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Highlights

- Social wasps are considered as effective biocontrol agents
- Predation by a Polistinae was studied using a light trap to attract insect prey
- Foragers can carry 30.7% of their load capturing up to six small prey
- Large prey are cut into two pieces; the wasps return to gather the second piece
- Social facilitation, a primitive form of nestmate recruitment was noted

The predatory behavior of the Neotropical social wasp *Polybia rejecta*

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ABSTRACT

We experimentally studied the predatory behavior of *Polybia rejecta* (Vespidae, Polistinae, Epiponini) towards 2-88 mm-long insects attracted to a UV light trap. Foragers, which began to hunt at 6:30, selected 4-14 mm-long prey insects. Prey detection by sight by hovering wasps was confirmed using decoys. After the wasps landed and walked along a sinuous path, prey were detected by contact or from a distance (1-3 cm). This was followed by seizure, stinging (contrarily to most other known cases), prey manipulation and retrieval. Prey that flew off might be caught in flight. The prey load, representing 30.7% of a forager's weight, was optimized by capturing up to six small prey or two medium-sized prey successively (both of which might be consumed *in situ*). The foragers cut off the wings of larger prey or cut them into two pieces and returned to gather the second piece. The handling time increased exponentially with the weight of the prey. Partial loading (i.e., retrieving a load much inferior to the maximum possible) was likely related to social facilitation, a form of nest-based recruitment that was demonstrated through the experimental elimination of local enhancement by removing foragers (both mechanisms favor the exploitation of favorable patches).

199 words < 200

Keywords

Epiponine wasps, Polistinae, predation, prey selection, recruitment, Vespidae

1. Introduction

Foraging is the basis for the survival, development and reproduction of individual animals. It permits their populations to endure while impacting other species, as seen through pollination, seed dispersal, parasitism and, for predators, the regulation of prey populations (Schoener, 1987; Kramer, 2001). To reduce the costs of food acquisition, animals must adapt their foraging behavior to spatially and temporally dynamic environments while avoiding their predators, so that theoretical models have been developed where the premise is that an optimization process results from natural selection (i.e., the notion of optimal foraging) (MacArthur and Pianka, 1966; Pyke et al., 1977).

In the case of a solitary predator a foraging bout includes the elements (1) search, (2) detection, (3) assessment resulting in pursuing or abandoning prey, (4) pursuit leading to prey contact and attack, (5) handling that includes mastering the prey, its preparation and consumption, and (6) processing or digestion (Kramer, 2001). Animals maximize benefits and minimize costs through an optimal diet based partly on the size of prey (i.e., a function of the time necessary to master them, or “handling time”), the choice of optimal patches to forage, the allocation of time spent in these patches, and the patterns of movement (i.e., foragers increase the sinuosity of their path and decrease their speed in favorable patches, known as “intensive search”; a patch is abandoned when the density of prey decreases). Therefore, when foraging, predators need to make decisions based on perceived cues related to prey density, quality and defenses, resulting in choices where risks are perceived as well as the possibility for inter- and intraspecific kleptobiosis (notion of decision rules; Iwaza et al., 1981; Stephens and Krebs, 1986; Kramer, 2001; Darracq et al., 2016).

Central place foragers, such as birds during the breeding season that return to their nests to feed their offspring or eusocial insects that feed their kin (i.e., nestmates and the brood of

the colony), need to use navigation and memory to return to the nest and then to favorable patches (Orians and Pearson, 1979; Schoener, 1979; Hölldobler and Wilson, 1994; Sutton, 2015). In eusocial insects, the foraging bouts of solitary hunters are composed of (1) an outward trip, (2) search, (3) mastering the prey, (4) loading, (5) a homeward trip and (6) unloading (Kramer 2001). Although it can occur, the consumption of the prey is no longer the main objective of the forager. “Social foragers” have, in addition, the ability to inform their nestmates of the location of favorable patches (e.g., recruitment trails in ants and the waggle dance in honeybees) (Hölldobler and Wilson, 1994; Beekman and Dussutour, 2009). Loading can be optimized by retrieving large prey or successively capturing several small prey and retrieving them all at one time. Alternatively, partial loading often occurs when recruiting nestmates is needed to rapidly deplete a food source. Moreover, the theory predicts that when the load affects the duration of the homeward trip, the optimal load size decreases with an increasing distance to the nest (Schoener, 1979; Kasuya, 1982; Wetterer, 1989; Dornhauss et al., 2006).

Because most social wasps (e.g., Vespinae and Polistinae including the swarm-founding Epiponini) are generalist predators preying mostly on caterpillars and adult Diptera and so can be used as biological control agents (Raveret Richter, 2000; Donovan, 2003; Jeanne and Taylor, 2009; Bichara Filho et al., 2010; Santana et al., 2012) they constitute a good model for studying their predatory behavior. The foraging bouts of social wasps begin with a flight towards a potential prey habitat. Then, search flights are composed of highly irregular loops alternating with phases of inspection where individuals hover while oriented toward a visible resource (Raveret Richter and Jeanne, 1991; Collett, 1995; Jander, 1997; Stürzl et al., 2016). Although prey, particularly live, fast-moving insects, are mostly detected by sight, odors also play a role (Raveret Richter and Jeanne, 1985; Hendrich et al., 1994; Raw, 1998; Jeanne and Taylor, 2009; Couto et al., 2014). The prey capture behavior of *Polistes dominula* foragers is

composed of the following phases: approach (generally walking), antennation, attack and biting various parts of the prey, butchering (slicing away pieces of flesh) and balling up (preparation of a small chunk of flesh to be transported). Finally, the ball of flesh is taken to the nest (Brown et al., 2012). The foragers of some Epiponini do not malaxate their prey, but rather transport them virtually intact or cut off only the non-edible parts, such as the wings; others retrieve only the most profitable part (e.g., the thorax of adult insects with the wing muscles), and still others cut large prey into pieces which are retrieved during successive flights (Jeanne, 1972; Hunt et al., 1987; Raveret Richter, 2000; Raveret Richter and Jeanne, 1991; Gomes et al., 2007; Jeanne and Taylor, 2009; Dejean et al., 2010, 2012; Polidori et al., 2013). Although foragers generally kill live prey by biting them, stinging, a facultative phase, is triggered when the prey struggle. This permits the wasps to economize their venom which is only used to master large and/or vigorous prey (Edwards, 1980; Olson, 2000).

Navigation using sunlight angles, visual landmarks in the environment and a cognitive map (Collett et al., 2016; Stürzl et al., 2016) permits the wasps to take a direct homeward path. Learning flights (i.e., the individuals back away from the goal in a series of arcs) occur just after leaving the nest and before leaving a large food resource, permitting the foragers to find them later (Zeil et al., 1996; Jander, 1997; Stürzl et al., 2016). Capable of 24-hour recall, foragers can undertake a series of return trips (Moreyra et al., 2016).

