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Daily and Seasonal Foraging Activity of the Oriental Non-army Ant Doryline *Cerapachys sulcinodis* Species Complex (Hymenoptera: Formicidae)

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Abstract

The ant subfamily Dorylinae contains the true army ant genera, the species of which are dominant predators, as well as non-army ants. Some of the non-army ant genera are closely related to true army ants, so they could be an important key in understanding the evolution of the army ant adaptive syndrome. Nevertheless, there has been little field research on the non-army ant doryline species because many of them are very rare. *Cerapachys* is one of the genera closely related to the Old-World army ants. We found some species of *Cerapachys* are commonly distributed in northern Thailand, so we investigated the daily and seasonal foraging activities of a non-army doryline ant of *Cerapachys sulcinodis* species complex in the seasonal tropical area of northern Thailand. Workers of the *C. sulcinodis* complex were diurnal and actively foraged during the rainy season, and their reproduction and foraging activity paused during the dry season. This report is the first on the foraging activity of non-army doryline ants under field conditions.

Introduction

The true army ants, consisting of eight genera in the subfamily Dorylinae, are known to exhibit several specific biological characters such as large colony size, group predation with several workers, nomadism, and permanently wingless queens, which together form the army ant adaptive syndrome (Gotwald, 1995; Kronauer, 2009). This subfamily also contains "non-army ant" genera, which do not exhibit the army ant adaptive syndrome (Borowiec, 2016). Several biological aspects of true army ants have been studied in the field (Reviewed in Gotwald, 1995; Kronauer, 2009), whereas the basic biology and behavior of non-army doryline ants are mostly unknown because of their rarity. The only exception is the clonal raider ant *Ooceraea biroi* (Forel, 1907), which has been the subject of detailed studies (e.g., Ravary et al., 2006; Oxley et al., 2014). However, this species shows an apparently atypical lifestyle because of not only clonal reproduction but also queenlessness and a "tramp" habit (Tsuji & Yamauchi, 1995; Wetterer et al., 2012). Therefore, there is almost no research on a comparative approach to the evolution of the army ant adaptive syndrome in this subfamily.

Research on daily and seasonal foraging activity is important in understanding the basic ecology and behavior of ants. The daily foraging schedule is a distinctive character of each ant species (Hölldobler & Wilson, 1990). Some ants exhibit diurnal or nocturnal foraging (e.g., Rosengren, 1977; Hölldobler, 1980; Ashikin & Hashim, 2015), whereas many species actively forage during the day and at night (e.g., Kaspari & Weiser, 2000; Peeters & Ito, 2015). In seasonal tropical regions, some species are active even during the dry season while many species rarely show foraging activity (e.g., Kaspari & Weiser, 2000; Chantarasawat et al., 2013). Such foraging patterns may relate to daily and/

or seasonal fluctuation in resource abundance, seasonality of brood production, and physiological adaptation to ambient temperature, humidity, and/or luminosity (Hölldobler & Wilson, 1990). In doryline ants, diurnal, nocturnal, and 24 h active species have been reported among epigaeic army ants (Gotwald, 1995), but there has been only limited observation of non-army ants because they are rare. In addition, body size and colony size of non-army ant doryline species are generally small, making it more difficult to observe them in the field. Most of the descriptions of foraging activity in the field are based on anecdotal observations.

Recently, we found that a few species of the non-army doryline genus *Cerapachys* are common in some areas in northern Thailand, and these ants seem to be good model species for quantitative studies on the biology of non-army ant dorylines. A molecular phylogenetic study suggests that three genera, *Cerapachys*, *Chrysapace*, and *Yunodorylus*, are related to the Old-World army ants, *Aenictus* and *Dorylus* (Borowiec, 2019). We started comprehensive research of the biology of the *Cerapachys sulcinodis* Emery, 1889 species complex in 2013. In this study, we present a report on the field observations of the daily and seasonal foraging activity of a species belonging to the *C. sulcinodis* species complex in a seasonal tropical region in northern Thailand. This report is the first on the quantitative observation of foraging behavior in non-army doryline ants in the field.

