



Colony composition, phasic reproduction, caste dimorphism, and prey preferences of the oriental non-army doryline ant *Yunodorylus eguchii* (Borowiec, 2009) (Hymenoptera: Formicidae: Dorylinae)

R. Mizuno¹ · K. Eguchi² · R. Satria³ · A. V. Dang^{2,4} · V. T. Bui⁵ · L. T. H. Phung⁴ · F. Ito¹

Received: 14 July 2022 / Revised: 11 January 2023 / Accepted: 13 January 2023
© International Union for the Study of Social Insects (IUSSI) 2023

Abstract

The ant subfamily Dorylinae consists of the so-called true army ants and their relatives. The latter (= non-army ant doryline genera) was formally known as cerapachyine ants. Among this non-army ant doryline genera, the genus *Yunodorylus* is part of a clade likely sister related to the Eastern Hemisphere army ants and has remarkable queen morphology (subdichthadiigyne). They are enigmatic ants, however, because of their limited distribution and rareness. Therefore, their behavior and biology have never been reported. In this study, we collected two colony fragments of *Yunodorylus eguchii*, (Borowiec in Zootaxa 2069(1):43–58, 2009) in Vietnam, and their behavior was observed under laboratory conditions. Both colonies were monogynous and included 300 and 450 workers, but their whole colony size was estimated to be much larger. The caste dimorphism was conspicuous; the head width of queens was notably larger than that of workers. The head width of workers was negatively allometric to their head length; the larger workers have a relatively broader head. The colonies showed phasic reproduction under laboratory-rearing conditions. The duration of an entire reproductive cycle was 56 and 63 days. The queens' abdomen became physogastric during the egg-laying phase. Colony emigration was frequently observed but never occurred while the queen was fully physogastric. The colonies predate on various prey arthropods offered in the laboratory, including ant brood, termites, mealworms, and killed cockroaches. Our results reveal unique biological traits in *Yunodorylus* that shed light on the evolution of the army ant adaptive syndrome.

Keywords Army ant adaptive syndrome · Cerapachyinae · Subdichthadiigyne · Ergatoid queen · Cerapachys sexspinus group · Physogastrism

Introduction

The army ants of the subfamily Dorylinae exhibit unique life history characterized by the combination of the following traits: group foraging, nomadism, obligate colony fission, extreme caste dimorphism with the specialized morphology of queens (dichthadiigyne), and specialized predation on social insects (Gotwald 1995, Kronauer 2020). To discuss the evolution of the army ants, biological knowledge of non-army ant doryline genera is necessary. However, it is still scarce because of its difficulty in discovery and biased distribution toward the tropics. To consider the biology of non-army ants in the context of army ant evolution, a comparison of the following life-history traits among the non-army doryline ants is important: colony size, degree of caste dimorphism and worker polymorphism, presence or

✉ R. Mizuno
m.riou112@gmail.com

¹ Faculty of Agriculture, Kagawa University, Ikenobe, Miki 761-0795, Japan

² Department of Biological Sciences, Graduate School of Science, Tokyo Metropolitan University, Hachioji 192-0397, Japan

³ Department of Biology, Faculty of Mathematics and Natural Sciences, Universitas Negeri Padang, Padang, Indonesia

⁴ Department of Soil Ecology, Institute of Ecology and Biological Resources, Vietnam Academy of Science and Technology, 18, Hoang Quoc Viet Rd., Cau Giay District, Hanoi, Vietnam

⁵ Vietnam National Museum of Nature, 18 Hoang Quoc Viet Rd, Cau Giay District, Hanoi, Vietnam

absence of phasic reproduction, foraging behavior and prey specialization (Ito et al. 2018, Mizuno et al. 2021). Among the non-army doryline ants, three genera (CCY clade; *Cerapachys*, *Chrysapace*, *Yunodorylus*) are likely closely related to the army ants in the Eastern Hemisphere (= Old World) (*Aenictus*, *Aenictogiton*, *Dorylus*) (Borowiec 2019). The authors have investigated the biology of the CCY clade as an important group for discussing the evolution of army ants in the Eastern Hemisphere (Mizuno et al. 2019, 2021).

The genus *Yunodorylus*, a member of the CCY clade, consists of four described species and occurs from mainland Southeast Asia to Borneo (Xu 2000, Borowiec 2009, 2016). Their workers have unique morphological characteristics that resemble the army ant genus *Dorylus*. Indeed, unlike other non-army doryline ants, the workers of *Yunodorylus* have no constriction between abdominal segments 3 and 4 as in the workers of *Dorylus* (Bolton 1990). Because of such striking morphological characteristics, this genus was thought to be the closest relative of the army ant genus *Dorylus* (Xu 2000). Recently, Eguchi et al. (2016) and Satria et al. (2018) reported that the queen of two species (*Y. eguchii* and *Y. doryloides*) show specialized morphology, namely subdichthadiigyne. Subdichthadiigyne is defined as partially possessing the morphological characteristics of army ants' dichthadiigynes, and is regarded as the intermediate condition between the "normal" ergatoid (= permanently wingless) queen and the dichthadiigyne (Borowiec 2016, Eguchi et al. 2016). Therefore, their ecological and behavioral characteristics are highly interesting, and indispensable for discussing the evolution of the army ant syndrome. However, biological information on *Yunodorylus* is scarce because of their rareness and hypogaecic lifestyle.

Eguchi et al. (2016) described the queen morphology of *Y. eguchii* but their behavior was almost unknown. In this study, we reared and observed two colonies of *Y. eguchii* which were also used for Eguchi et al. (2016). As a result of the observation, we report their large colony size, conspicuous caste dimorphism and worker polymorphism, the existence of phasic reproduction, and wide prey spectrum. From these biological traits, we argue that *Y. eguchii* is at a higher level in the evolution of the army ant adaptive syndrome compare to that in CCY genera *Cerapachys sulcinodis* species complex (Mizuno et al. 2021).

Materials and methods

Ants

Two colonies of *Y. eguchii*, colony A = Eg19ix15-01 and colony B = Eg20ix15-01 (Eguchi et al. 2016), were collected in lowland evergreen forest fragments of Lo Go Xa Mat National Park, Tay Ninh Province, Vietnam in September

2015. Collecting the entire colonies was impossible because of their hypogaecic nesting habit (Eguchi et al. 2016). The queen-right colony fragment including a single queen, hundreds of workers, and brood were collected for each colony nesting in the soil wall of termite mounds.

Caste dimorphism, worker polymorphism, and observation of workers' reproductive system

The maximum head width and length of both queens and 211 workers (randomly chosen from colony A) were measured. The head of a queen (colony A) and the workers was mounted on cardboard and photographed using a digital camera (Shimadzu moticam 2000) connected to a binocular microscope (Olympus SZX12), and measured based on the photographs using ImageJ software version 1.52 k (open source: <https://imagej.nih.gov/ij/>). Head width and length of the queen of colony B were measured from the specimen photo in Eguchi et al. (2016). The allometric relationship between workers' head width and length was assessed by standardized major axis regression (SMA) with R package "smart" version 3.4–8 (Warton et al. 2012). First, the correlation between head width and length was assessed. Then, their regression line (slope and y-intercept) was computed. The slope of the SMA regression line (= allometric coefficient) was compared with that of the *Cerapachys sulcinodis* species complex (Mizuno et al. 2021).

After the rearing of colony B, 13 workers were dissected to examine the ovariole numbers and the presence or absence of a spermatheca. The queens were not dissected and used in Eguchi et al. (2016).