When moving to a new nest site, the Epiponini recruit nestmates by laying scent trails (Jeanne, 1981, 1991; Francescato et al., 1993; Howard et al., 2002), but this mechanism has never been observed during food recruitment (see Jeanne and Taylor, 2009). Yet, in *Polybia occidentalis*, naïve individuals in the nest use food scent cues from the carbohydrates brought in by successful foragers to orient themselves to food resources (social facilitation; Jeanne and Taylor 2009; Shettleworth, 2010). Furthermore, in the field, the presence of conspecifics at a site attracts the foragers of different polistine species (local enhancement or increased

likelihood of visiting a place by virtue of observing others doing it) (Raveret Richter, 1990; Hrnčir et al., 2007; Schueller et al., 2010; Shettleworth, 2010; Taylor et al., 2012; Schueller and Jeanne, 2012; for Vespinae, see Santoro et al., 2015). Also, group hunting, likely related to a form of recruitment, has been noted in the Epiponini, illustrating the possibility of cooperation and coordination (O'Donnell and Hunt, 2013). Yet, except for tandem flights possibly performed by *Vespula germanica* foragers (Lozada et al., 2016), these types of information signals do not direct recruited individuals from the nest to the specific location of a food resource.

We studied the predatory behavior of *Polybia rejecta* (Epiponini) aiming to determine (1) when the wasps forage, (2) if visual cues are used to detect prey by using decoys, (3) the size/weight range of selected prey, (4) the differences in capture behavior according to prey size, (5) the impact of the prey-predator weight ratio on handling time, and (6) experimental manipulations to test for social enhancement, a form of recruitment to food resources.

2. Materials and Methods

2.1. Study sites and experimental set up

This study was conducted at the Hydreco field station at Petit Saut, Sinnamary, French Guiana (5°03'39" N; 53°02'36" W) between 2009 (preliminary observations) and 2015. The climate is tropical moist, with 3500 mm of annual precipitation distributed over 280 days. There is a major drop in rainfall between July and November (dry season) and another shorter and more irregular dry period in March.

The study area, the outer western wall of the Hydreco laboratory, is situated ≈ 200 m downstream from the center of the Petit Saut dam and, at ≈ 30 m height, overlooks the right bank of the Sinnamary River. There, we set up one or the other of two light traps to attract

nocturnal flying insects. The traps consisted of the white western wall (4x2 m) or a white plastic sheet (3x2 m) mounted on a frame, both lit by a self-ballasted 80-watt mercury vapor lamp emitting both white and UV light. The wall or the white sheet were hidden from the seven wasp nests used in this study by the buildings of the research station; the distance separating these nests and the experimental set-up varied from 60.5 m to 105 m.

Each series of observations and experiments was conducted during five consecutive nights without moonlight (two nights before and two nights after the new moon). The light traps attract numerous insects with small moths and small dipterans being particularly abundant. Because most of the insects attracted stay on the wall or the white sheet during the next day, we had the opportunity to work on the foraging behavior of *P. rejecta* wasps which began to hunt on the wall or the white sheet from the first morning of each experimental period (see Raveret Richter, 1990 for training social wasps to prey on furnished insects).

2.2. *The focal social wasp species*

These studies were conducted on the swarm-founding Neotropical social wasp *Polybia rejecta* (Fabricius, 1798) (Vespidae; Polistinae; Epiponini) (Fig. 1) whose nests, which are protected by an envelope, can reach 30 cm in diameter and 2 m in height, although most of them are less than 70 cm in height. These nests have frequently been noted as being associated with the large carton nests of the territorially dominant arboreal dolichoderine ant species *Azteca chartifex*. In this mutualistic association, the ants protect the wasps from army ant attacks, while the wasps protect the ant nests from bird attacks (Herre et al., 1984; Corbara et al., 2009; Somavilla et al., 2013; Le Guen et al., 2015).

Polybia rejecta individuals mainly prey on soft bodied arthropods, especially lepidopteran larvae, and are very aggressive toward humans, who are attacked from more than 15 m away without any “provocation”; their sting is very painful (Starr, 1985; Somavilla et al., 2013; Le

Guen et al., 2015). Note that foraging workers are old individuals whose remaining lifespan is probably short: only 20-25 days in another Epiponini wasp species with large nests (O'Donnell and Jeanne, 1992).

2.3. Selected prey size

During a first series of experiments, we left all of the insects immobilized on the wall or the white sheet during the day following the night-time use of the light trap. This permitted us to record when *P. rejecta* foragers began to hunt and what size classes of insects they select compared to those available. This study was conducted during three non-consecutive days for three different new moons between 6:00 and 9:30. The comparison of the distribution of the size classes of insects attracted by the light traps and those captured by *P. rejecta* foragers was conducted using the Mann-Whitney test.

2.4. Predatory behavior

To study the wasps' predatory behavior, a full repertoire of behavioral acts was first established from observations conducted during preliminary experiments. Referring to this complete list, we recorded each behavioral act performed during predatory sequences. We studied the predatory behavior of *P. rejecta* foragers confronted with three size classes of prey (i.e., 4 mm-long *Drosophila*, 5-6 mm-long Noctuidae and 9-11 mm-long Noctuidae). To select these prey, between 6:00 and 6:10, as the sun began to rise, we touched each insect of an inappropriate species or size that was immobile on the wall or the white sheet (UV-lit the previous night) with the tip of a fine paintbrush. This process caused them to fly away, so that only appropriate items remained; then, we waited for the arrival of the *P. rejecta* foragers.

For each class of prey, we then built a flow diagram where the transition frequencies between behavioral acts were calculated based on the overall number of transitions between each individual behavioral act, a method based on Bayesian procedures (see Dejean, 1980; Bernard et al., 1985).

Using a microscale (Mettler® AE 260), we weighed 25 *P. rejecta* individuals (≈ 15 mm total length) and one of each type of prey tested to calculate the prey-predator weight ratio and verify the upper limit in the selection of insects as prey in terms of size and weight.

During other series of observations of the predatory behavior, we recorded the handling time (from the seizure of a prey until taking off with the prey) corresponding to the capture of one, two and four 4-mm long *Drosophila* as well as 5-6 and 9-11-mm long noctuids (N = 18, 18, 15, 40 and 20, respectively). We conducted a log-normal linear model of handling time as a function of prey classes. Model fit was evaluated graphically by exploring residuals patterns (Bolker et al., 2009). A set of t-tests was performed for pairwise comparisons among prey class effects on log-transformed handling time data, and afterwards p-values were adjusted using False Discovery Rate (FDR) criteria. Also, to verify if visual cues alone can be used to detect prey, we made 30 decoys (triangular pieces of grey carton with a base of 4 mm and height of 10 mm) attached to the wall amid the prey using modelling clay.