Materials and Methods

We observed the foraging activity of *C. sulcinodis* species complex in northern Thailand. According to the key and description based on the worker diagnosis provided by Brown (1975), the species was identified as *C. sulcinodis*. However, two distinct types of ergatoid queen were found sympatrically in our study sites in northern Thailand, and each colony contained only one of the two queen types. Preliminary research on their molecular phylogeny indicated that they are separated into two monophyletic clades (Yamada & Eguchi, pers. comm.), indicating that these are two species. However, we could not conclude their taxonomic status because the taxonomy of this genus is still inadequate. In this paper, we call them the *C. sulcinodis* species complex. Colonies of the *C. sulcinodis* species complex are relatively large, having up to 2000 workers that exhibit group foraging with up to 100 workers on the ground surface, so observation of foraging behavior is easy. Workers attack ant colonies as is known in other non-army ant dorylines, but they also predate on other arthropods. Details of their foraging behavior, prey preferences, and colony composition will be published separately (Mizuno et al., in prep.).

Observations were carried out in the Omkoi National Forest (17° 50′ 49.79″ N, 98° 22′ 18.84″ E, alt. 950 to 1000 m) in Omkoi District, Chiang Mai Province, northern Thailand (Fig 1). The study site is a dry dipterocarp forest, belonging to the *Aw* type of the Köppen climate classification, showing well-defined dry and rainy seasons. Figure 2 shows the annual trend in monthly precipitation and temperature in the Omkoi study site within the research period. During the dry season (December to March), the forest floor was very dry, and macro soil animals were very rare on and under the leaf

Fig 1. Landscape of the survey route in the Omkoi study site during the rainy season (A, taken on 25 August 2017) and the dry season (B, taken on 20 March 2017).

litter on the ground where the *C. sulcinodis* species complex workers foraged. Some species of ants such as *Odontoponera denticulata* (Fr. Smith, 1858), *Diacamma violaceum* Forel, 1900, *Paratrechina longicornis* (Latreille, 1802), and *Dolichoderus* cf. *thoracicus* (Fr. Smith, 1860) were active during the dry season, but ant species richness was apparently poor.

A walking survey was conducted to determine the daily and seasonal foraging activity of the *C. sulcinodis* complex. Three survey routes (route 1, distance 670 m; route 2, 1030 m; and route 3, 400 m) were chosen (Fig 3). We walked those routes at various times during the day and night, and the number of foraging parties of the *C. sulcinodis* complex seen on the open surface was counted. The approximate duration of the survey for each route was 30 min for route 1, 45 min for route 2, and 20 min for route 3. The temperature and relative humidity were recorded at the start and the end of each survey.

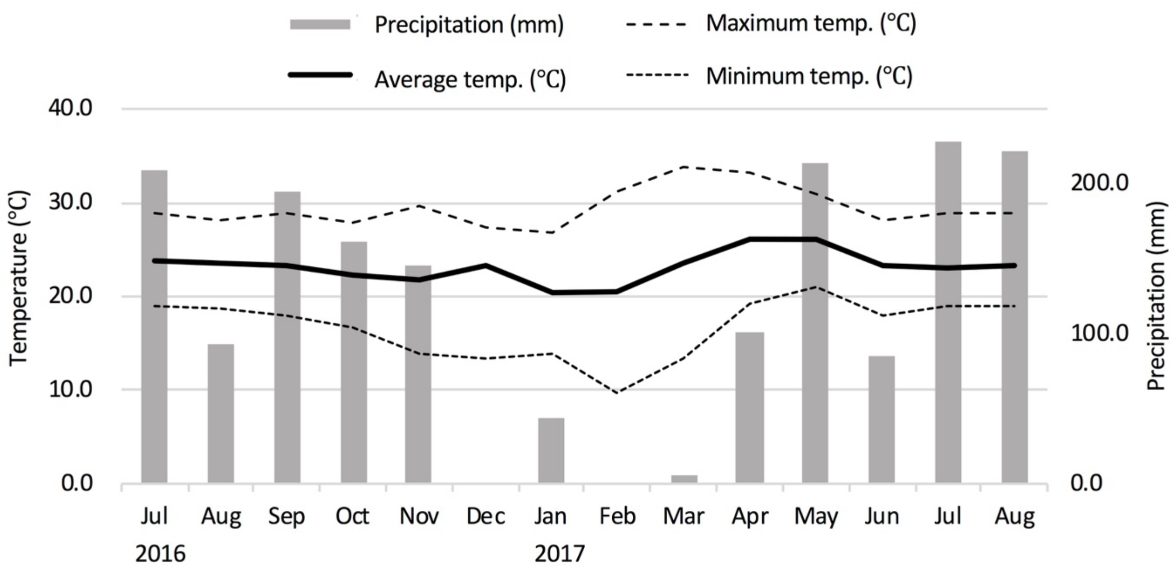

Fig 2. Precipitation and average temperature from July 2016 to August 2017 in the Omkoi study site.