Colony rearing under laboratory conditions

The colonies were reared in polystyrene boxes with plaster floors for keeping the humidity high. Nesting chambers were excavated in the plaster floors, and the top of the chambers was covered with glass plates (see "Observation of emigrations" for the detail of the layout of artificial nests). The colonies were placed under constant temperature (25°C) and day length (12L:12D).

The approximate number of each developmental stage of brood and the number of foraging workers were counted in both colonies almost daily. The duration of three developmental stages of brood was presumed from the daily change in brood composition as follows: egg stage, from the first egg to the hatching of the first larva; larval stage, from the first larva to the first cocoon; and the cocoon stage, from the first cocoon to the emergence of the first callow worker. The abdomen of the queens was swollen (physogastry), possibly with ovary development. The degree of physogastry was evaluated and recorded as follows: PL (physogastrism level) 0, the abdomen is fully contracted (Fig. 1a); PL1,



Fig. 1 Aqueen of *Yunodorylus eguchii* with contracted (a) and enlarged abdomen with exposure intersegmental membrane (b, shown by an arrow). a colony A, 19 Nov. 2015, the image was taken under anesthesia by CO₂. b colony B, 21 Dec. 2015

the abdomen is swollen but the intersegmental membrane between tergites and sternites is not visible; PL2, the abdomen is fully swollen, and the intersegmental membrane is visible in lateral view (Fig. 1b). The observations were continued for 142 days in colony A (6 October 2015 to 24 February 2016, when the queen died or was killed) and 146 days in colony B (8 October 2015 to 1 March 2016, until the queen was fixed for morphological description). Both colonies were reared under orphaned conditions after the queens died or were removed (duration of orphaned conditions: colony A = 38 days, colony B = 44 days).

Observations of prey preferences

Diverse arthropods, including ant brood and termites, were provided to the colonies. We placed a prey on the floor of the foraging arena and observed whether it was consumed or not within 24 h. In the case of prey with a hard exoskeleton (e.g., cockroaches, mealworms), whether *Y. eguchii*

accepted the prey or not was determined with confirmation of consumption of soft tissue. Due to the small body size of ant workers, large prey items were given as fragments or small individuals were chosen. If the prey was not killed or killed but intact after 24 h, we concluded that the prey was not accepted. The amount of prey given at once was coordinated to avoid overfeeding, which may affect prey acceptance. For example, a relatively large ant brood (more than 3 mm in body length, e.g., *Camponotus*) was given as one to three items at once, whereas smaller ant brood (less than 3 mm, e.g., *Monomorium*) was given up to 120 individuals together. Because the colonies' foraging activity was considerably changed with their colony reproductive cycle and condition (see Results), the examined prey was given when at least one worker actively foraged. To know their relative preference for each type of prey, four prey were given at once (cafeteria experiment): a mealworm (body length 10 mm); termites (4 mm, seven individuals); larvae of *Stigmatomma* sp. (5 mm, three individuals); and larvae of *Camponotus* (*Tanaemyrmex*) sp. (6 mm, two individuals). The prey items were placed on plastic dishes (35 × 35 × 3 mm) 10 cm away from the nest entrance. The cafeteria experiment was done once in colony A.

Observation of emigrations

To observe nest emigration, three types of artificial nests were used (Fig. 2). For Nest 2 and 3, multiple nesting chambers were provided. The chamber occupied by the colony was recorded every day. If the colony occupied a different chamber from one day before or stayed outside the chambers, it was regarded as an occurrence of nest emigration. The occupied duration (days) of each nesting chamber was calculated.

Colony A was reared in Nest 1 for 66 days (6 October 2015 to 9 December), then moved to Nest 3 and was reared for 76 days. Colony B was reared in Nest 2 for 89 days (8 October 2015 to 4 January 2016), then moved to Nest 3 for 57 days. Only for colony B in Nest 3, a small plaster floored nest box (chamber 5, 35 × 35 × 15 mm) was offered additionally (13 February 2016).

Results

Colony composition, caste dimorphism, and worker polymorphism

The two collected colony fragments each included a single queen, with approximately 300 and 450 workers. Observations in the field indicated that their true colony size was estimated as more than several thousand.

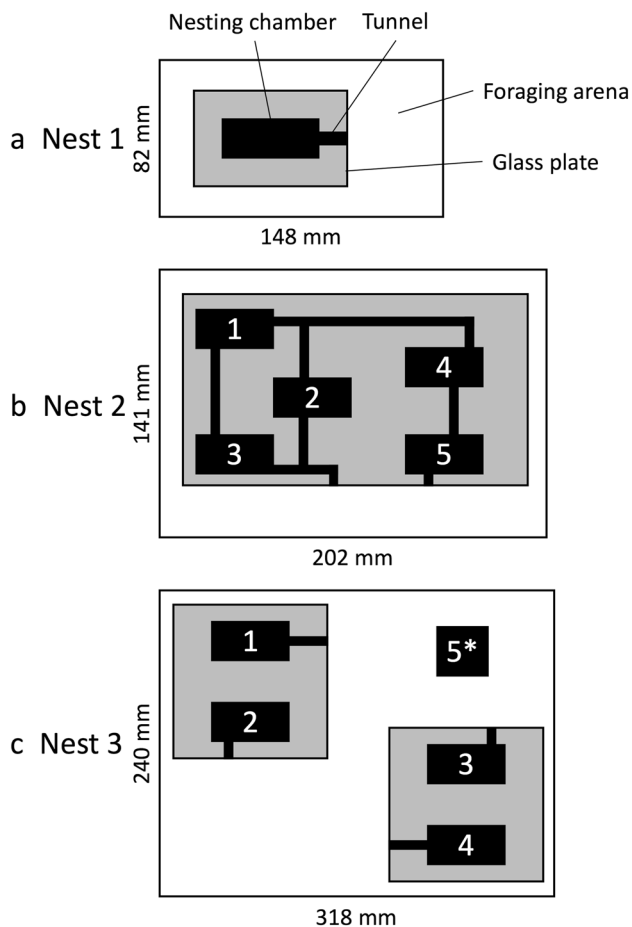


Fig. 2 Spatial structure of artificial nests used in this study. **a** Nest 1; **b** Nest 2; **c** Nest 3. *The chamber 5 consists of a small plastic box with a plaster floor was placed on the foraging arena of nest 3

The head width distribution of queens and workers is shown in Fig. 3. The head width of the two queens was 0.826 mm and 0.876 mm for colony A and B, respectively, and the average worker head width was $0.53 \pm \text{SD } 0.05$ mm ($n = 211$). The largest worker's head width (0.657 mm)

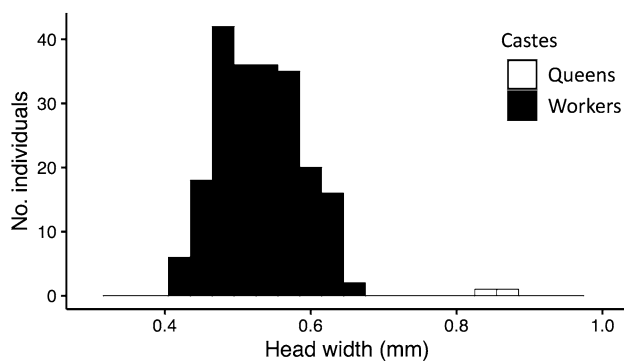


Fig. 3 Head width distribution of queens and workers of *Yunodorylus eguchii*

was 1.57 times larger than that of the smallest worker (0.418 mm). Head width distribution of workers did not fit the normal distribution ($W = 0.98$, $p = 0.01$, Shapiro–Wilk normality test). The average head width of the two queens was 1.59 times larger than that of the average head width of workers and was significantly different ($W = 0$, $p = 0.01$, Wilcoxon rank-sum test).