We also noted during eight days for two new moon periods (involving two different nests), the number of cases when the *P. rejecta* foragers captured and retrieved only one or several (i.e., up to six items) 4-mm long *Drosophila*. As with the study on the predatory behavior, these small prey were captured on the UV-lit white sheet the previous night whereas, in addition, we placed ≈ 100 freeze-killed *Drosophila* on the ground at the base of the sheet. Using R software (R Development Core Team, 2016), we compared the reactions of the first individuals that came to forage on the white sheet (between 6:30 and 7:30) with those that came to forage between 8:25 and 8:35 and then between 9:25 and 9:35). We compared

the number of cases when foragers retrieved one, two and up to six small prey using a repeated measure ANOVA and the Tukey *post-hoc* test (assumptions of normality and homoscedasticity passed).

2.5. Testing the possibility of nestmate recruitment

First, during four days (from two days before the new moon to the day following it) and for three non-consecutive new moons (i.e., 12 cases), between 6:30 and 11:30, we registered every hour the number of wasps foraging on the wall that was UV-lit the previous night. Using the R packages *car* (Fox and Weisberg, 2011) and *glmmADMB* (Skaug et al., 2014) software, we analyzed the results with a generalized linear mixed model (GLMM) where the response variable (i.e., the number of foraging wasps recorded per time unit) was modeled using discrete hourly time units as fixed factor (five levels) and case identity as random factor. A Poisson error distribution was selected. Model fit was evaluated graphically by exploring residuals patterns. Multiple comparisons between time units were conducted using the Tukey HSD test (R package *multcomp*; Hothorn et al., 2008).

Second, we tested if a kind of recruitment (e.g., nest-based social facilitation, local enhancement in the field, or both) occurs by noting the number of wasps foraging on the wall at 15:00 after all of the prey had already been captured and again 20 minutes later. The following day, we conducted the same type of verifications but this time we also placed a plate containing 50 freeze-killed *Drosophila* at the base of the wall at 15:00. This protocol was repeated twice during seven new moon periods plus once for another new moon; 15 cases in total. Using R software, we analyzed the difference between the numbers of wasps foraging once flies were provided, *versus* non-provided flies situations (considered as a control), by means of a GLM with a Poisson error distribution. Model fit was evaluated graphically by exploring residual patterns.

In a third series of experiments conducted three times (covering three new moon periods), we aimed to distinguish social facilitation from local enhancement in the field. During “controls” occurring two days before the new moon, we noted the number of wasps foraging on the white sheet (it was UV-lit the previous night) every 5 minutes during 35 minutes from the arrival of the first foraging wasp (around 6:30). The next day (preceding the new moon), each wasp coming to forage between 6:30 and 7:05 was captured and temporarily placed in a tube. This permitted us to record the total number of wasps visiting the sheet every 5 minutes, constituting an experimental lot (“all wasps captured”) eliminating both possible local enhancement and social facilitation or any other form of communication. These wasps were freed at the end of the experiment, permitting them to return to their nest; 15 of them were individually marked on the thorax with spots of quick-dry paint (Edding 750® paint marker) of different colors (see LaPierre et al., 2007). The next night (that of the new moon), the white sheet was not lit to limit the effect of the wasp remembering the presence of this favorable patch (24-hour recall is known in another social wasp species; Moreyra et al., 2016). The day after the new moon, the unmarked *P. rejecta* wasps that came to forage on the white sheet were captured until the first marked one arrived and, during the 20 subsequent minutes, all other wasps were captured (as previously, all of these captured wasps were freed at the end of the experiment). The marked wasp was left free to forage, capture a prey and return to its nest. After 20 minutes, we noted the number of wasps that came to forage every 5 minutes during 35 minutes. So, for this second experimental lot (“first marked wasp free, all others captured”) only local enhancement, if any, was eliminated at least at the beginning of the experiment, while possible social facilitation or other kinds of recruitment were permitted. Using R software, we modeled, with a GLM, the number of foraging wasps from the arrival of the first individual as a function of the covariate length of time (in minutes) combined with the experimental protocol applied factor (fixed factor with three levels: “control”, “all wasps

captured”, “first marked wasp free, all others captured”). A Poisson error distribution was selected and a model fit was evaluated graphically by exploring residual patterns. We tested the interaction to detect changes in the temporal pattern of recruitment according to the different experimental protocols. We contrasted model predictions with the least-square means procedure with a fixed significance level of $\alpha=0.05$ using the R package `lsmeans` software (Lenth, 2016).

Because we again lit the sheet during the next new moon period, we verified if the wasps marked with paint still foraged.

3. Results and Discussion

3.1. Size range of the prey / Cafeteria experiments

The first *P. rejecta* foragers began to hunt at 6:30 both during preliminary observations and when we noted the range of size of the prey selected by these foragers.

While the length of the insects attracted varied from 2 mm to 88 mm, the *P. rejecta* foragers captured only 4-14-mm long individuals (Fig. 2). Observations in the field permitted us to note that these wasps mostly hunt small caterpillars, grasshoppers and flies (see also Bichara Filho et al., 2010 for *Polybia sericea*). So, *P. rejecta* foragers are able to adapt very quickly to the possibility of a favorable patch, although the insects here were adults (see also the frequent capture of swarming ants and termites by different epiponine species; Richards, 1978; Raveret Richter, 2000; Jeanne and Taylor, 2009; Dejean et al., 2011).

3.2. Prey capture behavior

Each tested *P. rejecta* forager likely detected the potential presence of prey from a distance as they flew toward the wall or the plastic sheet covered with insects. When

approaching the wall, the foraging wasps began with a concentrated search, hovering up and down ≈ 10 cm from the wall. The contrast of the prey against the wall likely serves as a visual cue because all the 30 decoys made of grey paper were visited by the foraging wasps once or several times (53 visits noted), although they were abandoned immediately after antennal contact.

All types of tested prey can be detected from a distance (up to 8 cm) by hovering wasps, but 4-mm long flies and 5-6-mm long noctuids were rather detected by contact after the wasps landed and walked along a sinuous path; the prey, particularly large ones, can be detected from 1-3 cm (Fig. 3). In all cases, detection was followed by a short antennal contact which preceded the seizure of the prey (i.e. classically, the wasps closed their mandibles on the prey body). Then, a stinging phase followed by a backward movement and prey manipulation occurred if the prey did not escape by flying away. The tested prey were taken to the nest at different percentages. However, 1.66% of the 4-mm long flies and 6% of the 5-6-mm long noctuids were consumed on the spot before the wasps resumed their sinuous path to capture another or several other item(s). Alternatively, the wasps resumed their sinuous path to capture other items keeping the first ones captured between their mandibles. Larger 9-11-mm long noctuids were never eaten on the spot. Instead, the wasps cut off their wings in 66.7% of the cases or cut them into two pieces (16.67%) and transported one piece immediately. They then returned to collect the other piece (Fig. 3).