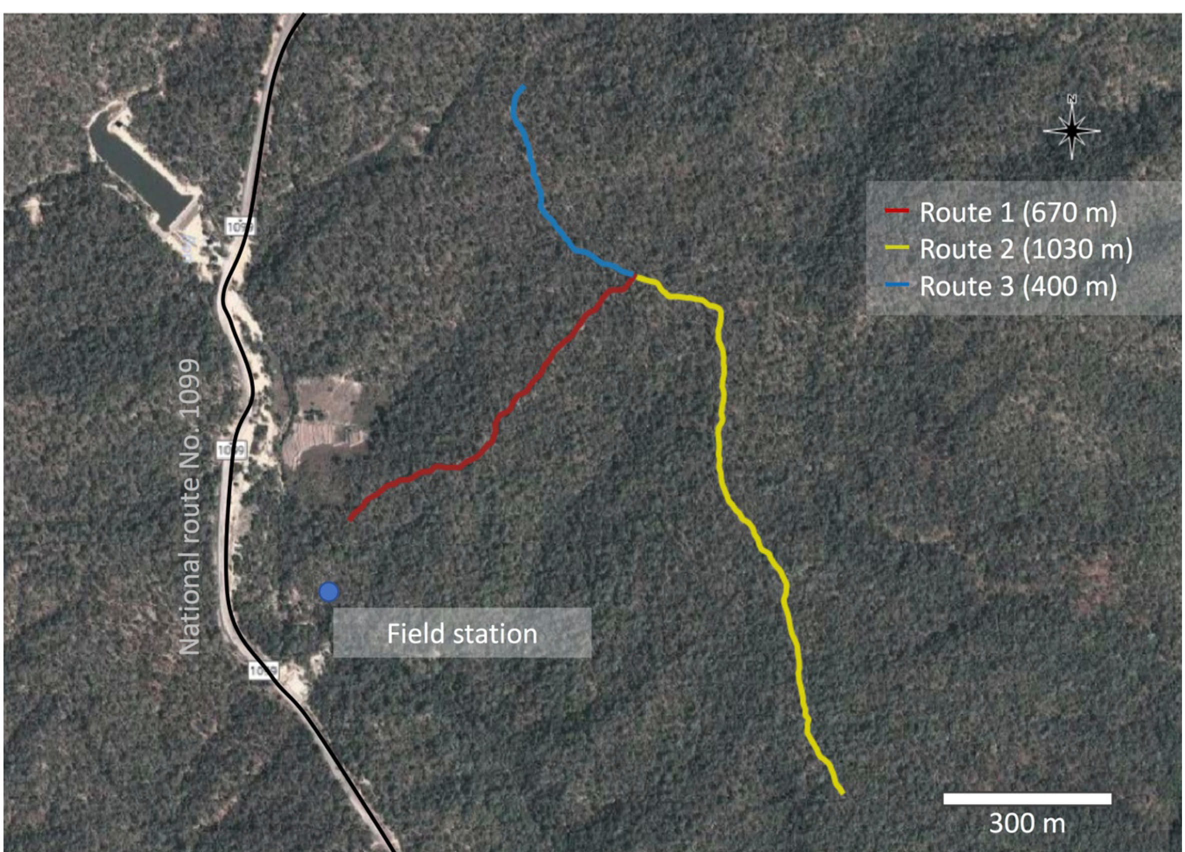

Fig 3. Map of three surveyed routes in the Omkoi study site.

The median between the data at the start and at the end was considered as representative data for the survey of the course. This survey was conducted 206 times in total (total walking distance was 141.8 km) from September 2016 to July 2017. Of the 206 records, temperature and humidity was not measured 22 times between March and July 2017 because of a device failure. There was no significant difference in the average number of foraging groups per 100 m among the three routes (Tukey multiple comparisons of means: Route 1 vs. Route 2, $p = 0.4168155$; Route 1 vs. Route 3, $p = 0.061$; Route 2 vs. Route 3, $p = 0.664$); thus, the data from the three routes were combined. Foraging activity was compared between the dry season (December 2016 to March 2017) and the rainy season (all other months). Statistical comparisons of the observed foraging activity, temperature, and humidity between the categories of seasons and periods of time were performed with R software (Version 3.5.0), using a multiple comparison test after the Wilcoxon signed-rank test (function *pairwise.wilcox.test*).

