

ORIGINAL ARTICLE



Predator–prey encounters: deciphering the robbery relationship between highwayman flies and their ant victims

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Abstract

Examples of predator–prey interactions in which flies rob ants are uncommon. To date, this behavior has only been recorded in the genus *Bengalia* Robineau-Desvoidy (Bengaliinae, Diptera, Calliphoridae). These predatory flies ambush ants, and rob them of the food or offspring that they are carrying. However, because of the rarity of this behavior, the reasons and consequences (evolutionary advantages) are unknown, and indeed, the behavior has been sometimes considered anecdotal. In this study, we employed field investigations and behavioral analyses to investigate whether the sex of the fly *Bengalia varicolor*, or the weight and quality of the food carried by *Pheidole nodus* ants influenced fly–ant interactions in their natural habitats. We show that food weight and quality influenced the behavior of *B. varicolor* independent of the fly's sex. Robbing behavior by the flies was more successful when the food robbed was of high-quality and light in weight. Furthermore, the weight of the food robbed modulated the escape distance the flies could carry it. This then may affect the food quality and weight transported by the ants. This is a novel example of deciphering the relationship between highwayman flies and their ant victims. Given the widespread distribution of *Bengalia* flies, we suggest that such interspecific predator–prey encounters may shape the robbery interactions and the carrying behavior of further ant species in nature.

Key words: *Bengalia*, kleptoparasitism, *Pheidole*, predatory flies, robbing

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INTRODUCTION

Predator–prey interactions play key roles in ecosystems (Pimm & Pimm 1982; Andrew 2018). Interaction between marine mammals and their prey is known to influence the structure and dynamics of marine ecosystems (Andrew 2018). Kleptoparasitism, in which one species feeds by stealing food from another species, is an important form of predator–prey interaction that is

widespread in both invertebrates and vertebrates (Iyengar 2008). Broadly speaking, predators steal or plunder the resources of another species in order to reduce the time and energy required to find and process food (Nishimura 2010). There are three main forms of kleptoparasitism: overt aggression, competitive scramble, and stealth (Giraldeau & Caraco 2000), of which robbery is one of the most effective strategies. For example, hyenas rob prey from African wild dogs to increase their own food intake while minimizing the energy spent getting it (Gorman *et al.* 1998), and the spider *Curimagua bayano* appears to be an obligate kleptoparasite of other spider species, gaining all its food from this behavior (Vollrath 1978). Such interactions have significant ecological and evolutionary consequences for species survival and for the dynamic equilibrium of animal communities (Nishimura 2010).

Sexual size dimorphism and body size often impact animal's reproductive mode, carrying behavior, attacking ability, and clutch size (Li *et al.* 2021; Krasnov *et al.* 2022; Liang *et al.* 2022). Recent studies into robbing behavior in animals suggest that the predator's sex and behavior will influence the size, quality, and density of the prey species and food they carry, as well as potentially altering prey behavior (Martisova *et al.* 2009; Schmidt *et al.* 2012; Wimp *et al.* 2021). Under laboratory conditions, when the dragonfly *Rhodotomias rufa* attacks another species, males have higher predation success rate than that of females (Goutam *et al.* 2016). In addition, the difference in body size between predators and prey affects the efficiency of predatory attacks and can even lead to the occurrence of anti-predation behavior (Aljetlawi *et al.* 2004; Kaushik & Banerjee 2021). For example, the predation success rate of the common hawkler *Aeshna juncea* on *Daphnia magna* larvae decreases with increasing prey size (Hirvonen & Ranta 1996). A further important factor in predator choice is the nutritional content of the prey. For example, experienced wolf spiders prefer to feed on fruit flies with higher nutritional value (Schmidt *et al.* 2012), and herring gulls have been observed to preferentially attack puffins carrying larger prey (Busniuk *et al.* 2020).

Kleptoparasitism in flies was reviewed by Sivinski *et al.* (1999) and included robber flies, blowflies, and chloropid flies recorded from different regions (Tschirnhaus *et al.* 2014; Barahona-Segovia & Painao 2020; Zhao *et al.* 2021). Some small kleptoparasitic flies are quick enough to rob invertebrate prey from slow-eating predators (Sivinski *et al.* 1999). For example, *Desmometopa* flies are kleptoparasites of honeybees killed by *Misumena vatia* (Thomisidae) spiders (Tschirnhaus *et al.* 2014). Fly species of the Sphaeroceridae, Milichiidae, Calliphoridae,

Chloropidae, and Phoridae are able to rob prey or resources from predatory arthropods such as praying mantises and spiders, as well as from dung beetles (Petersson & Sivinski 1996; Iyengar 2008; Tschirnhaus *et al.* 2014). However, how the sex and size of the predatory flies, as well as taxon, size, and quality of the prey and food shape the robbing behavior of the flies is not well understood.