Compared to other studies, stinging, or at least flexing the gaster in a movement normally linked to stinging, occurred in all cases (see also Olson, 2000 and papers cited therein), a major difference from most other studies dealing with social wasp predatory behavior (Edwards, 1980; Raveret Richter, 2000). Although the sting-insertion itself was not observable, we deduced that the venom acted when the tip of the wasps' gaster came into contact with the prey because the latter almost immediately stopped struggling. The use of the

stinger during predation by *P. rejecta* is in contradiction with the fact that sting apparatus autotomy is thought to occur in this wasp species (Overall et al., 1981). However, we were frequently stung by these wasps and never noted this fact. Moreover, the stingers observed on 50 individuals from eight colonies were smooth (i.e., not barbed), allowing them to sting several times.

As with several other epiponine wasps, *P. rejecta* foragers do not malaxate their prey (Raveret Richter, 2000; Raveret Richter and Jeanne, 1991; Jeanne and Taylor, 2009). When the prey were able to escape, the wasps, seemingly excited, increased both their speed and the sinuosity of their path and immediately seized and stung any newly encountered items and then flew away to take them to their nest (Fig. 3). This behavior increases the probability of finding the escaped prey again and securing it quickly (for non-winged insects). Here, because the targeted prey escaped by flying away, the wasps were able to capture another item with the peculiarity of such excited wasps transporting these heavy prey whole in all cases (while in the “normal situation” the wasps more frequently cut off the wings of these prey or cut them into two pieces; Fig. 3).

3.3. Load size and prey capture behavior

Because only 6.66% of the 9-11-mm long noctuids were transported whole, they likely constituted the maximum load for *P. rejecta* foragers corresponding to 12.60 ± 0.05 mg (mean \pm SE; N = 25 items weighed for each type of tested prey and for the wasps). Indeed, the wasps cut off the wings of 66.67% of other items or cut into two pieces the remaining 16.67% (Fig. 3) and all larger 12-14-mm long moths captured during the cafeteria experiment (see Fig. 2) were cut into two pieces.

Some *P. rejecta* foragers tended to attain this maximum load by retrieving two 5-6-mm long noctuids 6.24 ± 0.04 mg each, so ≈ 12.48 mg, or up to six 4-mm long flies 2.1 ± 0.04 mg

each, so ≈ 12.60 mg. Yet, this occurred only for 1.66% and 2% of the cases for 4-mm long flies and 5-6-mm long noctuids, respectively. This maximum weight of prey captured, ≈ 12.60 mg, corresponds to 30.7% of the mean *P. rejecta* worker wet weight, or 41.05 ± 1.5 mg. The median size of captured prey being 6 mm (see Fig. 2), thus ≈ 7.00 mg, corresponds to ≈ 17.05 % of the mean *P. rejecta* worker wet weight, a value lower than the 24.7% of the mean prey weight for *Polybia sericea* (Bichara Filho et al., 2010).

These results were obtained from wasps belonging to a nest situated 105 m away, but the same studies conducted with foragers from a nest situated 60.5 m away from the light trap led to in similar results (i.e., up to six small flies retrieved and same maximum load of ≈ 12.60 mg; very similar percentages as in Fig. 3). However, based on the central place foraging theory, we expected larger loads due to smaller distances. It seems that in the range of their foraging area the *P. rejecta* foragers react similarly to each prey size and weight, at least in the particularly favorable situation of our experimental set up. By comparison, the *P. rejecta* flight range (105 m x 2 = 210 m in this study) is high compared to other *Polybia* species: *P. scutellaris* 150 m; *P. occidentalis* 126 m; *P. sericea* 75 m and in the range of that found for two *Polistes* species (Bichara Filho et al., 2010 and papers cited therein).

The handling time was significantly higher when the prey was heavier (Fig. 4A) and it increased exponentially with the weight of the prey (Fig. 4B). The capture by *P. rejecta* foragers of only one small prey (i.e., 4-mm long *Drosophila*) rather than several as they can retrieve up to six items (Fig. 3) needs to be considered at the colony level if a form of recruitment is deemed possible. Because the handling time for small prey (i.e., 4-mm long flies) varied significantly with the number of individuals captured (Fig. 4A), we cannot exclude that a given forager favors the recruitment of nestmates and captures only one small prey, while others retrieve several. This might be the case because the individuals that foraged on the white sheet between 6:30 and 7:30 retrieved one small prey in 62.5% of the cases,

while those that foraged later (8:25-8:35 and 9:25-9:35) rather retrieved two to six small prey (Fig. 5).

3.4. Testing if a form of nestmate recruitment exists

We firstly noted that the number of *P. rejecta* foragers on the wall UV-lit the previous night naturally increased until 9:30 and then decreased as the number of remaining potential prey was extremely reduced (Fig. 6A).

Second, when at 15:00 the wall UV-lit the previous night was devoid of prey, only a few *P. rejecta* continued to forage; this situation remained the same during the 20 subsequent minutes. Yet, when the following day at 15:00 we placed a plate containing 50 freeze-killed *Drosophila* at the base of the wall, after 20 minutes we noted a significant increase in the number of *P. rejecta* foragers (Fig. 6B). Here, local enhancement is unlikely due to the small number of foragers involved.

Third, during the experiment conducted early in the morning, when the foragers were captured while they hovered in front of the wall, we noted a significantly lower increase in the number of foraging wasps (see “all wasps captured”; social facilitation and local enhancement eliminated; Fig. 6C) in comparison to the two other experimental situations (i.e., “control”: all of the wasps were free to forage on the wall, opening up the possibility of multiple recruitments; “first marked wasp free-all others captured”: only one wasp marked two days before with paint was allowed to return to its nest where it can eventually recruit nestmates; “all wasps captured”: all the wasps were captured as they arrived to forage on the wall, so that they cannot return to their nest and recruit nestmates). Because the number of *P. rejecta* foragers increased the most during the 35-minute monitoring period in the control series (see “Control”; Fig. 6C), a form of recruitment is likely; both social facilitation and local enhancement could be involved in this process. A very similar trend, not significantly

different, was observed when we left only one marked forager to capture a prey and transport it to the nest (see “First marked wasp free; all others captured”; Fig. 6C); this time, only social facilitation was permitted. This paint-marked forager was found again among nestmates registered first 20-25 minutes later (i.e., 20 minutes corresponds to the first observation recorded in this case), but we cannot assert that tandem flights occurred as suggested for *V. germanica* (Lozada et al., 2016). Indeed, the exponential shape of the cumulative curves in the two last cases is likely the result of a kind of recruitment if compared to the linear shape of the first case.