Results

A summary of the survey in each month is shown in Table 1. Foraging activity was rarely observed in the dry season, except at the very beginning (December). No foraging groups of *C. sulcinodis* were seen in February and March. The average number of observed foraging groups per 100 m was significantly different between the rainy and the dry seasons (rainy season = 0.16 ± 0.23 SD, dry season = 0.01 ± 0.04 SD, $t = -5.9291$, $df = 47.768$, $p < 0.01$, Welch two sample t-test). During the dry season, foraging groups were observed only five times in mid-December. Three of these raids (observed on 18 December 2016 at the beginning of the dry season on Route 1) were conducted by one colony (Mizuno personal colony code, 161218-1). The foraging groups were observed twice on Route 2, on 16 and 18 December. The temperature and humidity of the observed routes were 20.6 to 28.2 °C and 46.5 to 89.0%, respectively.

Table 1. The frequency of walking surveys on each route, total distances, and the number of observed foraging groups of the *C. sulcinodis* complex.

			Frequency of walking surveys					
	Year	Month	Route 1 (670 m)	Route 2 (1030 m)	Route 3 (400 m)	Total	Total distance (km)	No. observed foraging groups
Dry season	2016	Dec.	17	13	19	49	32.38	5
	2017	Feb.	14	14	14	42	29.40	0
	2017	Mar.	18	14	14	46	32.08	0
		Subtotal	49	41	47	137	93.86	5
Rainy season	2016	Sep.	11	9	9	29	20.24	19
	2017	May	5	2	2	9	6.21	8
	2017	Jun.	6	4	4	14	9.74	33
	2017	Jul.	9	4	4	17	11.75	16
		Subtotal	31	19	19	69	47.94	76
		Total	80	60	66	206	141.80	81

Most of the foraging groups were observed during the daytime (Fig 4). The frequency of the foraging activity was significantly different between daytime (6:01 to 19:00, 0.11 ± 0.18 SD) and nighttime (19:01 to 6:00, 0.02 ± 0.07 SD) ($t = 3.507$, $df = 74.608$, $p = 0.000771$, Welch two sample t-test, data for two months with no foraging activity observed omitted from the comparison). Foraging activity at night (after 19:00) was observed only twice during the rainy season (Fig 4, shown with arrows). One of the observations was recorded on Route 3 at 23:29 (temperature 23.4°C, humidity 81%) on 23 September 2016. A group of 10 workers walking on the forest floor was observed at the site 30 cm away from their nest entrance. These workers did not have any brood or prey. The other observation of night foraging was recorded at 20:40 (temperature 24.0 °C, humidity 86%) on 14 July 2017 on Route 1. There were about 30 workers in the foraging group. They did not carry any brood and walked up to 1.5 m from the nest entrance hole on the surface.

The range of temperatures during the daytime in the dry season (12.6 to 35.0 °C) was broader than that in the rainy season (15.6 to 30.1 °C), but the median temperature was not different between the two seasons (Fig 5). In contrast, at night the temperature was significantly lower in the dry season than in the rainy season. Humidity was higher in the rainy season than in the dry season during the day and at night (Fig 5). The range of temperatures and humidity where foraging groups were observed was 20.6 to 30.1 °C and 46.5 to 96.0%, respectively (Fig 6). Of the 98 daytime surveys conducted during the dry season, 23 were in this range of temperatures and humidity, but foraging groups were found only five times as mentioned above.