Calliphoridae flies are well known as scavengers and pollinators. An interesting case is that species from the genus *Bengalia* rob or prey on various ant and termite species (Maschwitz & Schönegege 1980; Zhao *et al.* 2021). *Bengalia* is a genus of about 80 species, distributed across tropical and subtropical regions (Zhao *et al.* 2021). Studies into 13 species of *Bengalia* suggest that up to six genera of ants are subject to predation by *Bengalia* (Zhao *et al.* 2021). Indeed, our recent review also demonstrated that *Bengalia* flies can rob prey carried by several different ant species (Zhao *et al.* 2021). It has also been reported that larger, more aggressive or faster moving ants lead to increased robbery failure in *Bengalia* flies (Maschwitz & Schönegege 1980), and ferocious *Odonotomachus monticola* ants can even kill the *Bengalia* flies (Chen & Chomicki 2020). To date, although we are now sure that ant species can be subject to robbery by *Bengalia* flies, deciphering the robbery relationship between highwayman fly and its ant victims remains unclear.

Predator-prey relationships are determined by the characteristics of the species involved (Abrams 1992). In this study, we used the fly *B. varicolor* and the ant *P. nodus* as a study system to address the following questions: (a) Does the sex and size of the *Bengalia* fly individual affect the success rate and frequency of theft of ant prey? (b) Does the weight of the food carried by the ants affect the success rate and frequency of fly-ant interactions? (c) Are the success rate and frequency of ant pupa theft different from those of food theft? (d) Finally, by measuring the distances between the sites of theft (robbing points) to the food points and to the ant colonies, we plan to explore choice of robbery points when *B. varicolor* flies are robbing food from *P. nodus* ants.

MATERIALS AND METHODS

Study location and materials (fly and ant species)

In this study, all experiments were conducted from May to October 2019–2020 in Guishan National Forest Park, Shilin County, Yunnan Province, China (103°33′27″E, 24°37′22″N; 1966 m asl). The area has a typical subtropical monsoon climate. The annual mean temperature is about 13.2°C and the average annual precipitation is

about 968 mm. The rainfall is concentrated from May to October every year (Duan 2016). The habitat of Guishan is within the natural distribution area of the studied *Bengalia* flies and ant species.

To identify the *Bengalia* fly species taxa and the targeted ant species taxa, a total of 500 pieces of food pieces (bread crumbs) were placed in different places in the forest park to attract ants and *Bengalia* flies. The distance between each food pile was more than 10 m. The food piles were then observed for 30 min, and the frequencies of absence or presence of ant and/or fly species and their numbers were recorded. Fifty food pieces were used per day during 12:00–12:30 and the experiments were repeated 10 days to collect the flies and ant taxa data. Most (470, 94.0%) of the food piles were visited by both ants and flies, 28 food piles (5.6%) were visited only by ant species, and 2 food piles (0.4%) were visited by neither ants nor flies.

During the observation period, none of the *Bengalia* flies fed directly on the food piles, but they robbed the ants carrying the food away. Of the ants attracted to those food piles, 81.3% were *Pheidole nodus*, 10.4% were *Aphaenogaster* sp., 3.2% were *Camponotus* sp., and 5.1% were other ant species (*Odontomachus* sp., and *Crematogaster* sp.). Because of its abundance at the sites, *P. nodus* was the main ant species targeted by the *Bengalia* flies. We caught the *Bengalia* flies using an insect net, and Professor Chun-Tian Zhang identified the *Bengalia* fly species as *B. varicolor* (Fabricius, 1805), *B. emdeniella* (Lehrer, 2005), and *B. fani* Feng & Wei, 1998. *Bengalia varicolor* individuals represented 80% of the total number of flies ($n = 1000$). Therefore, we focused on *B. varicolor* and *P. nodus* in our investigation of the interactions between these flies and the ants they rob.