Therefore, we argue that a kind of recruitment occurred. In this situation, the indication of the general direction from the nest is insufficient due to the presence of buildings between the wasp nests and the targeted favorable patch represented by the wall or the white sheet covered with potential prey. Indeed, one to three flight angles were necessary to go around the buildings and reach the targeted food source. Because local enhancement was eliminated at least during the beginning of the experiment where the first marked wasp remained free and all of the others were captured, social facilitation was involved as is known for other vespid wasps (Hrncir et al., 2007; Schueller and Jeanne, 2012; Taylor et al., 2010, 2012). This is likely facilitated by the ability of foragers to detect food at a relatively long distance (see Raveret Richter, 2000).

Note that during the new moons following these experiments, we never recorded paint-marked *P. rejecta* foragers. This is likely because wasps are able to tear off the paint marks or to the fact that foragers are already old with a short remaining lifespan (only 20-25 days for *Polybia occidentalis*; O'Donnell and Jeanne, 1992).

In conclusion, *P. rejecta* foragers exhibit a flexible foraging behavior, enabling them to capture several types of prey from favorable patches that were depleted in approximately 3

hours (06:30-09:30) in our experiments. Experimental evidence supports nest-based social facilitation as a mechanism of recruitment to prey- rich resources.

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Figure legends

Fig. 1. A *Polybia rejecta* forager marked with a spot of paint.

Fig. 2. Comparison of the percentages of size classes of insects attracted by the light trap and those selected as prey by *Polybia rejecta* foragers. Statistical comparison conducted from the baseline data; Mann-Whitney test; $N = 45$ in both cases; $U = 390.5$; $P < 0.0001$.

Fig. 3. Flow diagrams representing the sequences of acts during prey capture by the *Polybia rejecta* foragers. The percentages were calculated from the total number of cases.

Fig. 4. A. Handling time in five situations: flies are 4-mm long *Drosophila*, small moths are 5-6-mm long noctuids and large moths are 9-11-mm long noctuids. Statistical comparisons: ANOVA ($F = 31.44$, $P < 0.0001$); T-test pairwise comparisons *post-hoc* test adjusted by False Discovery Rate (FDR), different letters indicate a significant difference at $P < 0.01$. B. Relationships between the handling time and the corresponding wet weight of the prey.

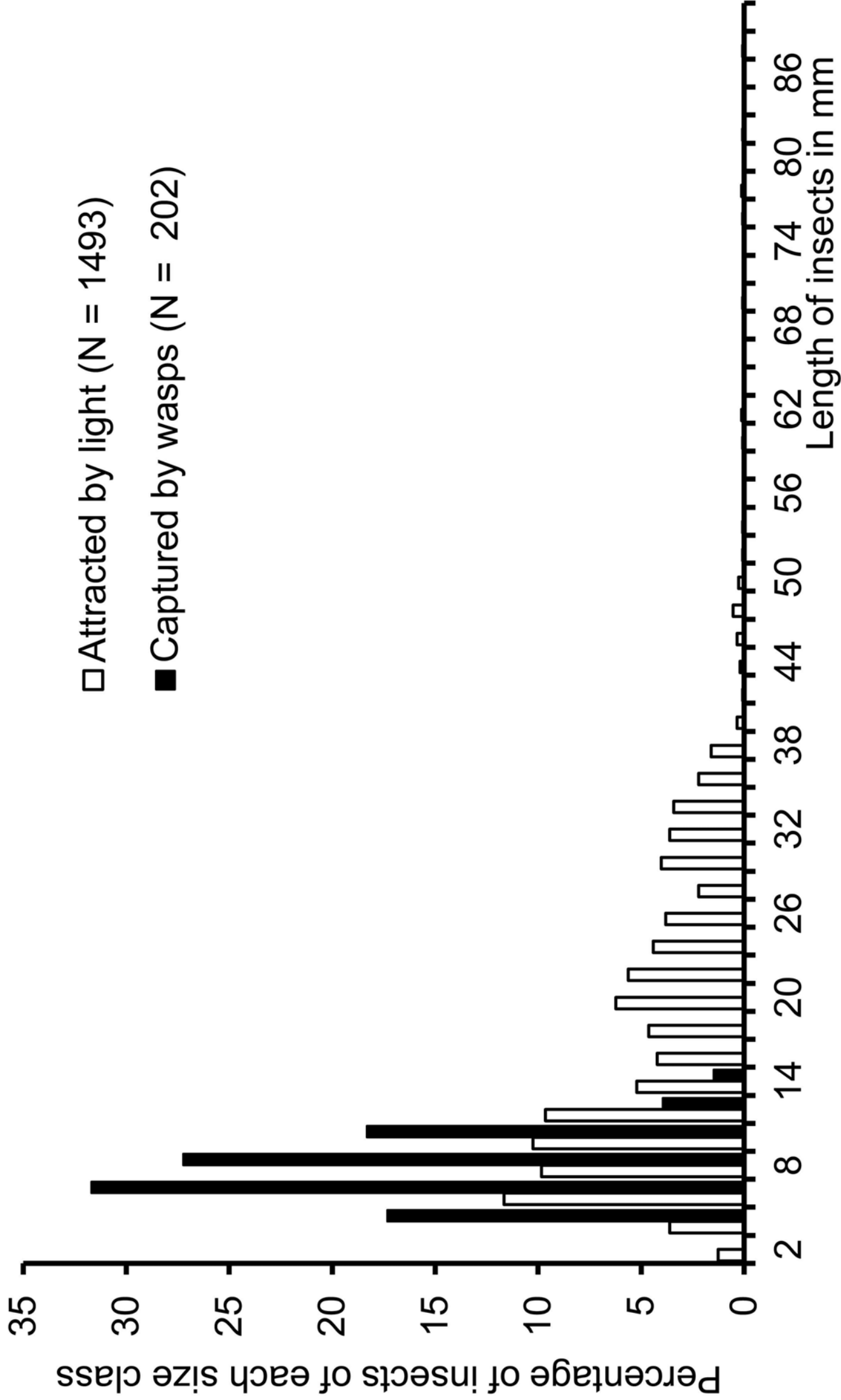
Fig. 5. Comparison of the percentages of cases when the *Polybia rejecta* foragers confronted with small prey (i.e., 4-mm long *Drosophila*) captured and retrieved one item or several (up to six). Statistical comparisons: ANOVA ($F = 20.25$, $P < 0.0003$); Tukey *post-hoc* test, different letters indicate a significant difference at $P < 0.01$.