The allometric relationship between head width and length is shown in Fig. 4. A significant correlation was observed in workers' head width and length ($r^2 = 0.83$, $p < 0.01$). The slope of the SMA regression line (= allometric coefficient) was 0.738, and the y-intercept was -0.038 . The allometric coefficient was significantly smaller than 1 ($r = -0.59$, $df = 210$, $p < 0.01$); therefore, the relationship is negatively allometric. The largest worker has a relatively wider head (HW (0.657 mm)/HL (0.642 mm) = 1.02), while the smallest worker has a more slender head (HW (0.418 mm)/HL (0.499 mm) = 0.84). The dots of the two queens appear above the regression line of workers (Fig. 4); thus, queens have more slender heads.

All dissected workers had two ovarioles (1–1) without a spermatheca ($n = 13$).

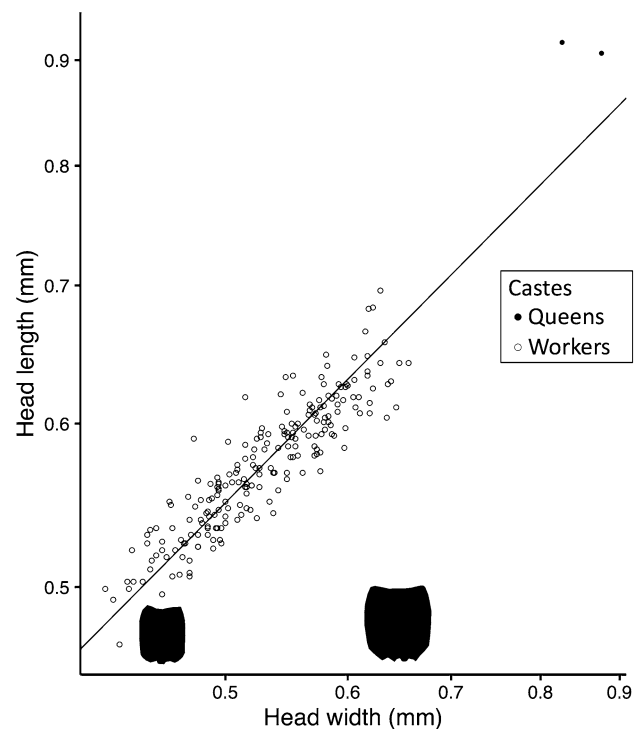


Fig. 4 Relationship between head width and head length in queens and workers of *Yunodorylus eguchii*. Both axis are a logarithmic scale. Allometric relationship shown by a solid line was computed only in workers. Head shape of a large (HW = 0.64 mm) and a small (HW = 0.42 mm) worker are shown

Phasic reproductive cycle under laboratory conditions

The successive change in brood composition and queen physogastry of colony A is shown in Fig. 5a. The queen's abdomen became physogastric on 13 October 2015, and then the first egg pile consisting of 10 eggs appeared on 16 October. Hereafter, the observation results are described with the number of days from the start of egg-laying. The number of eggs increased up to 150 on the 13th day and apparently did not increase after that. The first 30 larvae hatched on the 19th day. All the eggs hatched before the 30th day; 108 larvae existed at this time. The workers dug the plaster inside the nest chamber and attached the plaster powder on the larval bodies on the 42nd day, probably for the assistance of cocoon spinning. Then the first five cocoons appeared on the 43rd day. However, the number of increased cocoons was not equal to the decrease in the larval number, possibly because of failure to pupate. The cocoons increased to 35 on the 46th day, but only two survived until the 57th day. The queen started to be physogastric from the 52nd day, but the egg pile was not observed until the 63rd day. The egg number increased to 90 on the 67th day but eggs disappeared on the 79th day, and no larvae hatched from these eggs. Two workers emerged from the cocoons on the 70th and 71st day. The next egg-laying was observed from the 93rd day to the 102th day. Up to 80 eggs appeared but the number decreased and they disappeared on the 111th day. No larvae hatched. Almost no workers foraged after the 116th day. The provided prey was never consumed. The queen died or was killed on the 132nd day, and the queen's dead body was fragmented. Although the workers were reared under this orphaned condition, all died before the 170th day. The duration of each developmental stage (egg, larva, and cocoon) were 19, 24, 27 days, respectively. The entire colony cycle

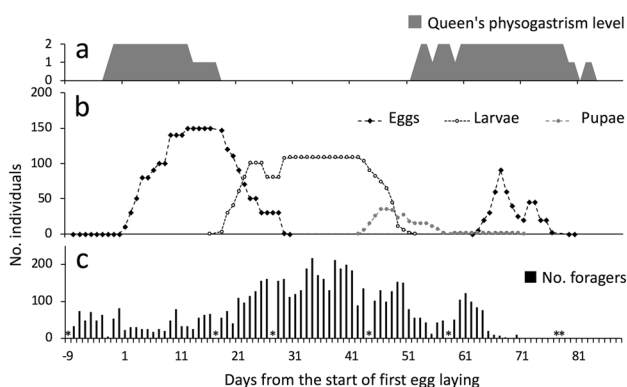


Fig. 5 Successive change in queen physogastrism (a), brood composition (b), and forager number (c) in colony A. * The colony was not observed for these seven days

(the duration between the first egg-laying to the next egg-laying) was 63 days.

Colony B also showed the same phasic reproductive cycle once, but the second batch of eggs never hatched and disappeared, possibly due to cannibalism by adults. The duration of each developmental stage (egg, larva, and cocoon) were 16, 26, 28 days, respectively. The entire colony cycle was 56 days.

The workers did not lay eggs under the orphaned condition in both colonies.

Foraging

The number of foragers was relatively high: sometimes almost half of the entire colony stayed outside the nest. The foraging workers walked along the trail of other workers or less frequently walked alone. When foraging workers encountered prey (termites or mealworms), they grabbed it, bent their abdomen, and stung the prey (Fig. 6a, b). When a worker started an attack, surrounding workers converged and joined the attack together. During the attack, nestmates were recruited from the nest and joined the attack or prey retrieval. Nestmate recruitment could not be observed in detail and we did not notice any conspicuous trail-laying behavior. Small and less moveable prey such as small ant brood were usually grasped by the mandibles and dragged (Fig. 6c).

The number of foragers matched the number of larvae in the colony (Fig. 5b). However, many workers still foraged on the days without larvae (a maximum of 122 workers foraged during the cocoon phase, on the 61st day).

Prey preferences

The majority of ant brood of 16 species belonging to Amblyoponinae, Formicinae, Myrmicinae, and Ponerinae were accepted as prey (Table 1). Exceptionally, larvae of *Temnothorax congruus* were completely ignored by colony B.

Most of the non-ant prey including two species of termites were also accepted (Table 2). Small mealworms were killed and fed on. The fragments of large mealworms were also accepted. The prey items with less or no movability (e.g., dermapteran eggs) were easily consumed. On the other hand, larger and/or agile prey (e.g., cockroaches, crickets, springtails) was not killed by *Y. eguchii* but cockroaches and crickets were accepted after being artificially immobilized. Dipteran larvae and pupae, Geophilomorpha centipedes and isopods were ignored.