Characteristics of flies and marking of flies with tags

To test potential differences in body weight and length between male and female *B. varicolor* flies, these two characteristics were measured from newly captured *B. varicolor* individuals. We weighed flies by placing a single adult *B. varicolor* in an insect box and weighing it on an electronic balance (Sartorius, accuracy 0.1 mg), then deducting the weight of the insect box. Vernier callipers were used to measure the body length of the flies, and the lengths were measured from the antennae to the excretory hole.

The 500 adult individuals of *B. varicolor* captured and determined as male or female were then placed in 120

mesh nylon insect cages (30 × 30 cm × 30 cm; 30–50 individuals per cage) for experiments the following day. The bottoms of the cages were each lined with a 5-cm thick layer of coconut soil in advance, in order to maintain the humidity in the cage. Because the flies were to be released the following day, there was no need to specially feed them. To monitor the robbing behavior of the individual flies, all flies were labeled with a tag bearing a unique number, according to the method of Chen *et al.* (2018). The diameter of the tag was 2.5 mm and the weight was 2.0 mg. The tags were stuck to the backs of the flies and did not affect their flight or predation. The next day, we used a test tube to transfer the marked flies from their cages to the vicinity of an ant nest where food had been placed. The flies then slowly and tentatively climbed out of the mouth of the test tube, stayed on the grass blades above or near the test tube mouth, and cleaned their whole bodies using their mouthparts and feet. Sometimes fright caused the flies to fly away directly, but as long as there were ants carrying food nearby, marked flies continued to appear. We marked a large number of flies.

In order to reduce the possible activity range of the flies, we initially used four sticks and four ropes to make a 1 × 2 × 4 m cage of mosquito netting around the anthill and put the marked flies into it. However, most flies only flew to the top of the net, with only a few stopping near the bottom of the nest to rob the ants. Therefore, we released the flies without a cage to observe their robbery processes without limitation. Although not all of them returned, our repeated experiments still managed to accumulate observation data on hundreds of the fly food thefts from ants. During the whole process, we remained crouched near the source of food, where the ants were carrying the food, and observed the robbing behavior of the flies.

Relationships between fly sex, weight and quality of food, and robbing behaviors

To study the impacts of fly sex and weight and quality of food on the thefts from the ants, we recorded the behavior of 396 labeled *B. varicolor* individuals (♀:♂ = 226:170) toward *P. nodus* ants from 28 ant colonies. Food weight was assessed using by bread crumbs of different sizes (10, 30, and 50 mg), and food quality was assessed using ant pupae and bread crumbs of similar weight. The main nutritional composition of the bread was: protein 80.0 mg/g, lipid 215.0 mg/g, and carbohydrate 475.0 mg/g (Man Yue Fu Food). Previous studies suggested that the main nutritional components of ant pupae include: protein

177.8 mg/g, lipid 81.7 mg/g, and carbohydrate 290.9 mg/g (Mukhopadhyay & Sannigrahi 1993). In this study, we consider a high-quality food is with more protein.

Many *P. nodus* nests and foraging ants were present on both sides of the path running through the park. The predatory flies hide in the grass on both sides of the path, waiting for opportunities to rob. Bread crumbs of different sizes were placed in the way of the foraging *P. nodus*. Tagged female and male flies were released after the ants had picked up the bread crumbs. A few minutes after release, some of the flies were attracted to the foraging ants and stole the bread being carried by the ants. The times and results (success or failure) of each attempted theft were recorded for each fly within 30 min of release.

To study how the flies reacted to ant broods, we destroyed the entrances of *P. nodus* nests ($n = 7$), and when the ants picked up the larvae or pupae to take them to safety escape, we released the marked *B. varicolor* (♀:♂ = 14:15). The weight of an ant pupa or larva is about 10 mg. Robbery success rate was calculated as the number of successful thefts divided by the number of robbing events for each fly within 30 min. A theft was considered to be successful robbery if the fly's forefoot made contact with the food and if the ants then gave up the food. The frequency of robbery was defined as all the times a particular fly attempted a theft within 30 min.

When the flies robbed the ants, to reduce the chance of ant's counterattack, the flies flew away from the location rather than feeding in situ (Zhao *et al.* 2021). To explore the effect of food weight on the distance that *B. varicolor* would fly after the theft of food, we placed bread crumbs of six different weights (10, 20, 30, 40, 50, and 60 mg) near the ant colonies. Twenty marked flies were observed to rob the *P. nodus* ants in this experiment. We recorded the flight distance of the flies carrying the food from the site of the robbery, using a tape measure (accuracy 0.1 cm) to measure the distance in a straight line between the robbing location and point where the flies touched down and fed on the robbed food (feeding point).