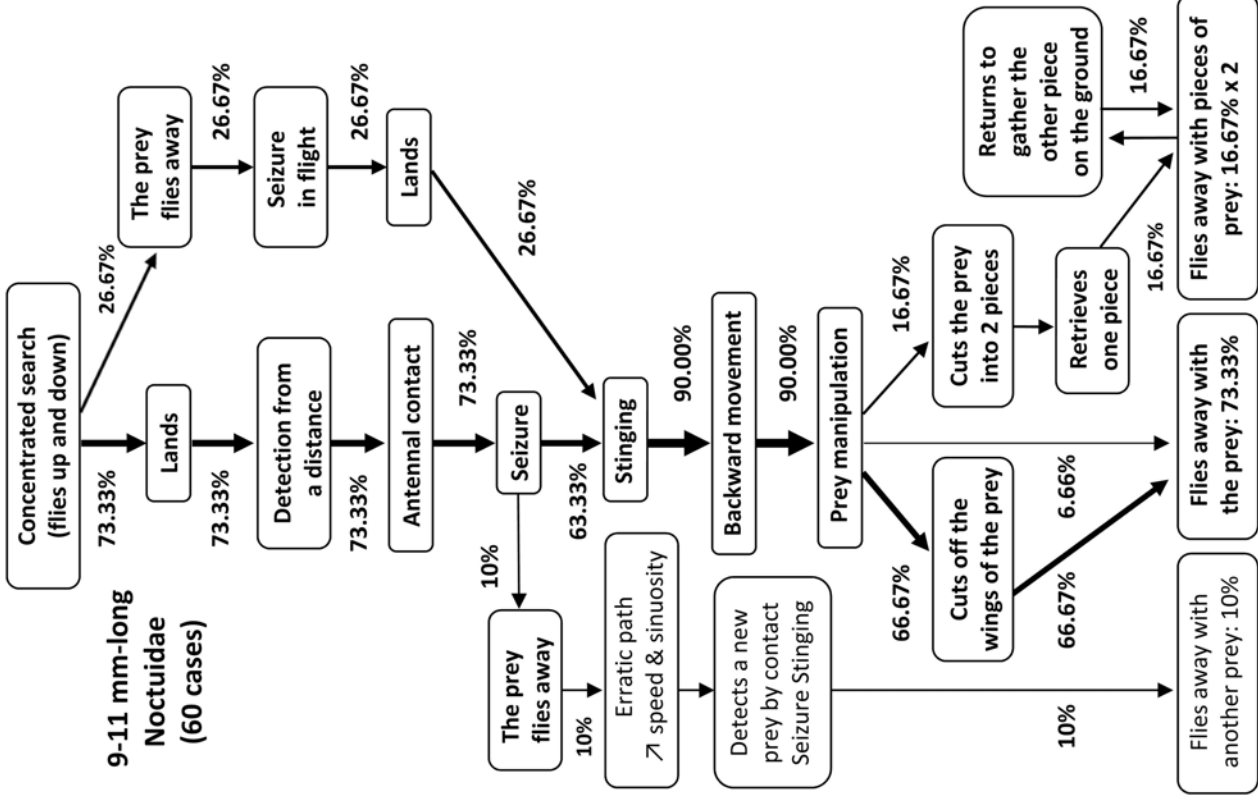
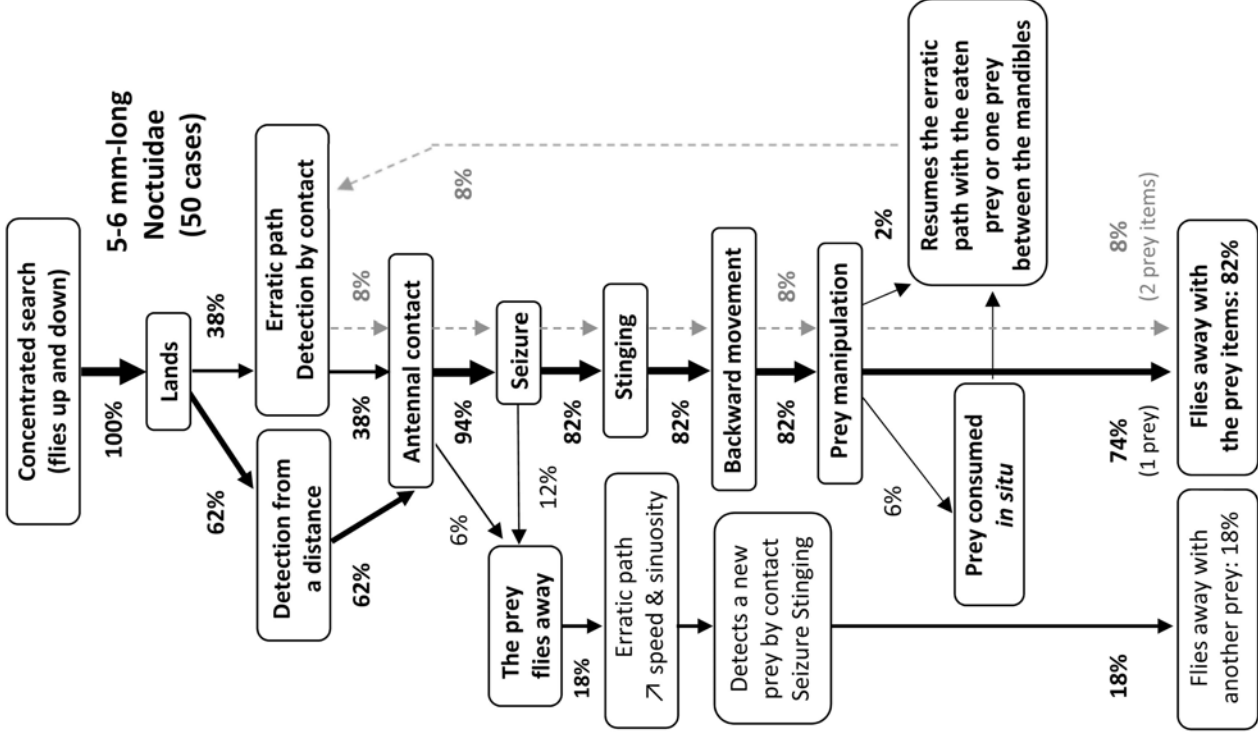
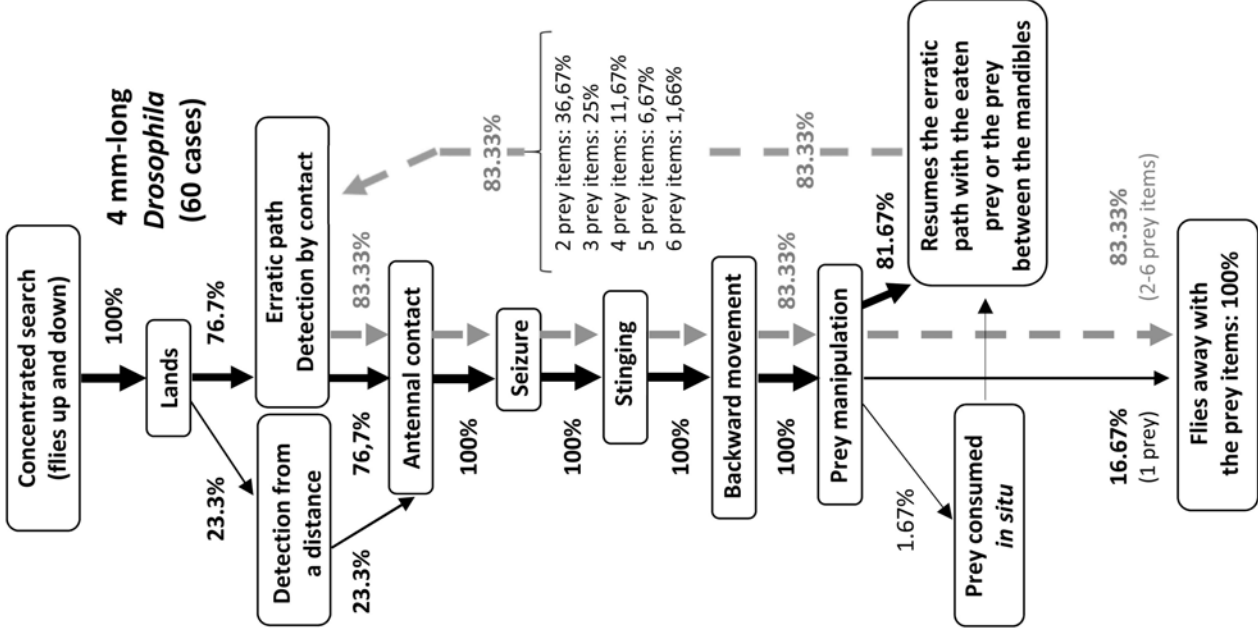
Fig. 6. Search for the existence of a kind of recruitment in *Polybia rejecta*. A. Sequence of the *P. rejecta* forager arriving on the wall lit the night before (means \pm SE ; 12 cases; three non-consecutive new moons; three replicates per new moon). Statistical comparison: GLM with a Poisson error distribution ($F = 19.78$, $P < 0.0001$); Tukey HSD *post-hoc* test, different letters