The prey items were carried to the nest chamber or consumed at the foraging arena. The larvae of *Y. eguchii* were placed on the prey items and fed on them. Feeding of the larvae was also observed outside the nest entrance ($n = 5$), especially when the prey was large and difficult to retrieve.

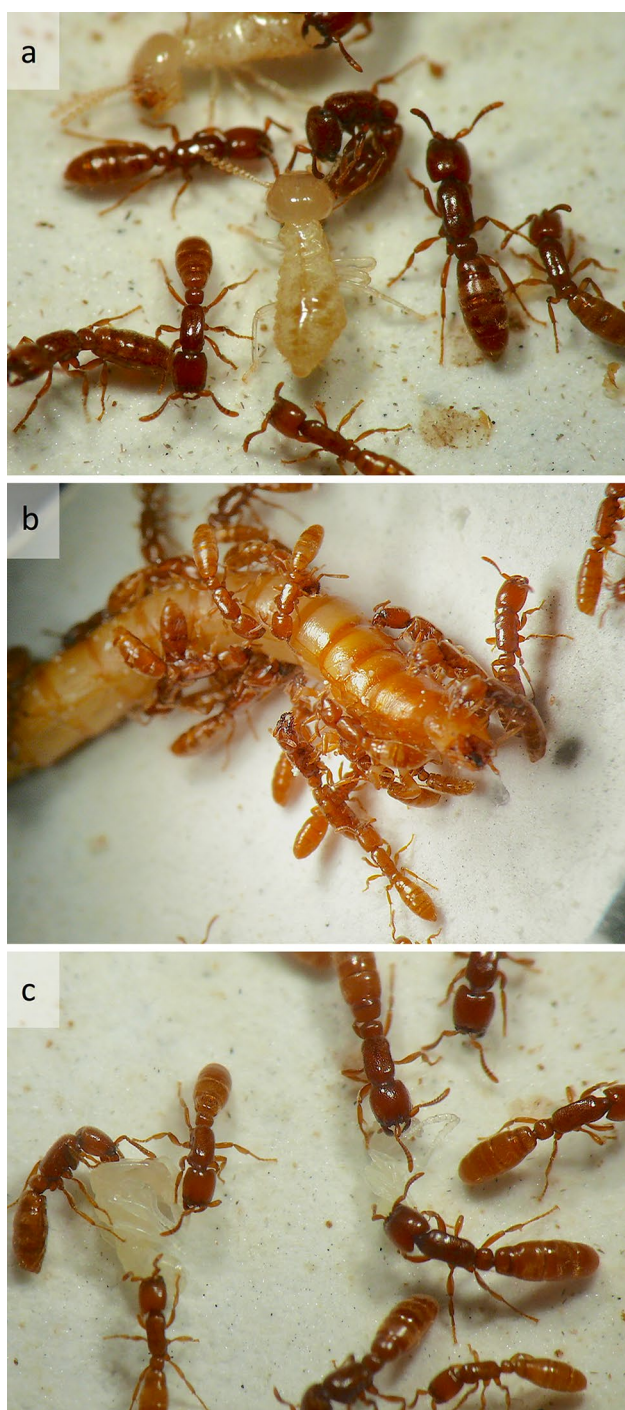


Fig. 6 Foragers of *Yunodorylus eguchii* attacking termites (*Reticulitermes speratus*, **a**), a mealworm (**b**), and ant pupae (*Pheidole megacephala*, **c**)

The accepted ant larvae had been completely consumed within 24 h; long-term storage was never observed. Non-accepted preys decayed on the spot in the foraging arena. Larger prey-like mealworms were consumed for more than 24 h.

When the cafeteria experiment was done, 104 workers actively foraged. After 20 min, approximately 10 workers were attracted to each prey. The mealworm and one termite were already killed at this time. Two hours later, *Y. eguchii* workers started to eat the mealworm and ant larvae, but still, four termites were alive. The next day (24 h later), all the given ant larvae were completely consumed, but the remnants of mealworms and termites remained at the given site. Thus, they consumed all the given prey, of which the ant larvae were eaten first.

Colony emigration under laboratory conditions

Table 3 shows the colony emigrations observed in the laboratory colonies. Emigration was observed once in colony A and seven times in colony B. Nesting duration (the days between an occurrence of emigration to the subsequent emigration) varied from one to 74 days. The emigration was observed in both the larval phase (3 times) and the cocoon-egg phase (4 times). Thus, the brood composition of the colony is not related to their emigration. In contrast, emigration was never observed while the queen was fully physogastric.

Discussion

Queen morphological specialization and fecundity

Colony fragments of *Y. eguchii* were large and included a single morphologically specialized queen (subdichthadiigyne). The queen ovariole number could not be assessed in this study, but queen's ovariole numbers should be higher than that of the *C. sulcinodis* species complex (approximate 40/queen, Mizuno et al. 2021) because, the queen of *Y. eguchii* shows strongly specialized morphology, including physogastry. In fact, the number of eggs laid per queen during the single egg-laying phase was higher in *Y. eguchii* (up to 200 eggs per queen) than that of the *C. sulcinodis* complex (20–100 eggs per queen) (Mizuno et al. 2021). Overall, the queen morphological specialization and fecundity of *Y. eguchii* is higher than that of the *C. sulcinodis* complex. Such strong morphological specialization may be related to their monogynous social structure. However, we have no strong evidence to show their monogyny because of the difficulty of completing colony excavation. If *Y. eguchii* is truly monogynous, the social structure of *Y. eguchii* might be similar to that of the army ants and different from some other non-army ant dorylines that are known as polygynous (*C. sulcinodis* complex, Mizuno et al. 2021; *Zasphinctus steinheili*, Buschinger et al. 1989). Subdichthadiigynes are known in four non-army ant genera: *Acanthostichus*, *Leptanilloides*, *Ooceraea*, and *Zasphinctus* (Borowiec 2016). These four genera also include species with alate queens or

Table 1 List of provided ant brood and its acceptance rate by *Yunodorylus eguchii*

Subfamily	Species	Stage ^a	Approx. body length range (mm)	Colony A		Colony B		Acceptance (%)
				No. given indiv	No. accepted indiv	No. given indiv	No. accepted indiv	
Amblyoponinae	<i>Stigmatomma</i> sp.	L	2–3	2	2	2	2	100
Formicinae	<i>Camponotus vitosus</i>	L	2–3	–	–	33	33	100
	<i>C. kiusiuensis</i>	L	2.5	30	30	30	30	100
	<i>C. devestivus</i>	L	1.5–5	2	2	25	25	100
	<i>Camponotus (Tanaemyrmex)</i> sp.	L	2.5–5	8	8	8	8	100
	<i>Lasius hayasi</i>	C	4–5	2	2	2	2	100
Myrmicinae	<i>Aphaenogaster famelica</i>	L	2.5	–	–	28	28	100
		C	4	–	–	5	5	100
		PP	5	1	1	–	–	100
	<i>Crematogaster osakensis</i>	P	5	5	5	–	–	100
		L	2	17	17	–	–	100
	<i>Monomorium intrudens</i>	P	3	1	1	–	–	100
		L	1–2	210	210	100	100	100
	<i>Myrmica kotokui</i>	P	2	10	10	–	–	100
		L	2	–	–	7	7	100
	<i>Pheidole megacephala</i>	P	2–3	24	24	20	20	100
	<i>P. noda</i>	L	1.5–3	14	14	14	14	100
		P	3	10	10	10	10	100
	<i>Temnothorax congruus</i>	L	2	–	–	53	0	0
<i>Tetramorium bicarinatum</i>	L	2–4	–	–	6	6	100	
	PP	4	–	–	5	5	100	
	P	4	–	–	2	2	100	
Ponerinae	<i>Odontomachus simillimus</i>	L	2.5	–	–	1	1	100
	<i>Diacamma</i> sp.	L	2–3	4	4	–	–	100

^aL larvae, PP prepupae, P pupae

normal ergatoid queens having less specialized morphology (*Acanthostichus*, alate queen; *Leptanilloides* and *Ooeceraea*, ergatoid queen; *Zasphinctus*, alate and ergatoid queen; Borowiec 2016). In contrast, two species of *Yunodorylus* have a subdichthadiigyne (*Y. eguchii*, Eguchi et al. 2016; *Y. doryloides*, Satria et al. 2018), and there is no report of alate or “normal” ergatoid queens in this genus so far.