Our previous observations suggested that the *B. varicolor* might employ a sit-and-wait strategy to rob foraging ants (Zhao *et al.* 2021). To determine whether the flies had a location preference for robbing the ants, we sprinkled bread crumbs evenly over an area between 0–3 m away from the ant nest and observed where the robberies took place. In this experiment, we used 10 *B. varicolor* individuals and targeted three *P. nodus* colonies. When the ants were carrying food, we marked the location from which

the food had been collected (food points). When a robbery took place, we marked the location of the robbery (robbery point) and measured the both the distance from the robbery point to the food point and the robbery point to the nest in a straight line.

Statistical analysis

All the analyses were conducted in SPSS25.0 software (SPSS Inc., Armonk, NY, USA), and all data were examined using normality tests. Independent samples *T* tests were used to compare differences in body weight and body length in male and female flies. Chi-square tests were used to analyze the differences (success rate and frequency) between thefts of different types of foods. Non-parametric tests of K independent samples were used to compare the distances flown by *B. varicolor* individuals after robbing food of different weights. Bivariate Spearman tests were used to investigate correlations between the robbery-food point distance and the ant colony-food point distance.

RESULTS

Characteristics of flies and ants

In this study, we found that weight and the body lengths of female and male *B. varicolor* individuals were not significantly different (female: 57.86 ± 1.37 mg and 11.31 ± 0.13 mm vs. male: 62.51 ± 1.44 mg and 11.18 ± 0.10 mm, respectively, both ratios $P > 0.05$). The process by which *B. varicolor* robs *P. nodus* ants of their pupae or food is illustrated in Fig. 1.

Interactions between *B. varicolor* flies and *P. nodus* ants

Robbing success rate was not significantly different in male and female *B. varicolor* in this study (Fig. 2a). The success rate of robbing decreased significantly with increasing food weight, and *B. varicolor* had significantly higher rates of success robbing ant pupae than bread crumbs ($\chi^2 = 448.631$, $P < 0.001$; Fig. 2a). We observed no significant differences in the frequency with which different weights of food were robbed by the flies, nor was there a significant difference in the frequency with which female and male flies attempted robbing ($\chi^2 = 2.737$, $P = 0.434$; Fig. 2b).

When *B. varicolor* successfully stole food from ants, the flies often flew away with the food for some

