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ARTICLE

Non-mimetic jumping spider responses towards three species of ants and their mimics

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Abstract

Ants and jumping spiders are prominent invertebrate predators in terrestrial ecosystems. Many jumping spiders are thought to avoid ants and their ant mimicking spiders, yet little is known if they discriminate among different species of ants or mimics. Chances of encountering multiple ants, and mimics all in a relatively short stretch of time and space is fairly common in the tropics, but how all these species interact with each other is not known. In a laboratory setup, we first examined the behavioral response of three ant species (*Oecophylla smaragdina*, the weaver ants; *Camponotus sericeus*, the golden backed carpenter ants, and *Leptogenys processionalis*, the procession ants), and their mimics in the genus *Myrmarachne* towards the non-mimetic jumping spider *Plexippus paykulli*. We then examined the response of *P paykulli* towards the three ant species, and their mimics. Our results suggest that weaver ants and procession ants are more aggressive towards non-mimetic jumping spiders as compared to golden backed ants. The three mimics also differed in their response towards the non-mimetic jumping spider: both weaver ant mimics and golden backed ant mimics charged at the non-mimetic jumping spiders as compared to the procession ant mimics. On the other hand, *P. paykulli* did not treat all ants similarly: while they looked, and approached the black procession ants by visual cues, they stayed away from weaver ants and golden backed ants. However, *P. paykulli* treated the three ant mimicking spiders similarly: while they looked at the mimics, they rarely approached or attacked them. Jumping spiders and ants are sympatric, and it may be advantageous to selectively avoid some ants over others. Studies, such as ours go a step closer in understanding multispecies predator–prey interactions.

Keywords Ant mimicking spider · Weaver ant · Visual cues · *Myrmarchane*

Introduction

Predator–prey interactions are important in maintaining the dynamics of ecological communities. Predators have both consumptive and non-consumptive effects on prey, and thus the identity of predators often influences prey behavior (Turner et al. 1999; Catano et al. 2017). These in turn influence prey's interaction with other predators and conspecifics and foraging decisions (Lima 1998). Predators' decisions to attack certain prey over others in an area may also be driven by experience, internal state, cognitive abilities, etc., as well as relative abundance, spatiotemporal distribution and, habitat complexity in which prey is located (Ware 1972; Crowder and Cooper 1982; Li et al. 2003; Jakob et al. 2011; Powell et al. 2019).

Ants are one of the top invertebrate predators in tropical and subtropical ecosystems (Hölldobler and Wilson 1990; Roslin et al. 2017). They compete for resources (including prey or nesting areas) with other arthropods, leading to non-consumptive effects on arthropod communities (Halaj et al. 1997; Ibarra-Isassi and Oliveira 2018). Because of their ubiquitous presence, aggressive nature and communal defense, ants are particularly dangerous to small arthropods.

Jumping spiders are another group of dominant arthropod predators that have diversified extensively, especially in the tropics (Coddington and Levi 1991). Jumping spiders are known for their unique vision, as they have achieved a high degree of spatial resolution, as well as a wide field of view (Land 1972; Forster 1985; Harland et al. 2012). Studies have shown that jumping spiders can tell prey from non-prey based on the certain key features, such as movement,

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shape, or color; the salience of one feature over the other depends on the species of jumping spider studied, context, or biological relevance of the stimulus (Nelson and Jackson 2006; Bednarski et al. 2012; Dolev and Nelson 2016). For example, *Phidippus audax* preferred motion cues rather than the shape of the prey to make predatory decisions (Bednarski et al. 2012). *Evarcha culicivora* on the other hand used shape of dead lures to identify its preferred mosquito prey (Nelson and Jackson 2006). Both naïve and field-caught *Habronattus pyrrithrix* avoided crickets that were painted red (Taylor et al. 2014), but they could also be trained to prefer them (Taylor et al. 2016), demonstrating flexibility in color learning during foraging. Spiders' ability to tell prey from non-prey may also depend on the microhabitat structures, and various other arthropods present in that habitat (Powell et al. 2019).

Ants and jumping spiders overlap in their habitats, and are often intraguild predators (Okuyama 2002; Sanders and Platner 2006; Sanders et al. 2008). Although ants pose a threat to various spiders (Halaj et al. 1997), jumping spiders can potentially escape ant attacks because of their good vision. Earlier research suggests that jumping spiders avoid live ants, as well as motionless ant dummies by using visual cues (Nelson et al. 2006, 2020). But detailed observations of interactions between ants and jumping spiders is needed.