Worker polymorphism

Among the doryline army ant genera, *Dorylus*, *Eciton*, and *Labidus* show an extreme worker polymorphism: the body length of the largest worker is three times larger than that of the smallest worker (Kronauer 2020). The workers of *Y. eguchii* are moderately polymorphic; the range of worker head width of *Y. eguchii* was 1.58 (max HW/min HW). This range of worker polymorphism is narrower than in polymorphic army ants but wider than in the monomorphic army ant *Aenictus* (Table 4). Among the genus *Aenictus*, *A. inflatus*

shows a relatively wide range of worker body size (max HW/min HW = 1.3, Yamane and Hashimoto 1999), but is still inconspicuous compared to that of *Y. eguchii*.

Unlike these polymorphic army ants, almost all non-army ant dorylines are considered to have monomorphic workers except for a few genera (Table 4); Borowiec (2016) describes “monomorphic to moderately polymorphic” only in *Yunodorylus* and *Cerapachys* whereas 17 other genera are “monomorphic”. Allometric difference in worker body shape is suggested in some non-army ant species (e.g. *Parasyscia polynikes*, Wilson 1959; *Simopone grandidieri*, Bolton and Fisher 2012), but there is no quantitative analysis except for the *Cerapachys sulcinodis* complex (Mizuno et al. 2021). Based on the range of head width, worker polymorphism of *Y. eguchii* is more conspicuous than in other non-army ant dorylines. The allometric coefficient observed between head width and length of *Y. eguchii* workers (0.738) is significantly lower than that of *C. sulcinodis* “S-type” (0.970, Mizuno et al. 2021,

Table 2 List of provided non-ant prey and its acceptance rate by *Yunodorylus eguchii*

Order	Family	Species	Stage	Approx. body length range (mm)	Colony A		Colony B		Acceptance (%)
					No. given ^a	No. accepted ¹	No. given ^a	No. accepted ^a	
Blattodea	Termitidae	<i>Hodotermopsis sjostedti</i>	Young indiv	2–4	3	3	–	–	100
			Worker	2–5	151	144	83	83	97
			Solider	4	3	3	1	1	100
	Blattidae	<i>Shelfordella lateralis</i>	Young indiv	8	2	2	–	–	100
			Parted adult	6–10	4	4	10	9	93
Coleoptera	Tanebrionidae	<i>Tanebrio molitor</i>	Small larva	5–11	76	76	57	54	98
			Pupa	17	1	1	–	–	100
			Parted larva	5	2	2	6	6	100
Diptera	Drosophilidae	<i>Drosophila melanogaster</i>	Larva	3–4	5	0	–	–	0
			Pupa	4	5	0	–	–	0
Orthoptera	Gryllidae	<i>Gryllus bimaculatus</i>	Nymph	2–3	6	0	–	–	0
			Killed nymph	2–3	2	2	–	–	100
Archaeognatha	Machilidae	Unidentified	Adult	20	1	1	–	–	100
Collembola	Entomobryidae	Unidentified	Adult	1	5	0	–	–	0
Dermaptera	Unidentified		Egg	1	5	5	–	–	100
Lithobiomorpha	Unidentified		Adult	10	–	–	1	1	100
Geophilomorpha	Unidentified		Adult	60	1	0	1	0	0
Isopoda	Porcellionidae	Unidentified	Nymph	4	1	0	–	–	0

– not examined

^aNo. of individuals or parted fragments**Table 3** Details of the colony emigration observed in the laboratory

Colony	#Relocation (#artificial nest)	Observed date	#Nesting chamber		Nesting duration at origin chamber (days)	Brood composition (PL) ^a
			Origin	Destination		
A	1 (3)	13 Dec., 2015	1	2	2	2C (1)
B	1 (2)	13 Oct., 2015	1	4	5	None (0)
B	2 (2)	26 Dec., 2015	4	Outside	74	ca. 80L (0)
B	3 (2)	27 Dec., 2015	Outside	2	1	ca. 80L (0)
B	4 (2)	4 Jan., 2016	2	Outside	8	ca. 110L (0)
B	5 (3)	13 Feb., 2016	4	Outside	39	ca. 100E (0)
B	6 (3)	14 Feb., 2016	Outside	5	1	ca. 40E (0)
B	7 (3)	15 Feb., 2016	5	1	1	ca. 40E (0)

^aE eggs, L larvae, C cocoons, PL queen's physogastrism level

Table 4 Range of worker body size in army and non-army doryline ants

Genus	Species	Range of head width (mm)	Range ratio (Largest HW/Smallest HW)	References
Army ants				
<i>Aenictus</i>	<i>A. laeviceps</i>	0.70–0.82	1.17	Jaitrong and Yamane 2011
	<i>A. inflatus</i>	0.38–0.50	1.31	Yamane and Hashimoto 1999
<i>Dorylus</i>	<i>D. orientalis</i>	0.48–1.41	2.94	Eguchi et al. 2014
	<i>D. laevigatus</i>	0.48–1.98	4.12	Berghoff et al. 2002
<i>Eciton</i>	<i>E. burchellii</i>	ca. 0.7–3.5 ^a	5.00	Franks 1985
Non-army ants				
<i>Ooceraea</i>	<i>O. alii</i>	0.37–0.39	1.05	Bharti and Akbar 2013
	<i>O. quadridentata</i>	0.70–0.75	1.07	Yamada et al. 2018
<i>Syscia</i>	<i>Sy. reticularis</i>	0.46–0.50	1.09	Jaitrong et al. 2020
<i>Lioponera</i>	<i>L. anokha</i>	0.60–0.63	1.05	Bharti and Akbar 2013
	<i>L. nayana</i>	0.48–0.51	1.06	Bharti and Akbar 2013
	<i>L. daikoku</i>	0.44–0.51	1.16	Idogawa and Dobata 2018
<i>Zasphectus</i>	<i>Z. obamai</i>	0.44–0.47	1.06	Hita Garcia et al. 2017
	<i>Z. sarowiwai</i>	0.64–0.77	1.20	Hita Garcia et al. 2017
<i>Chrysapace</i>	<i>Ch. costatus</i>	0.90–0.97	1.08	Yamada et al. 2019
	<i>Ch. sauteri</i>	0.87–1.08	1.24	Yamada et al. 2019
<i>Parasyscia</i>	<i>P. schoedli</i>	0.44–0.46	1.05	Bharti and Akbar 2013
	<i>P. seema</i>	0.52–0.56	1.08	Bharti and Akbar 2013
	<i>P. lindrothi</i>	0.69–0.75	1.08	Wilson 1959
	<i>P. polynikes</i>	0.52–0.66	1.27	Wilson 1959
	<i>P. zimmermani</i>	0.66–0.87	1.32	Wilson 1959
<i>Cerapachys</i>	<i>Ce. sulcinodis</i> "L-type"	0.83–1.12	1.35	Mizuno et al. 2021
	<i>Ce. sulcinodis</i> "S-type"	0.76–1.13	1.49	Mizuno et al. 2021
<i>Tanipone</i>	<i>T. hirsuta</i>	0.86–1.02	1.19	Bolton and Fisher 2012
	<i>T. maculata</i>	0.53–0.75	1.42	Bolton and Fisher 2012
<i>Vicinopone</i>	<i>V. conciliatrix</i>	0.32–0.42	1.31	Bolton and Fisher 2012
<i>Simopone</i>	<i>Si. wilburi</i>	0.64–0.75	1.17	Bolton and Fisher 2012
	<i>Si. trita</i>	1.14–1.46	1.28	Bolton and Fisher 2012
	<i>Si. grandidieri</i>	0.53–0.92	1.74	Bolton and Fisher 2012
<i>Yunodorylus</i>	<i>Y. eguchii</i>	0.50–0.76	1.52	Borowiec 2009
	<i>Y. eguchii</i>	0.42–0.66	1.57	Present study
	<i>Y. paradoxus</i>	0.42–0.67	1.60	Borowiec 2009
	<i>Y. sexspinus</i>	0.43–0.73	1.70	Xu 2000