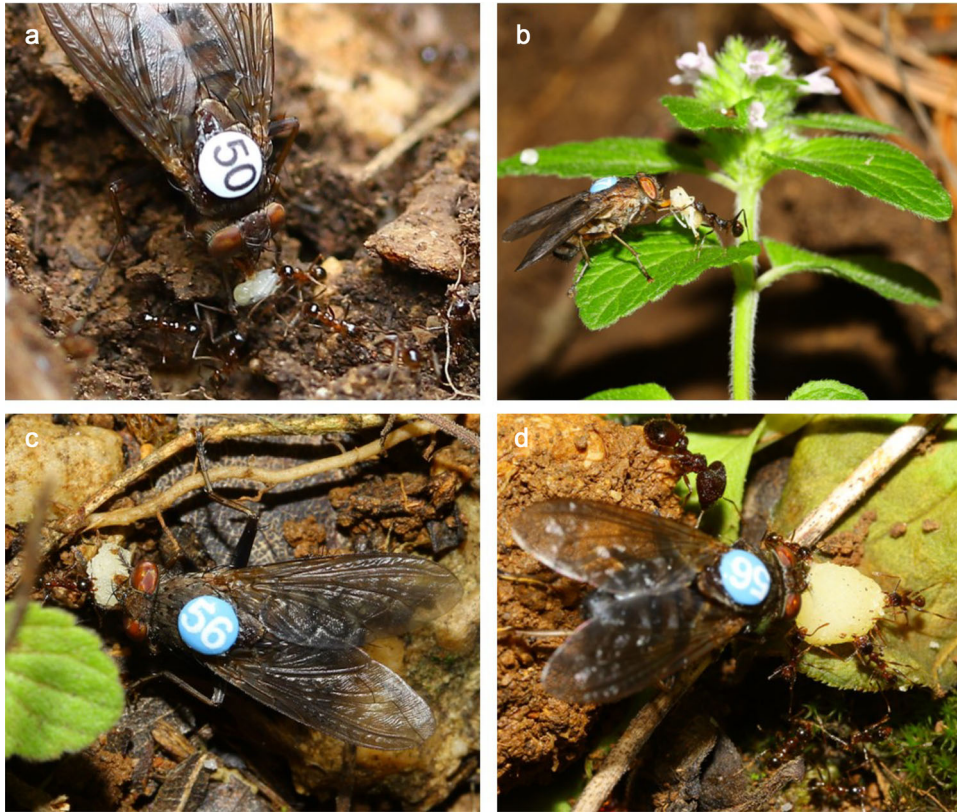


Figure 1 The process of *Bengalia varicolor* robbing pupae or food from *Pheidole nodus* ants. (a) An individual of *B. varicolor* robbing a *P. nodus* pupa from a destroyed nest. (b) A fly flew to a leaf, carrying an ant pupa with the ant still holding on to the pupa. (c) A *B. varicolor* individual robbing a single ant carrying a 10-mg crumb of bread. (d) A *B. varicolor* individual robbing several ants which are together carrying a 50-mg crumb of bread.

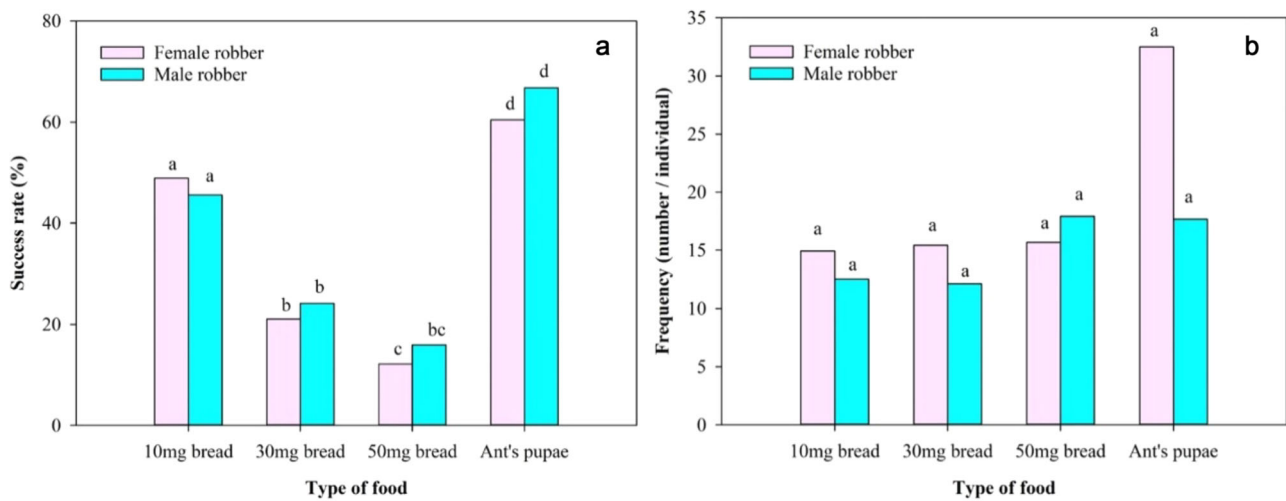


Figure 2 The success rate (a) and frequency (b) of *Bengalia varicolor* theft from *Pheidole nodus*. Bars marked with the same letters represent differences with $P > 0.05$, and different letters represent differences of $P < 0.05$.

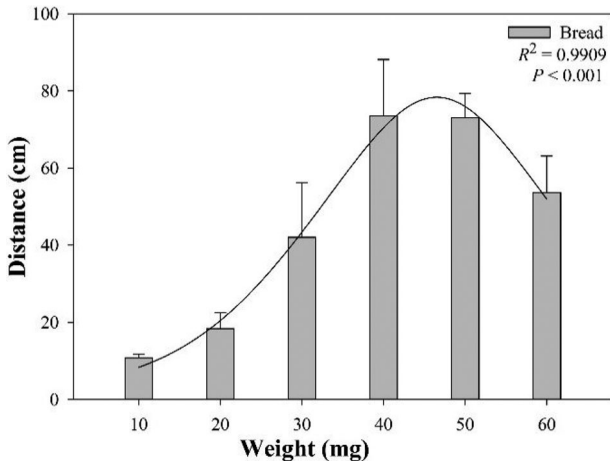


Figure 3 Food weight is related to the distance flown by *Bengalia varicolor* flies after they have stolen the food.