Why might it be important to study responses of ants and jumping spiders towards each other? First of all, not all ants are similar—ants may differ in terms of their movement, territoriality, foraging behavior, aggressiveness etc. (Hölldobler and Wilson 1990). In such cases, it makes sense for spiders to employ a 'safety first' approach, and stay away from aggressive ants. Spiders, however, could afford to forage closer to less aggressive ant species, and sometimes even prey on insects tended by ants (Del-Claro and Oliveira 2000; Mody and Linsenmair 2003). Second, ant-mimicking spiders are Batesian mimics, and are perfectly edible prey of jumping spiders (Cushing 1997 and references therein; Nelson 2012). Among other visually oriented arthropods, jumping spiders are considered a driving force behind the evolution of ant mimicry (Huang et al. 2011). Spiders in at least 13 families exhibit morphological and behavioral resemblance towards ants; jumping spiders in the genus *Myrmarachne* in particular have some astonishingly striking mimics (Cushing 1997). Few studies have looked into the responses of *Myrmarachne* towards its own model ants or non-mimetic jumping spiders (Nelson and Jackson 2007). Third, chances of encountering various species of ants or their mimics in a short stretch of time is fairly common in the tropics. Previous work has examined jumping spider responses to dead lures of ants and mimics (Nelson et al. 2006), one particular species of ant and its mimic (Huang et al. 2011), or how multiple spiders respond to one specific ant species (Nelson et al. 2020). Studies of detailed behavioral responses of different ant species towards non-mimetic jumping spiders, and responses of non-mimetic jumping spiders towards ants and their mimics are rare (Nelson et al. 2006; Huang et al. 2011; Durkee et al. 2011; Nelson 2012).

The objective of this study is twofold. First, we examined the response of three tropical ant species and their mimics towards generalist, non-mimetic jumping spider predators in the genus *Plexippus* Three species of ants, the weaver ant (*Oecophylla smaragdina*), the golden backed ants (*Camponotus sericeus*), and the procession ants (*Leptogenys processionalis*) differ in their natural history. Although weaver ants and procession ants are known to be aggressive towards many arthropods (Maschwitz et al. 1989; Hölldobler and Wilson 1990), there are no such reports on golden backed ants. Moreover, there are no experimental studies on how these ants respond towards *P. paykulli*, which are found in habitats similar to these ants. *P. paykulli* mostly feed on several kinds of insects up to twice its body size, but also on conspecific and heterospecific spiders (Jackson and Macnab 1989, pers obs).We also examined the response of three sympatrically occurring ant-mimicking spiders in the genus *Myrmarachne* towards *P. paykulli*. Although there are several studies examining the response of jumping spiders towards the mimetic spiders, studies looking from the mimetic perspective are rare (Nelson and Jackson 2007; Ceccarelli 2009). Second, we examined if *P. paykulli* differentiate between these ants and mimics using visual cues by performing behavioral assays where tactile and chemical cues were controlled for. Our study attempts to understand how multiple species of co-occurring ants, ant mimicking and non-mimetic jumping spiders perceive and respond towards each other.

Methods

Study species collection and maintenance

We chose three tropical ant species of comparable sizes that differed in their natural history, and that were abundant in the habitat occupied by the non-mimetic jumping spider *Plexippus paykulli* Audouin, 1826. Weaver ants (*Oecophylla smaragdina* Fabricius 1775), are reddish orange in color, and form trails while foraging; procession ants (*Leptogenys processionalis* Jerdon 1851) are black in color, and also form trails while foraging (Maschwitz et al. 1989); and golden backed ants (*Camponotus sericeus* Fabricius1798) have a prominent golden abdomen with a black head and thorax, and are solitary foragers (Hölldobler et al. 1974). The three species of mimics were, the weaver ant mimic (*Myrmarachne plataleoides* Cambridge 1869), golden backed ant mimic (*Myrmarachne* sp.), and a black mimic (*Myrmarachne melanocephala* MacLeay 1839) (Fig. 1). Although