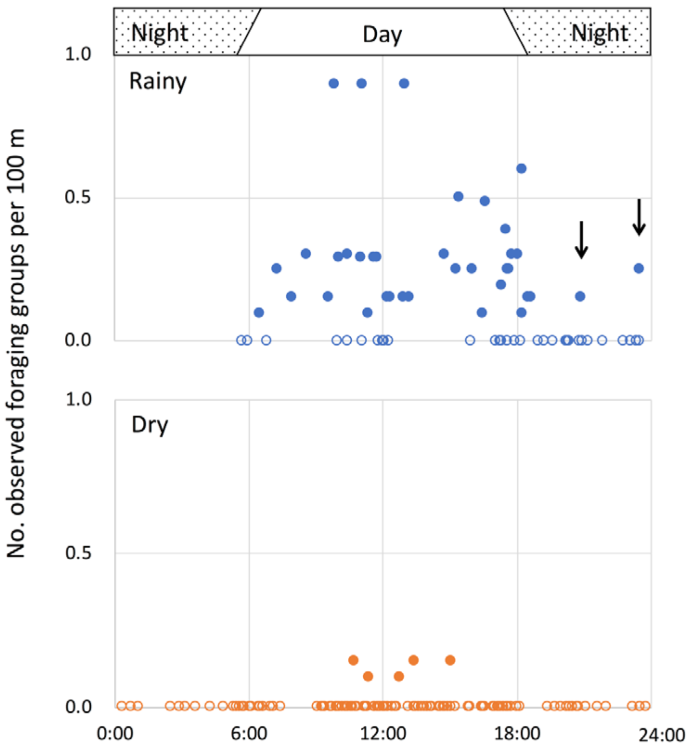

Fig 4. The number of observed foraging groups of the *C. sulcinodis* complex at 100 m intervals during the day in the rainy season (upper, September 2016; May, June, July 2017) and the dry season (lower, December 2016; February, March 2017). The observations with no foraging activity are shown as open circles on the base line. Nocturnal activity is indicated by arrows on the upper plot.

During the night in the rainy season, temperature and humidity were also in the range all nine times, but foraging groups were observed only twice. In other words, although the temperature and humidity were suitable during the dry season and at night, the foraging activity of *C. sulcinodis* stopped.

Discussion

The study field in Omkoi National Forest is located in the seasonal tropical mountainous region, where there is a strong dry season. Many ant species stop foraging during such dry seasons (e.g., Kaspari & Weiser, 2000; Chantarasawat et al., 2013) because terrestrial arthropods are generally sensitive to desiccation (Hood & Tschinkel, 1990). Some desert ants change their daily foraging schedule during the dry season to escape the extreme hot temperatures, e.g., *Cataglyphis* spp. and *Ocymyrmex* spp. (Wehner & Wehner, 2011), *Pogonomyrmex* spp. (Whitford et al., 1976; MacKay & MacKay, 1989), and *Aphaenogaster senilis* Mayr 1853 (Caut et al., 2013). Our study shows that colonies of the *C. sulcinodis* complex are completely inactive during the dry season, especially in February and March. Even during these two months, humidity and temperature often fall in the range where workers of the *C. sulcinodis* complex actively foraged during the rainy season. Thus, other factors regulate foraging activity.

