as molecular-based paternity analyses.

As discussed under the section on walking above, the higher mobility in male millipedes may increase their opportunity for finding a mate and mating, while the lower movement in females may increase the available time for feeding and resting to accumulate energy for egg production in the breeding season. This notion was supported by previous studies (Wise 1975, Ballinger 1977, Boggs and Ross 1993), which reported that fecundity was positively related to food and energy availability.

Other adaptations for survival and reproduction

The behavior of *Z.* cf. *viridescens* in a deciduous forest during the rainy season was dominated by feeding, in accordance with other millipedes studied previously (Dangerfield et al. 1992, Kadamannaya and Sridhar 2009). Feeding appears to be the most important activity, presumably for accumulating and storing energy reserves for the forthcoming dry season, and for reproduction in terms of either future reserve allocation to egg production in more-sedentary females, or investing in walking in more-active males for mate finding and mating. In addition, Lawrence (1984) stated that the intestines of giant pill-millipedes in relation to body length were longer than in most other millipede groups and bent in an 'N' shape for storing enough food material to supply the large body size, a potential adaptation for diapause during the dry season.

In a tropical deciduous forest, food components like leaf litter and soil particles are not limiting because they remain abundant on the soil surface throughout the year. The mobility of *Z.* cf. *viridescens* in part reflects its optimal foraging strategy, where walking to new areas assists in searching for a high-quality diet within its habitat; this is consistent with previous studies on *Julus scandinavius* (in the order Julida) (Kheirallah 1979) and *Alloporus uncinatus* (in the order Spirostreptida) (Dangerfield and Telford 1993). Sakwa (1974) mentioned that the important factors that affect food acceptance for millipedes include the nitrogen content, sugar level, and moisture content of the leaf litter (see also Mahsberg 1997). Therefore, dietary selection could result from nutritional requirements, food availability, food type, and the microhabitat of millipede species. However, no theoretical approaches, such as optimal foraging or game theory-based models, have evaluated the foraging strategy of millipedes in heterogeneous habitats, nor has the quality of the habitat been assessed.

In this study, *Z.* cf. *viridescens* was observed to walk and use sensorial cones on its antennae to make contact with the surrounding area (Fig. 4A). Since male *Z.* cf. *viridescens* can find females in the habitat while walking, it is possible that females secrete sex pheromones onto the forest floor to attract males in the breeding season, as was reported in some other millipede species including *Glomeris marginata* (in the order Glomerida) and *Ommatoiulus moreletii* (in the order Julida), which produce pheromones to attract each other over very short distances (Hopkin and Read 1992). Moreover, in many other millipede species, males cannot successfully mate if they do not have their antennae (Haacker 1974), suggesting the involvement of semiochemical signals in mate finding, recognition, and acceptance.

In contrast to the courtship behavior of pill-millipedes in the genus *Sphaerotherium* (Haacker 1974, Wesener et al. 2011), *Z.* cf. *viridescens* males produce no sound, but use body contact and wait for females to unroll (Fig. 4C). However, the mating behavior of *Z.* cf. *viridescens*, such as the male's backward walk to the female and their reversed copulation position with their ventral sides adjacent to each other (Fig. 4D), is similar to that reported in other pill-millipedes (Haacker 1974, Wesener et al. 2011). In addition, a male *Z.* cf. *viridescens* was observed to follow a female and attack another male who came close to her (Fig. 4G, H). If supported by future observations, this is of interest as there are no previous reports on precopulatory mate guarding in millipedes. Postcopulatory mate guarding, which was not observed in *Z.* cf. *viridescens*, was reported in *Alloporus uncinatus* (in the order Spirostreptida) (Telford and Dangerfield 1990) and *Nyssodesmus python* (in the order Polydesmida) (Adolph and Geber 1995). Both types of mate guarding can increase mating success and fitness of the male (Parker 1974, Waage 1979).

During the rainy season, some *Z.* cf. *viridescens* individuals were observed to burrow into the shallow layer of the upper soil to rest (Fig. 4E), which is similar to the burrowing behavior for resting reported in European millipedes (Haacker 1967 1968) and Indian giant pill-millipedes (Kadamannaya and Sridhar 2009). The burrowing behavior for diapause of *Z.* cf. *viridescens* was also observed at the end of Sept. in the late rainy season. This result is similar to observations of other millipede species, such as paradoxosomatids and gomphodesmids (in the order Polydesmida), which enter a chamber at the same time for diapause (Lewis 1974).

CONCLUSIONS

This field study of *Zephronia* cf. *viridescens* revealed that the principal activity in the rainy season was feeding, followed by resting and walking. In general, the activity of *Z.* cf. *viridescens* was related to the RH and temperature. Males were significantly more active than females, being observed to be walking more often and to cover a significantly greater total minimum daily distance and daily displacement. Moreover, males were more active at night than during the day, while females were less active at night; nighttime is likely to be when most mating behavior occurs. Thus, given that the observed microhabitat preference of *Z.* cf. *viridescens* was under leaf litter, then sampling methods to evaluate the population structure, including the home range size, population size and structure, and population genetics should take into account the different mobility of males and females and consequentially be based upon active searching methods, such as quadrat sampling or hand collection. Moreover, these results are consistent with the notion that males are likely to allocate more of their energy to mate searching (and so potentially show increased immigration/emigration levels compared to females), while females allocate more energy to reproduction and reducing predation risks.

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