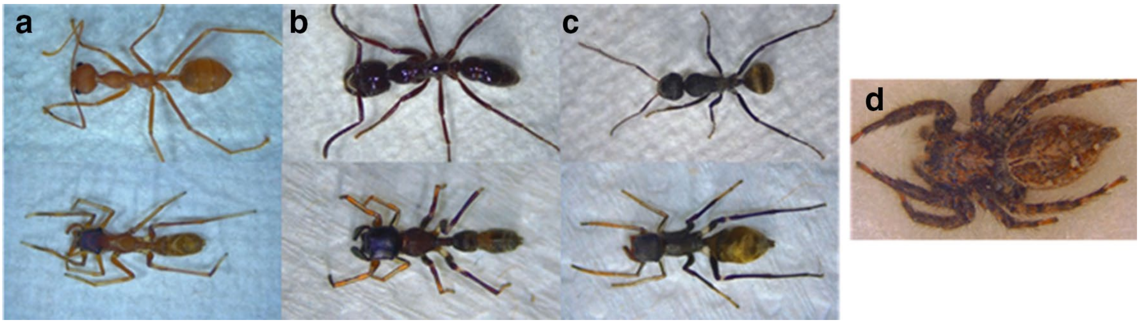

Fig. 1 Three ant species, their mimics and the jumping spider used in the study: **a** weaver ant (*Oecophylla smaragdina*) and its mimic (*Myrmarachne plataleoides*). **b** Procession ant (*Leptogenys processionalis*) and a generic black mimic (*Myrmarachne melanocephala*). **c** Golden backed (*Camponotus sericeus*) ant and its mimic (*Myrmarachne* sp.). All ants are in the top panel, and mimics in the bottom. **d** *Plexippus paykulli*, jumping spider. Ants were on an average 7.71 ± 0.62 mm, mimics 6.4 ± 0.88 mm, *P. paykulli* were 7.91 ± 1.39 mm in length

weaver ant and golden backed ant mimics resembled specific model ants (Mathew 1954; Borges et al. 2007), from our observation, black mimics resembled a generic black ant, including procession ant. Potential model ant species for *M. melanocephala* has not been reported in the literature.

Ants, non-mimetic jumping spiders and ant mimicking spiders were collected from different areas of Bangalore, Karnataka, India. *Plexippus paykulli*, one of the most abundant species found, were collected two days prior to experiments. After capture, the spiders were individually housed in 8 cm diameter plastic boxes with holes for ventilation, and a moistened piece of cotton for hydration. Female ant mimicking spiders were collected one to four days prior to the experiment, and maintained in the same way as *P. paykulli* spiders. Only female ant mimicking spiders were collected due to their greater resemblance to ants as compared to males, and because they were found be more common in the study area (pers. obs.). Mimics or non-mimetic spiders were not fed prior to the experiments. Non-mimetic jumping spider *P. paykulli* on an average were 7.9 ± 1.4 mm, ant and ant mimic sizes were as follows: Weaver ant: 8.2 ± 0.08, golden backed ant 7.4 ± 0.08 mm, and procession ants 7.63 ± 0.33 mm. Weaver ant mimic 6.37 ± 0.88 mm, golden backed ant mimic 5.97 ± 0.58, and black ant mimic was 6.38 ± 1.2 mm. Foragers of all three species of ants were collected on the day of the experiment. For ant responses towards non-mimetic spiders, both *Plexippus paykulli* and *P. petersi* were used, but for all other experiments, only *P. paykulli* was used, as that was the most abundant non-mimetic spider found.

Ant response towards non-mimetic jumping spiders

To examine response of ants towards non-mimetic jumping spiders, we carried out the following experiment in June-Jan 2017–2018. An individual of weaver ant, procession ant and golden backed ant, ($n = 16$ for each ant species), and a non-mimetic jumping spider (*Plexippus petersi* or *Plexippus paykulli*) was enclosed in a 5 cm^3 transparent tube and the latency of the ant to bite the spider in 3 min was recorded. An ant opening and closing its mandibles on any part of a spider's body was considered as a bite. Latency of the ants to bite non-mimetic jumping spiders were analyzed with Mann–Whitney *U* test. All statistical tests were carried out on R version 3.3.2 (R Core Team 2018). No statistical tests were performed if sample sizes were below 5, as the *p* value can be inaccurate for very low sample sizes.