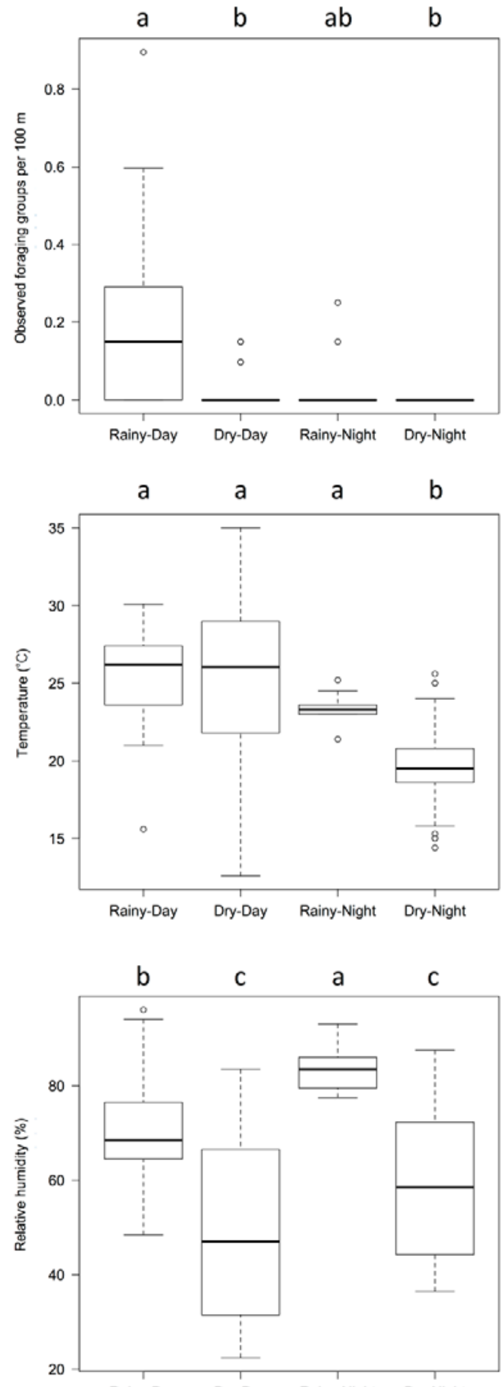

Fig 5. Foraging activity, temperature, and humidity during the day and at night in each season. Different letters indicate significant difference by multiple comparison test after Wilcoxon signed-rank test (function *pairwise.wilcox.test* in R), $p < 0.01$.

One possibility is the remarkably low density of prey arthropods including ants during the dry season. Furthermore, the colony collection data of the *C. sulcinodis* complex shows there is no brood in the early dry season, mid-November, suggesting that their reproduction pauses during the dry season (Mizuno et al., in prep.). In the case of the phasic ant *O. biroi*, the foraging behavior of workers is driven by social signals emitted by the larvae (Ravary et al., 2006; Ulrich et al., 2016).

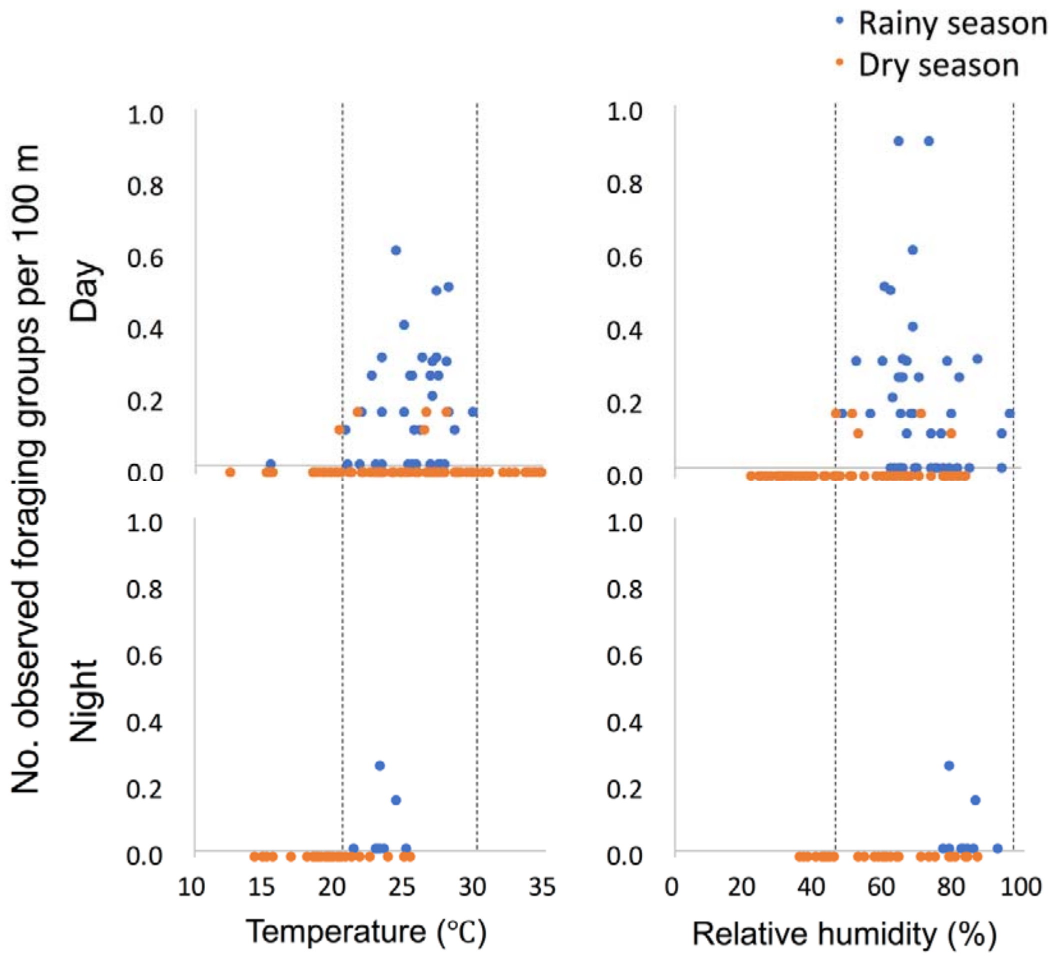

Fig 6. The relationship between foraging activity and temperature (left) and relative humidity (right) of the *C. sulcinodis* complex during the day and at night in each season. Dotted lines indicate threshold value of foraging activity.