The species descriptions with relatively large sample sizes ($n > 5$) are cited

^aEstimated from the figure in the referred article because the actual measuring value is not provided

$p < 0.01$) but not significantly different from that of *C. sulcinodis* "L-type" (0.758, Mizuno et al. 2021, $p = 0.30$). Furthermore, the head width range of *Y. eguchii* (max HW/min HW = 1.57) is wider than that of the *C. sulcinodis* complex (max HW/min HW = 1.41 in *C. sulcinodis* "L-type", 1.48 in *C. sulcinodis* "S-type"). The maximum head width of *Y. eguchii* described by Borowiec (2009) is wider than that we report in the present study, suggesting further body size range variations depending on the colony and location. The head width range of congeneric

species *Y. sexspinus* and *Y. paradoxus* is wider than that of *Y. eguchii* (Table 4, Xu 2000, Borowiec 2009), suggesting that worker polymorphism is a common characteristic in this genus.

Foraging behavior

Foragers' behavior suggests that trail pheromones and volatile pheromones attract the foragers nearby, although it is still unknown which exocrine glands are used for emitting

these pheromones. In the field, the foragers walk along underground trails in tubular cavities (Mizuno pers. obs.), also suggesting the existence of trail pheromones. This pheromone communication is also used in the spontaneous mass raids of army ants (Chadab and Rettenmeyer 1975, Topoff and Miranda 1975). However, our observations are not enough to conclude that *Y. eguchii* perform mass raids like the army ants. The foraging system and chemical communication of *Y. eguchii* should be studied in the future.

Predation on general prey

Brood of the majority of ant species was accepted as prey, suggesting that no preference for specific ant species exists. An exception is larvae of *T. congruus*: although workers of *Y. eguchii* actively foraged in the foraging arena, they did not retrieve the larvae of *T. congruus*. The reason is unknown. The larvae of *T. congruus* were accepted and consumed by a colony of non-army ant doryline genus *Cerapachys* (Mizuno unpublished). The laboratory colonies accepted not only the ant brood or termites but also other general prey; therefore, we concluded that *Y. eguchii* is a generalist predator. This is further supported by the observation that the workers attacked mealworms, termites, and small cockroaches without hesitation, although the ant brood of two species was preferentially consumed in the cafeteria experiment. However, the long-term colony rearing was not successful due to the high mortality of pupae and the low hatching rate of the second batch of eggs, although the reason for these phenomena is unknown. One of the possibilities is that the food resources given to us were not suitable for the ants. Unlike other non-army doryline ants with specialized ant predation, completely ignore the given non-ant prey (Ito et al. 2018), *Y. eguchii* feed on the given general prey. Therefore, there is no doubt that *Y. eguchii* is a generalist predator. However, termites might be a possible main prey because *Y. eguchii* colonies were found in a soil wall of termite mounds (the two examined colonies in the present study, Eguchi et al. 2016; two orphan bivouacs in Vietnam and Thailand, Eguchi pers. obs., Mizuno pers. obs.). The wide prey spectrum observed in *Y. eguchii* and the *C. sulcinodis* complex (Mizuno et al. 2021) is in marked contrast to other non-army doryline ants that are specialized predators of other ants (e.g., Hölldobler 1982, Buschinger et al. 1989, Idogawa and Dobata 2018, Ito et al. 2018). This contrast gives us a preconception that general predation had occurred in species with relatively larger colony sizes such as *Y. eguchii* and the *C. sulcinodis* complex. However, other *Cerapachys* spp. with smaller colony sizes also actively predate on mealworms and cockroaches under laboratory conditions (Mizuno et al. in prep.), and many of the army ants with extremely large colony sizes still show the specialized predation on ants (e.g., Hirose

et al. 2000, Hoenle et al. 2019). For these reasons, the prey spectrum extension and the colony size enlargement are not always associated with each other.

Emigration

Frequent occurrence of colony emigration suggests a nomadic lifestyle similar to true army ants. The frequency of emigration was highly different between the two colonies and was observed in both the larval phase and the cocoon-egg phase; therefore, unlike the epigaeic army ants (e.g., *Eciton burchellii*, Schneirla 1971), colony reproductive cycle might not be related to their emigration. However, the emigrations were not observed when the queens were fully physogastric. The African driver ant *Dorylus molestus*, which shows non-phasic reproduction, also emigrates irregularly (Schöning et al. 2005). The interval of emigration is three to 111 days, and queens stop ovarian development in a short term during an emigration (Schöning et al. 2005). The queens of *D. molestus* are unable to walk while their abdomen is physogastric (Schöning et al. 2005). The queens of *Y. eguchii* could walk when they were fully physogastric, but the physogastric abdomen with exposed intersegmental membranes may easily be damaged, particularly in underground cavities. Thus, the colonies of *Y. eguchii* may not emigrate at the peak of the queen's ovarian development.

Conclusion

Compared to other non-army ant dorylines reported so far (Table 5), our results indicate that *Y. eguchii* represents a higher level in the evolution of the army ant adaptive syndrome. Mizuno et al. (2021) considered that the *Cerapachys sulcinodis* complex has an atypical biology that is reminiscent of the army ant adaptive syndrome. In terms of colony composition, queen morphology and worker polymorphism, *Y. eguchii* seems to be more army-ant-like than the *C. sulcinodis* complex. Among other non-army ant doryline genera, *Leptanilloides* has a subdichthadiigyne (Borowiec 2016) and is likely closely related to the army ants in the Western Hemisphere (=New World, Borowiec 2019). Especially, *L. erinys* shares several biological features with *Y. eguchii*: monogyny (Borowiec and Longino 2011), possibly phasic reproduction (Brandão et al. 1999a, 1999b; Donoso et al. 2006; Borowiec and Longino 2011), and hypogaecic life (Brandão et al. 1999b). A comparison of the biology of non-army ant dorylines between the Eastern and Western Hemispheres will provide an important insight into the convergent evolution of the two army ant lineages.