Mimic response towards non-mimetic jumping spider

To examine mimics' responses towards non-mimetic jumping spider *P. paykulli*, we performed the following experiment in June–Jan 2018–2019. We restricted a mimic (weaver ant, golden backed ant, or black mimic) and *P. paykulli* in a Petri dish of 9 cm diameter and recorded latency of the mimic to charge (moving towards) the *P. paykulli* in 5 min. 20 weaver ant mimic (*Myrmarachne plataleoides*), 22 golden backed (*Myrmarachne* sp.), and 11 black mimic (*Myrmarchne melanocephala*) trials were conducted. Ant and mimic aggression trials are not directly comparable due to differences in the types of behaviors shown. Latency of the mimics to charge non-mimetic jumping spiders were analyzed with Mann–Whitney *U* test.

Non-mimetic jumping spider responses towards ants and mimics

To examine the visual response of non-mimetic jumping spider *P. paykulli* towards ants and mimics, we designed the following setup. A Petri dish (9 cm) was modified to include an inner ring of 2.8 cm diameter made with a strip of clear acetate. The transparent ring controlled for tactile cues, thus allowing visual cues to be seen from either side of the ring.

To make sure the spiders could see through the transparent ring, we put a housefly inside the ring, and examined hunting behavior of jumping spiders towards the fly. In 37 out of 44 trials (84.1%), *P. paykulli* attacked the flies, showing that the transparent ring setup did not hamper the spiders' ability to recognize prey and perform normal hunting behaviors. After this experiment, we used the same experimental setup to test response of *P. paykulli* towards ants and mimics.

Each ant was released inside the transparent ring. Adding a *P. paykulli* into the outer portion of the dish commenced a trial which was video-recorded using a Sony handycam (HDR-PJ600VE) for 5 min in a well-lit arena. After each trial, we wiped the arena with ethanol to remove chemical cues. Spiders or ants were used only once for all the trials, and a total of 14 trials with weaver ants, 16 trials with procession ants, and 10 trials with golden backed ants were carried out.

To examine the visual response of *P. paykulli* towards mimics, each individual spider was presented with a weaver ant mimic ($n = 24$), golden backed ant mimic ($n = 22$), or black mimic ($n = 11$) in the same setup as used for ants. All test animals were used only once.

Response of *P. paykulli* towards ants/mimics were coded using BORIS, a video coding software (Friad and Gamba 2016) as follows: (1) look: Spider orients its cephalothorax towards the stimulus (ant or a mimic). This is typically the first component of jumping spider response where the spider faces the prey or a moving object. This behavior is elicited by a prey, predator, conspecific spiders, or any moving stimulus (Forster 1977) (2) Approach: spider moves towards the stimulus, (3) Attack: spider pounces on the wall of the outer ring at the stimulus. (4) Avoid: spider moves away from the stimulus, while oriented towards it. The proportion of time spent and the frequency of these behaviors in 5 min was measured. Kruskal–Wallis test followed by Dunn's test with Bonferroni correction (Pohlert 2014) was used to analyze response of *P paykulli* towards ants as well as ant mimics.

Results

Ants vary in their latency to bite non-mimetic jumping spiders

13 out of 16 weaver ants (81.25%), 12 out of 16 procession ants (75%), and only 4 out of 16 of the golden backed ants (25%) bit non-mimetic jumping spiders *P. paykulli, or P. petersi*. Latency to bite spiders by weaver ant and procession ants was on average less than a minute, while it was twice as much by golden backed ants (Table 1). There was no significant difference between the time taken to bite by the weaver ants and the procession ants (Mann–Whitney $U = 5$, $p = 0.134$). Since only 4 golden-backed ants bit non-mimetic spider, we did not compare their latency with other ants, as statistical tests for very low sample sizes can result in inaccurate p values.

Table 1 Latency of ants to bite non-mimetic jumping spider

Ant	Latency to bite (sec)
Weaver ant	36.8 ± 41.6
Procession ant	19.8 ± 34.9
Golden backed ant	87.6 ± 71

Table 2 Latency of ant-mimicking spiders to charge at non-mimetic jumping spider

Mimic	Latency to attack (sec)
Weaver ant mimic	52.69 ± 85.59
Black mimic	88.5 ± 122.81
Golden backed mimic	51.43 ± 65.56

Mimics do not vary in their latency to charge non-mimetic jumping spiders

13 out of 20 weaver ant mimics (65%), 14 out of 22 of golden backed ant mimics (63.63%), and 4 out of 11 black mimics (36.36%) charged at the non-mimetic spider *P. paykulli*. Unlike ants, charges by mimics rarely culminated in bites. Weaver ant and golden backed ant mimics did not differ in their latency to charge towards *P. paykulli* (Mann–Whitney $U = 101$, $p = 0.64$, Table 2). Since only 4 of the black mimics charged at the jumping spiders, we did not compare their latency with other mimics.