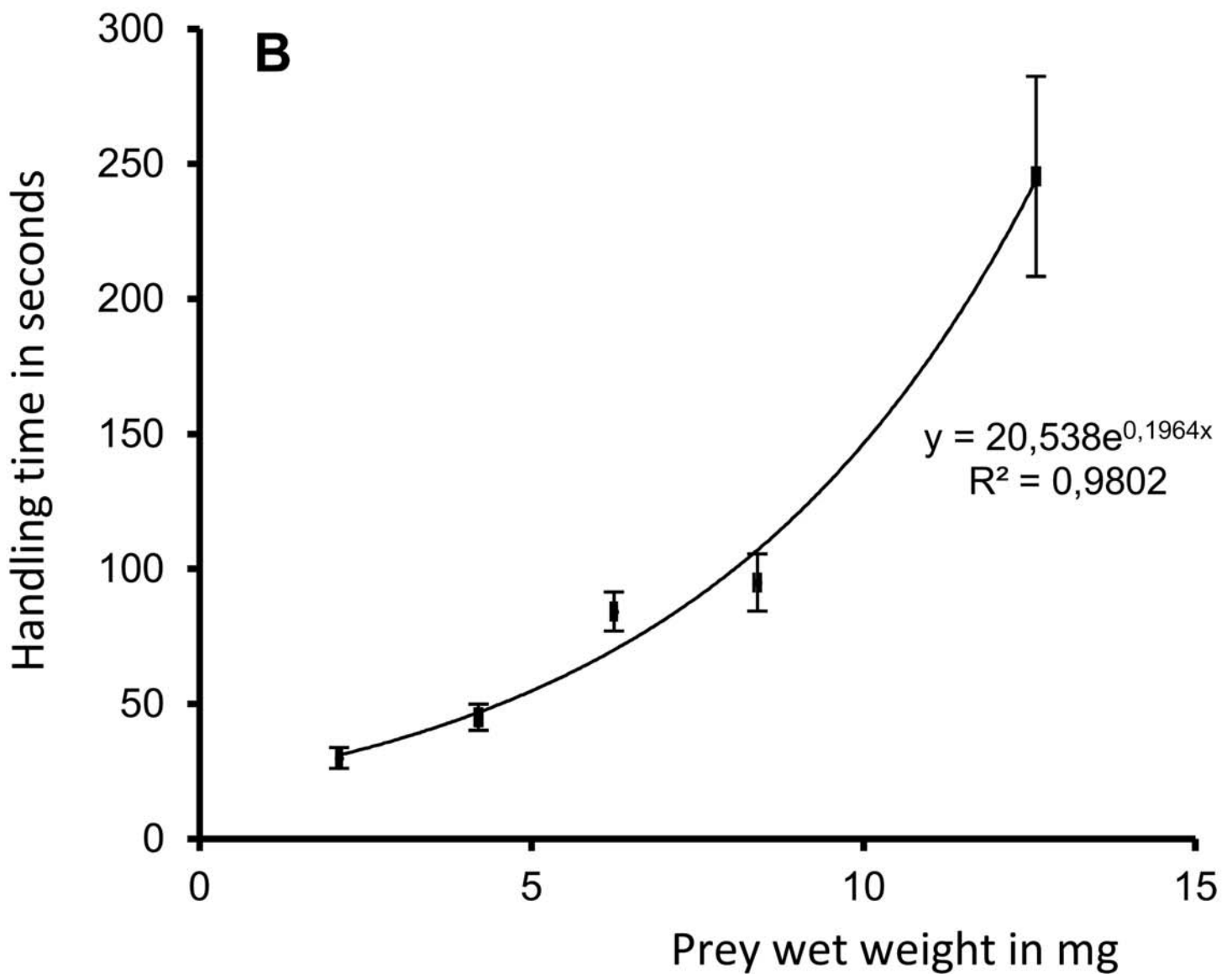
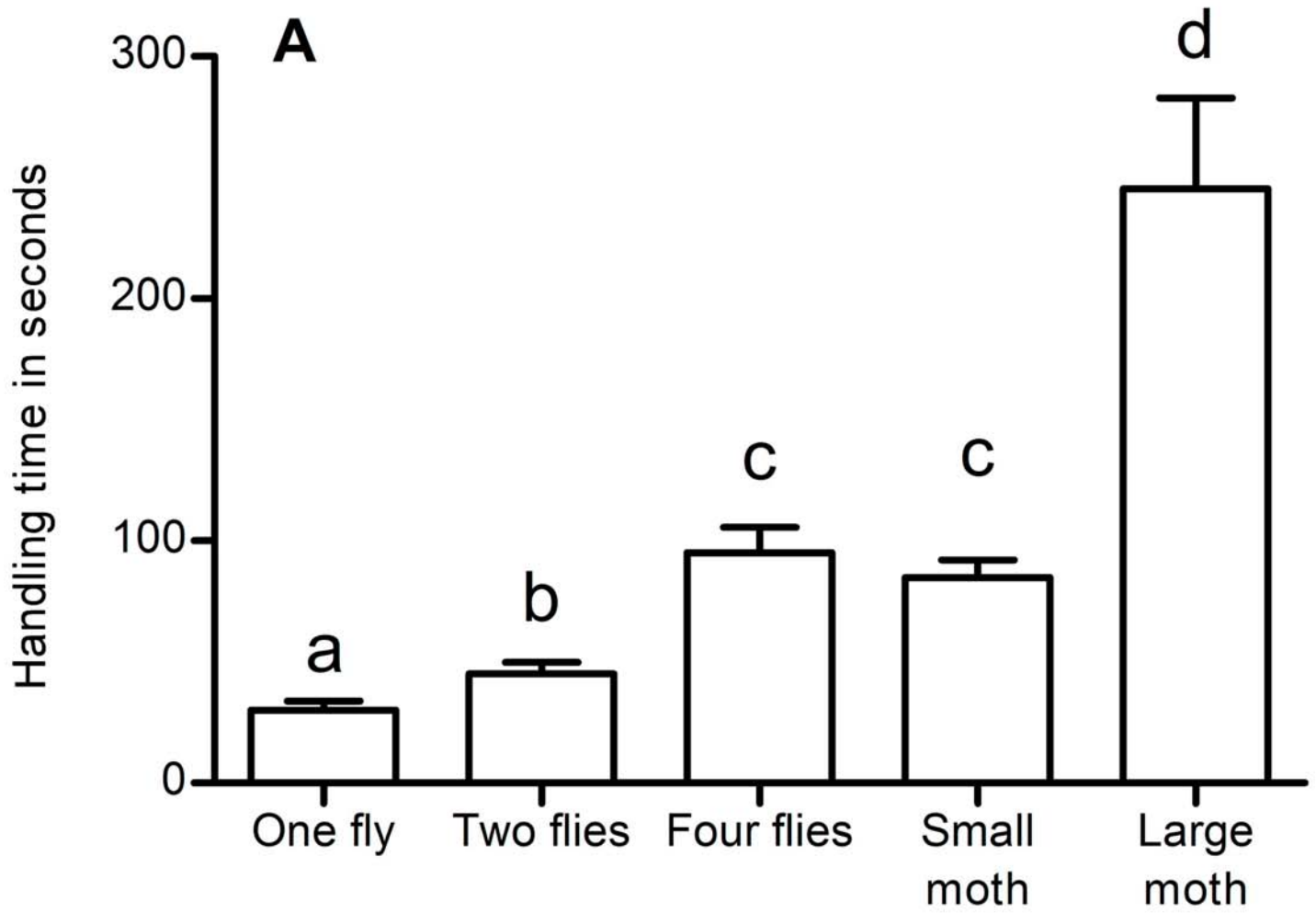
indicate significant differences at $P < 0.05$. B. At 15:00 after the wall was depleted of prey by foraging wasps, residual foraging individuals were counted and again 20 minutes later. The same experiment was conducted the following day, but 50 freeze-killed drosophila were placed at the base of the wall at 14:00. Statistical comparison: GLM with a Poisson error distribution ($Chi\text{-square} = 99.28$, $P < 0.0001$). C. Observed counts of foraging wasps and model projections under the three experimental protocols considered (i.e. "control", "all wasp captured" and "First marked wasp free; all others captured") arriving between 6:35 and 7:40 on the wall which was lit the previous night. Statistical comparisons: GLM with a Poisson error distribution; Covariate Length of time ($Chi\text{-square} = 190.37$, $P < 0.0001$); Factor Experimental protocol ($Chi\text{-square} = 50.48$, $P < 0.0001$); Interaction term Length of time x Experimental protocol ($Chi\text{-square} = 14.41$, $P = 0.0007$). Model prediction slopes contrast by least-square means; Control *vs.* First marked slopes did not significantly differ. All captured *vs.* Control and All captured *vs.* First marked differed at significant level of $\alpha = 0$.