Table 5 Comparison of biological features in army and non-army ant dorylines

Species	<i>Lioponera dai-koku</i> ^a	<i>Lioponera suscitata</i> ^b	<i>Zasphectus steinheili</i> ^c	<i>Cerapachys sulcinodis</i> species complex ^d	<i>Yunodorylus eguchii</i> ^e	Army ants (in general)
No. workers per colony	< 44	< 40	80–400	100–1850	Several thousand?	50,000 ^f –22,000,000 ^g
No. queens per colony	1–5	1	9–20	1–19	1	1 ^h
Reproductive cycle	Non-phasic	Non-phasic	Phasic	Phasic	Phasic	Phasic or non-phasic ^h
Queen morphology	Alate	Alate	Ergatoid	Ergatoid	Subdichthadi-igyne	Dichthadiigyne ^h
No. ovarioles per queen	4	4	4–11	32–52	?	600 ⁱ –2,400 ^j
No. ovarioles per worker	2	2	2	2	2	2–6 ^k
Degree of caste dimorphism	Weak	Weak	Relatively weak	Medium	Relatively strong	Strong
Degree of worker polymorphism	Low	Low	?	Low to medium	Medium	Low to high

^aIlogawa and Dobata 2018; ^bIto et al. 2018; ^cBuschinger et al. 1989; ^dMizuno et al. 2021; ^ePresent study; ^fSchneirla and Reyes, 1966, *Aenictus laeviceps*; ^gRaignier and Boven 1955, *Dorylus wilverthi*; ^hKronauer 2020; ⁱIto and Jaitrong unpublished, *Aenictus* sp.; ^jHagan 1954, *Eciton* spp.; ^kWhelden 1963, *Eciton* spp.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00040-023-00898-4>.

Acknowledgements We wish to thank Assoc. Prof. Dr. Tran Huy Thai (Former director of the Institute of Ecology and Biological Resources, Vietnam), Assoc. Prof. Dr. Nguyen Van Sinh (Director of the Institute of Ecology and Biological Resources), Prof. Dr. Nguyen Trung Minh (Director of Vietnam National Museum of Nature), Mr. Chau Van Van (Director of Lo Go Xa Mat National Park, Tay Ninh Province, Vietnam), and Mr. To Quang and other staff of the national park. We would like to thank Dr. Johan Billen, Dr. Marek Borowiec, Dr. Adam Khalife and an anonymous reviewer for careful reading and useful comments. This research is funded by the following foundations and societies: Vietnam National Foundation for Science and Technology Development (NAFOSTED, grant number 106.12-2012.16); the Japan Society for the Promotion of Science (JSPS) Grant-in-Aid for Scientific Research (B, 26304014, 24405010, 16H05769; C, 15K07193, 15K07805; young scientists 20J13490); Advanced Research Program of Asian Human Resources Fund by Tokyo Metropolitan Government.

Author contributions RM, KE and FI designed the research; KE, RS, AVD, VTB, LTHP performed a field study; KE identified ant species; RM and FI performed a laboratory study. RM analyzed the data and wrote the primary manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Funding This work was partly supported by the following foundations: Vietnam National Foundation for Science and Technology Development (NAFOSTED, grant number 106.12–2012.16); Japan Society for the Promotion of Science (JSPS) Grant-in-Aid for Scientific Research (B, 26304014, 24405010, 16H05769; C 15K07193, 15K07805) and young scientists (20J13490); Advanced Research Program of Asian Human Resources Fund by Tokyo Metropolitan Government.

Availability of data and material Data deposited as electronic supplementary materials.

Code availability Not applicable.

Declarations

Conflict of interest Not applicable.

Ethics approval Not applicable.

Consent to participate (include appropriate statements) All authors have approved contributing to the research of this manuscript.

Consent for publication (include appropriate statements) All authors have approved for submission of this manuscript.

References

- Berghoff SM, Weissflog A, Linsenmair KE, Mohamed M, Maschwitz U (2002) Nesting habits and colony composition of the hypogaecic army ant *Dorylus (Dichthadia) laevigatus* Fr. *Smith Insectes Soc* 49(4):380–387. <https://doi.org/10.1007/PL00012662>
- Bharti H, Akbar SA (2013) Taxonomic studies on the ant genus *Cerapachys* Smith (Hymenoptera, Formicidae) from India. *ZooKeys* 336:79–103. <https://doi.org/10.3897/zookeys.336.5719>
- Bolton B (1990) Abdominal characters and status of the cerapachyine ants (Hymenoptera, Formicidae). *J Nat Hist* 24(1):53–68. <https://doi.org/10.1080/00222939000770051>