Non-mimetic jumping spiders respond differently towards ants but not towards mimics

The non-mimetic jumping spiders *P. paykulli* differentiated ants in certain behaviors, such as looks and approaches. *P. paykulli* spent a significantly longer time looking at procession ants as compared to weaver ants (Kruskal–Wallis test: Looks: χ^2: 6.7649, $p = 0.034$, Fig. 2a, Table 3). Furthermore, while *P. paykulli* frequently approached procession ants, they rarely approached weaver ants or golden backed ants (Approach: χ^2: 7.7361, $p = 0.021$; Fig. 2b, Table 3). Spiders however rarely attacked any of the ants and avoided all of them similarly (Attacks: χ^2: 4.5179, $p = 0.10$; Avoid χ^2: 0.6775, $p = 0.7$, Fig. 2c, d).

P. paykulli did not perceive ant mimicking spiders as potential prey: although it spent time looking at the mimics it showed little interest in any other behaviors. Moreover, *P. paykulli* also did not differentiate among the three mimics (Kruskal–Wallis test: Looks: $\chi^2 = 3.55$, $p = 0.17$;

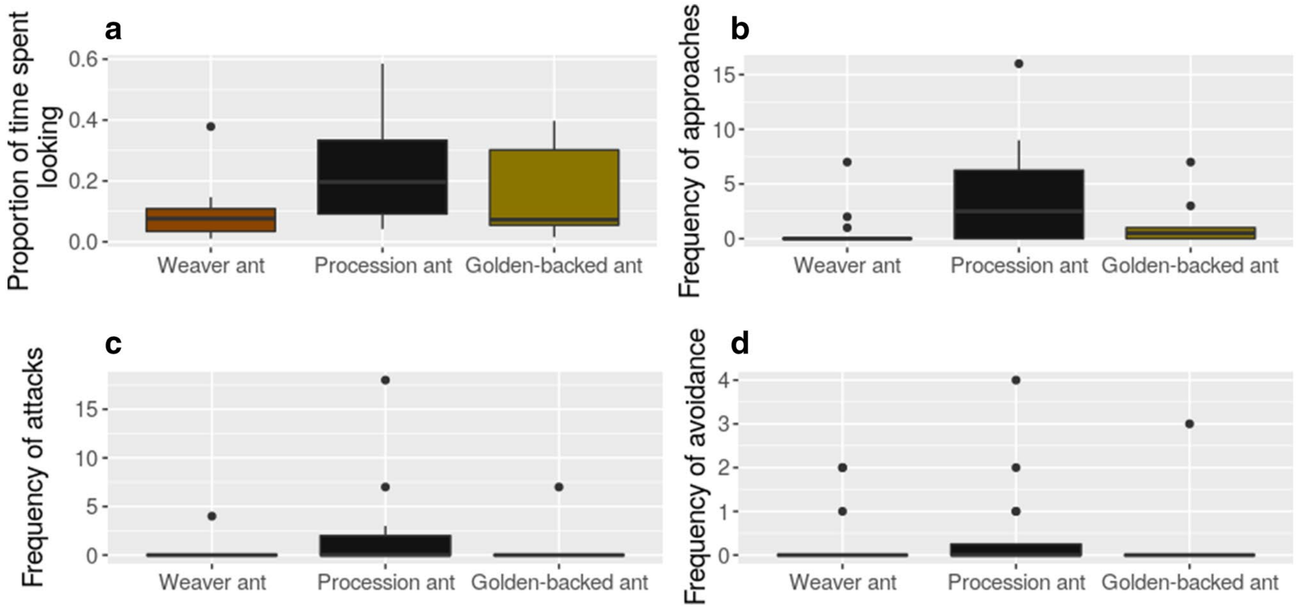

Fig. 2 Responses of *Plexippus paykulli*, a non-mimetic jumping spider to ants: Responses differed in terms of proportion of looks (**a**), and frequency of approaches (**b**), but not with attacks and avoidances (**c**, **d**). Box plot represents median values, with interquartile range, minimum, maximum values with dots representing outliers

Table 3 Non-mimetic jumping spider responses towards three ants: post hoc Dunn's test *p* values (for 'looks' and 'approaches') are presented below, where significant values are highlighted

Behavior	Weaver ant vs. golden backed ant	Weaver ant vs. procession ant	Procession ant vs. golden backed ant
Looks	1.000	0.031	0.436
Approach	0.925	0.017	0.431

Approaches: $\chi^2 = 1.03$, $p = 0.6$, Attacks: $\chi^2 = 0.15$, $p = 0.93$, Avoidances: $\chi^2 = 1.98$, $p = 0.37$; df = 2 for all categories, Fig. 3).