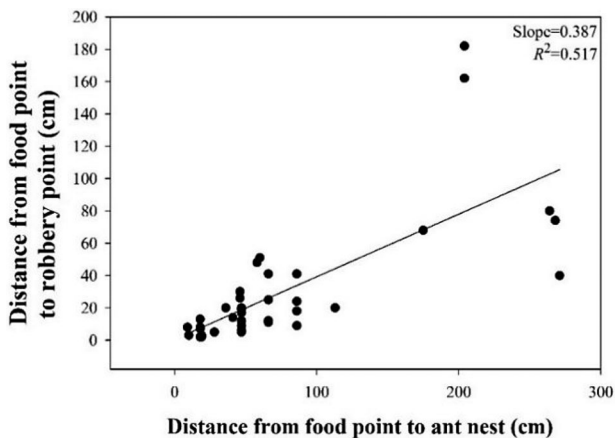


Figure 4 The relationships between the food–robbery point distance and the food–ant colony distance.

distance. In this study, the distance that the flies flew with the food correlated significantly with food weight ($R^2 = 0.9909$, $P < 0.001$, $n = 20$; Fig. 4). From our SigmaPlot 14.0 analysis, the curve model formula of flight distance was $y = 78.33[16.09\{1/1(x - 46.52)/b^2\} (1 - 3.507)e^{0.5(x - 46.52)/b^2}]$. The flight distance increased at first and then decreased with the weight of the foods. When the food weight reached 46.52 mg, the maximum flight distance was reached 78.33 cm (Fig. 3).

We found a significant positive correlation between the food–robbery point distance and the food point–ant colony distance ($R^2 = 0.517$, $P < 0.001$; Fig. 5). The Linearity Model formula generated in SigmaPlot 14.0 was $y = 0.387x + 0.537$ and the slope was 0.387 (Fig. 4).

DISCUSSION

The results indicated that dimorphism was absent from *B. varicolor* and that the success rate of robbery decreased significantly with increasing of food weight (Fig. 2a). We observed that bulky foods required more ants to transport, while the smallest breadcrumbs required only a single ant for transport, which correlates with ant payloads and social cooperation attributes. A single *Pheidole* ant normally carried 0–16 mg of food (Cerda *et al.* 1998), but when encountering large prey, the ants are known to recruit their nestmates to transport the prey collectively (Cerda *et al.* 1998; Folgarait & Gilbert 1999). For example, cooperative *Leptogenys* ants can easily kill and transport large prey (Peeters & De Greef 2015). This may be the main reason for the decline in the success rate of attempted fly robberies of large pieces of food. We suggest that these highly cooperative social ants found it easier to counter predator attack when flies attempted to steal the 50-mg bread crumbs because many workers were carrying the food and could retaliate against the fly when it attacked. Similar results have been reported from predation in other species of ants (Cangialosi 1990; Peeters & De Greef 2015). There was no significant change in the frequency of flies attempting to steal bread crumbs of different weights (Fig. 2b), suggesting that the size of the prey does not affect the number of robberies by the predator. This has also been reported in the kleptoparasitic spider *Argyrodes ululans* (Cangialosi 1990).

We found that the *B. varicolor* attempts to rob *P. nodus* pupae were more effective than attempts of theft of bread crumbs (Fig. 2a), suggesting that ant offspring were more important to the flies. This is likely to be because predators preferentially target prey with high nutritional value to maximize their net energy intake (Pyke *et al.* 1977; Redford & Dorea 1984). In nature, prey quality (nutrition) is a major factor in predator survival, growth, and behavior (Pyke *et al.* 1977; Redford & Dorea 1984; Mayntz & Toft 2001; Wilder *et al.* 2010). Insect larvae are known to be protein-rich, and the consumption of prey protein can result in insect predators producing more eggs with higher quality (Mukhopadhyay & Sannigrahi 1993; Schmidt *et al.* 2012; Barry & Wilder 2013; Latney & Clayton 2014). The predators can therefore optimize their kleptoparasitic foraging strategy by targeting more profitable hosts (Busniuk 2020). The protein content of ant pupa is about 177.8 mg/g (Mukhopadhyay & Sannigrahi 1993) and that of the bread is about 80.0 mg/g (Manyuefu Food Technology Company), meaning that the pupae were the higher quality food.