2 mm







□ 1 prey ▨ 2 prey ▩ 3 prey ▧ 4 prey ▦ 5 prey ■ 6 prey

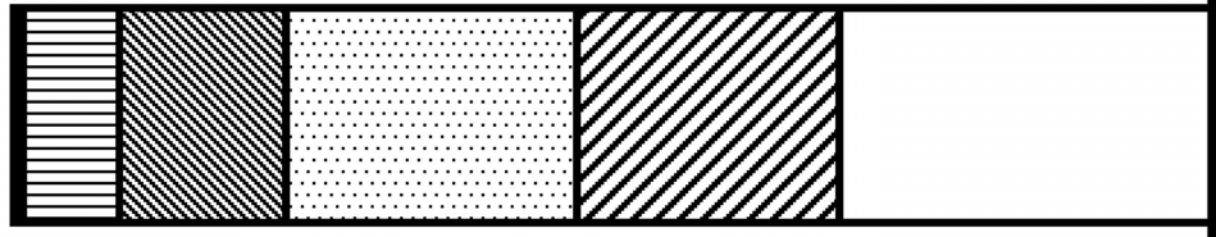
a

100%
80%
60%
40%
20%
0%



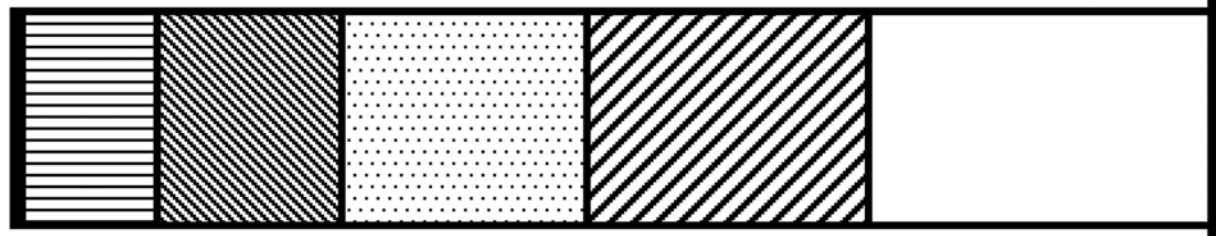
N = 24

b



N = 87

b



N = 98

6:30-6:40

8:25-8:35

9:25-9:35