- Bolton B, Fisher BL (2012) Taxonomy of the cerapachyine ant genera *Simopone* Forel, *Vicinopone* gen. n. and *Tanipone* gen. n. (Hymenoptera: Formicidae). *Zootaxa* 3283(1):1–101. <https://doi.org/10.11646/zootaxa.3283.1.1>
- Borowiec ML (2009) New ant species related to *Cerapachys sexspinus* and discussion of the status of *Yunodorylus* (Hymenoptera: Formicidae). *Zootaxa* 2069(1):43–58. <https://doi.org/10.11646/zootaxa.2069.1.3>
- Borowiec ML (2016) Generic revision of the ant subfamily Dorylinae (Hymenoptera, Formicidae). *Zookeys* 608:1–280. <https://doi.org/10.3897/zookeys.608.9427>
- Borowiec ML (2019) Convergent evolution of the army ant syndrome and congruence in big-data phylogenetics. *Syst Biol* 68(4):642–656. <https://doi.org/10.1093/sysbio/syy088>
- Borowiec ML, Longino JT (2011) Three new species and reassessment of the rare Neotropical ant genus *Leptanilloides* (Hymenoptera, Formicidae, Leptanilloidinae). *ZooKeys* 133:19–48. <https://doi.org/10.3897/2Fzookeys.133.1479>
- Brandão CRF, Diniz JLM, Agosti D, Delabie JH (1999) Revision of the Neotropical ant subfamily Leptanilloidinae. *Syst Entomol* 24:17–36. <https://doi.org/10.1046/j.1365-3113.1999.00064.x>
- Brandão CRF, da Silva RR, Diniz JLM, Yamamoto CI, Castro-Mello C (1999) *Biologia de Leptanilloidinae*. Naturalia, São Paulo 24:45–47
- Buschinger A, Peeters C, Crozier RH (1989) Life-pattern studies on an Australian *Sphinctomyrmex* (Formicidae: Ponerinae; Cerapachyini): functional polygyny, brood periodicity and raiding behavior. *Psyche* 96:287–300. <https://doi.org/10.1155/1989/13614>
- Chadab R, Rettenmeyer CW (1975) Mass recruitment by army ants. *Science* 188(4193):1124–1125. <https://doi.org/10.1126/science.1215991>
- Donoso DA, Vieira JM, Wild AL (2006) Three new species of *Leptanilloides* Mann from Andean Ecuador (Formicidae: Leptanilloidinae). *Zootaxa* 1201:47–62. <https://doi.org/10.11646/zootaxa.1201.1.2>
- Eguchi K, Bui VT, Oguri E, Maruyama M, Yamane Sk (2014) A new data of worker polymorphism in the ant genus *Dorylus* (Hymenoptera: Formicidae: Dorylinae). *J Asia-Pac Entomol* 17(1):31–36. <https://doi.org/10.1016/j.aspen.2013.09.004>
- Eguchi K, Mizuno R, Ito F, Satria R, Dang AV, Bui TV, Phung LTH (2016) First discovery of subdichthadiigyne in *Yunodorylus* Xu, 2000 (Formicidae: Dorylinae). *Rev Suisse Zool* 123(2):307–314. <https://doi.org/10.5281/zenodo.155307>
- Franks NR (1985) Reproduction, foraging efficiency, and worker polymorphism in army ants. In: Hölldobler B, Lindauer M (eds) *Experimental behavioral ecology*, G. Fischer Verlag, Stuttgart, New York, pp 91–107
- Gotwald WH (1995) *Army ants: the biology of social predation*. Cornell University Press, Ithaca
- Hagan HR (1954) The reproductive system of the army-ant queen, *Eciton* (*Eciton*) part 3, the oöcyte cycle. *Am Mus Novit* 1665:1–20
- Hirosawa H, Higashi S, Mohamed M (2000) Food habits of *Aenictus* army ants and their effects on the ant community in a rain forest of Borneo. *Insectes Soc* 47(1):42–49. <https://doi.org/10.1007/s000400050007>
- Hita Garcia F, Fischer G, Liu C, Audisio TL, Economo EP (2017) Next-generation morphological character discovery and evaluation: an X-ray micro-CT enhanced revision of the ant genus *Zasphinctus* Wheeler (Hymenoptera, Formicidae, Dorylinae) in the Afrotropics. *ZooKeys* 693:33–93. <https://doi.org/10.3897/zookeys.693.13012>
- Hoelen PO, Blüthgen N, Brückner A, Kronauer DJC, Fiala B, Donoso DA, Smith MA, Jara BO, von Beeren C (2019) Species-level predation network uncovers high prey specificity in a neotropical army ant community. *Mol Ecol* 28(9):2423–2440. <https://doi.org/10.1111/mec.15078>
- Hölldobler B (1982) Communication, raiding behavior and prey storage in *Cerapachys* (Hymenoptera; Formicidae). *Psyche* 89(1–2):3–23. <https://doi.org/10.1155/1982/28390>
- Idogawa N, Dobata S (2018) Colony structure and life history of *Lioponera daikoku* (Formicidae: Dorylinae). *Asian Myrmecol* 10:e010006. <https://doi.org/10.20362/am.010006>
- Ito F, Jaitrong W, Hashim R, Mizuno R (2018) Colony composition, brood production and caste dimorphism in two species of the doryline genus *Lioponera* in the oriental tropics (Formicidae: Dorylinae). *Asian Myrmecol* 10:e010007. <https://doi.org/10.20362/am.010007>
- Jaitrong W, Yamane Sk (2011) Synopsis of *Aenictus* species groups and revision of the *A. currax* and *A. laeviceps* groups in the eastern oriental, Indo-Australian, and Australasian regions (Hymenoptera: Formicidae: Aenictinae). *Zootaxa* 3128(1):1–46. <https://doi.org/10.11646/zootaxa.3128.1.1>
- Jaitrong W, Wiwatwitaya D, Yamane Sk (2020) First record of the ant genus *Syscia* Roger, 1861 (Hymenoptera: Formicidae) from Thailand, with descriptions of two new species. *Far East Entomol* 411:1–9. <https://doi.org/10.25221/fee.411.1>
- Kronauer DJC (2020) *Army ants: nature's ultimate social hunters*. Harvard University Press, Cambridge
- Mizuno R, Suttiprapan P, Jaitrong W, Ito F (2019) Daily and seasonal foraging activity of the oriental non-army ant doryline *Cerapachys sulcinodis* species complex (Hymenoptera: Formicidae). *Sociobiology* 66(2):239–246. <https://doi.org/10.13102/sociobiology.v66i2.3775>
- Mizuno R, Suttiprapan P, Jaitrong W, Yamada A, Ito F (2021) Colony composition, phasic reproduction, and queen–worker dimorphism of an oriental non-army ant doryline *Cerapachys sulcinodis* species complex in northern Thailand. *Insectes Soc* 69(1):19–35. <https://doi.org/10.1007/s00040-021-00841-5>
- Raignier A, van Boven JKA (1955) Etude taxonomique, biologique et biométrique des *Dorylus* du sous-genre *Anomma* (Hymenoptera Formicidae). *Ann Mus R Congo Belg* 2:1–359
- Satria R, Itioka T, Meleng P, Eguchi K (2018) Second discovery of the subdichthadiigyne in *Yunodorylus* (Borowiec, 2009) (Formicidae: Dorylinae). *Rev Suisse Zool* 125(1):73–78. <https://doi.org/10.5281/zenodo.1196017>
- Schneirla TC (1971) *Army ants: A study in social organization*. W. H Freeman and Company, Gordonsville, Virginia
- Schneirla TC, Reyes AY (1966) Raiding and related behaviour in two surface-adapted species of the old world doryline ant. *Aenictus* *Anim Behav* 14(1):132–148
- Schöning C, Njagi WM, Franks NR (2005) Temporal and spatial patterns in the emigrations of the army ant *Dorylus* (*Anomma*) *moles-tus* in the montane forest of Mt Kenya. *Ecol Entomol* 30(5):532–540. <https://doi.org/10.1111/j.0307-6946.2005.00720.x>
- Topoff H, Mirenda J (1975) Trail-following by the army ant, *Neivamyrmex nigrescens*: responses by workers to volatile odors. *Ann Entomol Soc Am* 68(6):1044–1046. <https://doi.org/10.1093/aesa/68.6.1044>
- Warton DI, Duursma RA, Falster DS, Taskinen S (2012) smatr 3—an R package for estimation and inference about allometric lines. *Methods Ecol Evol* 3(2):257–259
- Whelden RM (1963) Anatomy of adult queen and workers of army ants *Eciton burchelli* Westw. and *E. hamatum* Fabr. (Hymenoptera: Formicidae). *J NY Entomol Soc* 71:14–30 ((90–115, 158–178, 246–261))
- Wilson EO (1959) Studies on the ant fauna of Melanesia. VI The tribe Cerapachyini *Pac Insects* 1:39–57

- Xu ZH (2000) Two new genera of ant subfamilies dorylinae and ponerinae (Hymenoptera: Formicidae) from Yunnan. *China Zool Res* 21(4):297–302
- Yamada A, Luong PTH, Eguchi K (2018) Description of a new species of the ant genus *Ooceraea* Roger, 1862 (Hymenoptera: Formicidae; Dorylinae) from the Vietnam's Central Highlands. *J Insect Biodivers* 7(1):17–23. <https://doi.org/10.12976/jib/2018.07.1.2>
- Yamada A, Lin CC, Eguchi K (2019) Taxonomic notes on the rare ant genus *Chrysapace* with description of a new species from Brunei (Hymenoptera: Formicidae: Dorylinae). *Acta Entomol Mus Natl Pragae* 59(2):467–480. <https://doi.org/10.2478/aemnp-2019-0036>
- Yamane Sk, Hashimoto Y (1999) A remarkable new species of the army ant genus *Aenictus* (Hymenoptera, Formicidae) with a polymorphic worker caste. *Tropics* 8(4):427–432. <https://doi.org/10.3759/tropics.8.427>

Springer Nature or its licensor (e.g. a society or other partner) holds exclusive rights to this article under a publishing agreement with the author(s) or other rightsholder(s); author self-archiving of the accepted manuscript version of this article is solely governed by the terms of such publishing agreement and applicable law.