Discussion

In this study, we found that weaver ants and procession ants were aggressive towards non-mimetic jumping spiders *P. paykulli* and *P. petersi*. Weaver ant mimic and golden backed ant mimics in the genus *Myrmarchne* also charged at *P. paykulli*. In addition, *P. paykulli* varied in its response towards ants, where they looked and approached procession ants more than weaver ants and golden backed ants. *P. paykulli*; however, treated all the three mimics similarly, where they rarely approached or attacked any of them. Earlier studies suggest that non-mimetic jumping spiders avoid ants and their Batesian mimics, but few have examined a detailed response of spiders towards different species of ants and their mimics that share similar habitats.

Weaver ants and procession ants were most aggressive, as they readily bit the non-mimetic jumping spiders in over 75% of the trials. Both weaver ants and procession ants are known for their aggressive attacks on arthropods (Maschwitz et al. 1989; Hölldobler and Wilson 1990). The golden backed ants, on the other hand, rarely bit the spiders (25% of the trials). Although ants are generally considered to be aggressive towards many arthropods, by comparing their latency to bite the spider, we have shown here that not all species are aggressive to a similar extent.

Ant mimicking spiders morphologically and behaviorally resemble their model ants (Cushing 1997). We found that the weaver ant mimic charged at *P. paykulli* in over 60% of the trials, suggesting their behavior may be similar to their model ants. Weaver ants attack any intruder by raising their abdomen, and antenna, and we found the weaver ant mimics to exhibit these very specific behaviors. Unlike its model ant, the golden backed mimic charged at the jumping spiders in over 60% of the trials, suggesting that the mimics may not be similar in their behavior with respect to their model ants.

Many jumping spiders are known to avoid ants (Cushing 1997; Nelson et al. 2006, 2020; Huang et al. 2011; Durkee et al. 2011). A recent study suggests that several species of jumping spiders innately avoid live army ants (Nelson et al. 2020). Our current study shows that *P. paykulli* can discriminate three species of ants by visual cues alone. By looking at detailed behavioral response of *P. paykulli* we can understand at what point a jumping spider categorizes ants as potential predators. Predator identity may help the spiders