If this mechanism works as a stimulus of foraging activity in the *C. sulcinodis* complex, foraging is not activated during the dry season.

The daily foraging schedule of the true army ants varies among species (Gotwald, 1995). In the New World, epigaeic species of *Eciton* forage during the daytime and emigrate at night (Gotwald, 1995). In contrast, the epigaeic species *Neivamyrmex nigrescens* (Cresson, 1872) is a nocturnal forager (Gotwald, 1995). The hypogaeic species *Labidus praedator* (Fr. Smith, 1858) and *Nomamyrmex esenbeckii* (Westwood, 1842) are active during the day and at night (Schneirla, 1971; Sánchez-Peña & Mueller, 2002). Workers of two genera of the Old-World army ants *Dorylus* and *Aenictus* are blind. Workers of *Dorylus nigricans* Illiger, 1802 and *D. wilverthi* Emery, 1899 in Africa are active during the day and at night (Gotwald, 1995). In *Aenictus*, three types of activity pattern are known: diurnal, nocturnal, and 24 h active. An intensive study by Schneirla and Reyes (1966) showed that *A. gracilis* Emery, 1893 is active during the day and at night. Such daily activity is also described with species description and/or faunal survey for several *Aenictus* species in Southeast Asia, e.g., *A. longinodus* Jaitrong and Yamane, 2012, *A. jawadwipa* Jaitrong and Yamane, 2013, *A. pinkaewi* Jaitrong and Yamane, 2013, *A. dentatus* Forel, 1911, *A. parahuonicus* Jaitrong and Yamane, 2011, and *A. hodgsoni* Forel1, 1901 (Malsh et al., 2003; Jaitrong & Yamane, 2011; 2012; 2013). Nocturnal species are also known: *A. doydeei* Jaitrong and Yamane, 2011 and *A. inflatus* Yamane and Hashimoto, 1999 are collected only at night (Yamane & Hashimoto, 1999; Jaitrong & Yamane, 2011), while *A. latifemoratus* Terayama and Yamane, 1989 is found only during the daytime (Jaitrong & Yamane, 2010). The present study indicates that, unlike the majority of *Dorylus* and *Aenictus*, workers of the *C. sulcinodis* complex are almost strictly diurnal foragers.

To date, there has been little quantitative field research on the foraging activity of species in the non-army ant doryline genera. Table 2 shows the daily activities of foraging and emigration in non-army ant dorylines. So far, observations of these behaviors have been reported in eight species from five genera. In all but one case, foraging or emigration activity was observed during the daytime. However, nocturnal activity was not investigated for all species except for in the present paper. Small body size and relatively few foraging groups may make it difficult to observe foraging activity at night. Further investigation of daily foraging activity of non-army doryline ants is necessary to determine whether diurnal foraging is common or not.

Table 2. Daily activity of non-army ant dorylines observed in the field. Activity type (Diurnal (D) or Nocturnal (N)) and observed behavior (Foraging (F) or Emigration (E)) are shown.

Species	Activity type	Observed behavior	Reference
Cerapachys sulcinodis species complex	D	F	Present study
Leptanilloides nomada Donoso, Vieira & Wild, 2006	N	E	Donoso et al., 2006
Lioponera cohici (Wilson, 1957)	D	F	Wilson, 1958
Lioponera near *punctatissima* (Clark, 1924)	D	F	Wilson, 1958
Lioponera potteri (Clark, 1941)	D	F	Clark, 1941
Lioponera (Australian small species)	D (crepuscular)		Clark, 1924
Lioponera (Australian large species)	D		Clark, 1924
Parasyscia desposyne (Wilson, 1959)	D	F	Wilson, 1959
Parasyscia opaca (Emery, 1901)	D	E	Wilson, 1959
Syscia augustae (Wheeler, 1902)	D	E	Borowiec, 2016
Zasphinctus sp.	D	F	Brize, 1984

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