Field observations revealed that *B. varicolor* did not stay *in situ* to consume the bread or pupae following theft. The flies often flew away a distance, probably to avoid counterattacks from the ants. The flight distance was significantly correlated to the weight of the food (Fig. 3). The explanation for this is that as food weight increases, so does the number of ants required to carry that food, and there are therefore more ants available for counterattacks against the flies. The flies thus fly further to reduce the risk of being attacked by the ants. However, the flight distance did not increase indefinitely, which means that the predator payload and energy consumption can mediate the flight distance. This is known from other insects. For example, a bee's payload is positively correlated with its body weight, and a bee cannot carry more food than its own payload (Brown *et al.* 2012). We also found that there was a significant positive correlation between the food–robbery point distance and the food point–ant colony distance (Fig. 4). In this study, the ratio to food–robbery point distance/food point–ant colony distance was about 0.387, indicating that flies prefer to predate the ants close to the food point rather than to the ant colonies (Fig. 4). *B. varicolor* are robbers that adopt a sit-and-wait strategy to ambush their ant prey when the ants return to their colonies carrying their food or offspring (Maschwitz & Schönegege 1980; Zhao *et al.* 2021). The robbing point may have a more profound significance in the evolution of the interactions between these flies and their ant prey and it is worth exploring in next study.

There are still many unresolved questions regarding the interactions between *B. varicolor* and *P. nodus*. First, how do the predatory flies accurately locate the ant hosts carrying their foods or offspring? It is possible that olfactory and/or visual signals from the ants may play important roles in attracting these flies (Zhao *et al.* 2021). A well-known case of this is the attraction of parasitic phorid flies to the alarm pheromone released by fire ants (Sharma *et al.* 2011), but whether this is also the case in *Bengalia* is unknown. The pheromones released during ant foraging or defense may be picked up unintentionally (eavesdropped) by the flies (Mathis 2011). In the example of the Phoridae flies, warning elements released for localization by red fire ants were “overheard” by the flies and parasitic behavior occurs (Sharma *et al.* 2011; Chen & Porter 2020). In the experiments described in our study, we destroyed the entrances to the ant nests. In doing so, we may have caused the ants to produce more warning elements than normal, meaning that in our experiments, signals from ants with ant pupae may have been more likely to be “overheard” by *B. varicolor* than signals from ants carrying food, causing the robberies to occur

more frequently. Second, what is the complete life cycle of *B. varicolor*? Some researchers have speculated that *B. varicolor* may lay eggs in ants' nests (Altson 1932; Maschwitz & Schönegege 1980). When we fed captive flies with ant pupae and bee pupae at room temperature, we were unable to harvest any fly eggs. Moreover, when flies were fed mating termites, 2 years of effort yielded only a single 3rd instar larvae, which eventually emerged into a male *B. varicolor* individual (Zhao *et al.* 2021). The egg laying requirements of adult flies and the diet of the fly larvae remain unclear. We speculate that the life history of *B. varicolor* may be related to termites rather than ants. Third is the location of the robbing point chosen by the trade-off between the predatory flies and the species of the robbed ants?

In conclusion, we reveal here for the first time that *B. varicolor* has no sexual dimorphism in body weight or length, and that the sex of the fly has no effect on the robbing behavior. We also demonstrate that the robbery success rate and the distance flown by *B. varicolor* individuals are both related to the characteristics of the food carried by the *P. nodus* ants. Interestingly, *B. varicolor* robs *P. nodus* pupae with a higher success rate than for food when controlling for weight. The results imply that *B. varicolor* predation of high-quality foods such as ant larvae and pupae and of food in small pieces may be under selection. Furthermore, our evidence suggests that flies rob ants at fixed points close to the food source, which may impact the evolutionary strategies of both species involved. Seed dispersal by animals is a complex ecological interaction, and the associations between long-term dynamics of seed fates and their dispersers may shape forest ecosystems (Chen *et al.* 2022; Liu *et al.* 2022). As we know, many ant species can disperse seeds of myrmecochorous plants in microhabitats. Maybe, the predatory flies also impact the seed fate and dispersal process of these plants and provide complementary seed dispersal at different spatial scales.

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