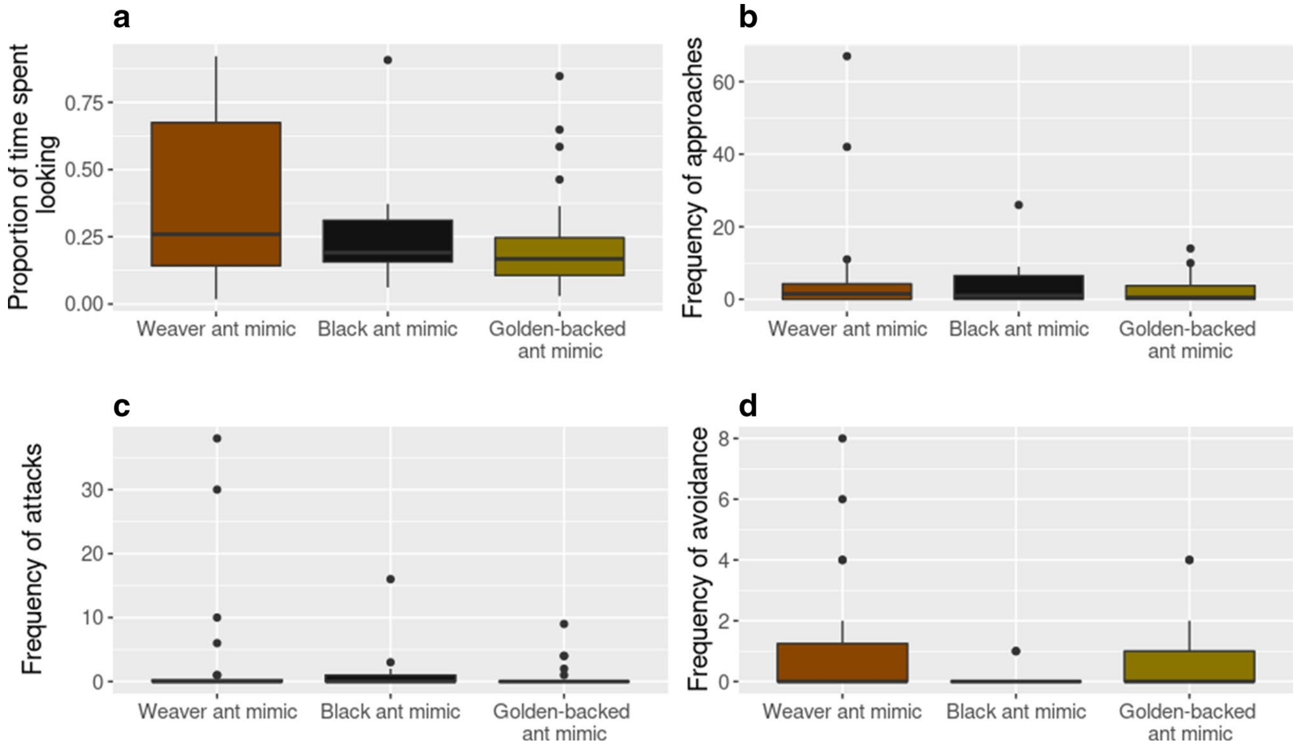

Fig. 3 Responses of *Plexippus paykulli*, a non-mimetic jumping spiders to mimics: Responses did not differ in terms of looks, approaches, attacks, or avoidances

to make a decision early in the hunting sequence to classify some ants as more dangerous than others.

Our results show that non-mimetic jumping spider *P. paykulli* looked, and approached black colored procession ants more than reddish-orange colored weaver ants through a transparent barrier. Both weaver and procession ants are trail-forming ants and are very aggressive in the laboratory, as well as in the field. Yet, spiders readily approached the procession ants. What might be the reason for this behavior? Some studies have shown that jumping spiders can learn to prefer or avoid red (Taylor et al. 2014, 2016). A recent study suggests jumping spider *Habronattus brunneus* show color bias against red over black, and this red aversion may depend on the prey availability and differences in microhabitat structure, such as proportion of grass, leaf litter, bare ground etc. (Powell et al. 2019). *P. paykulli* is commonly found on walls and on the ground covered with scrub, and chances of encountering reddish-orange weaver ant trails in the tropics are quite high. Weaver ants may taste bad, likely to be aposematic, and thus could be avoided by *P. paykulli*. On the other hand, black procession ants forage on the ground in similar habitats, often forming thick trails during early morning or late in the evening. *P. paykulli* do not forage during those hours, and are less likely to encounter these thick black trails of ants. A temporal separation in foraging activity might explain the observed responses. Golden backed ants, on the other hand are solitary foragers, and are not aggressive as compared to the other two ants. Yet, our results indicate that jumping spider responses towards golden backed ants lie in between weaver ants and procession ants. Golden-black color may be aposematic to a number of predators (Pekár et al. 2017).

Ant-like resemblance, and walking like an ant is indeed protective (Huang et al. 2011; Nelson and Card 2016; Shamble et al. 2017). But how mimics perceive other non-mimetic jumping spider are known to a lesser extent (Nelson and Jackson 2007). Even within the transparent barrier, mimics sometimes stalked, and tried to attack *P. paykulli*. For example, weaver ant and golden backed mimics displayed defensively, such as raising their antenna and abdomen. Ant-mimicking spiders are also salticids with acute vision. And it is possible that these mimics were looking at and tracking what was outside the ring, and this behavior may have influenced responses of *P. paykulli*. Another study suggests that praying mantids responded differently to black mimic and red mimics (Ramesh et al. 2016). Both jumping spiders and praying mantids have an acute sense of vision, but other factors, such as relative size of predator/prey and cognitive abilities of both predators may influence prey recognition and discrimination.

Responses of *P. paykulli* to weaver ants vs. weaver ant mimics (Fig. 2a, Fig. 3a), reveals certain interesting patterns.

Although jumping spiders spent less time looking at weaver ants, and rarely approached them, the spiders spent more time looking at weaver ant mimics, and approached them more frequently. A quick decision has to be made when an enemy or a potential prey is dangerous or fast moving. For example, bumblebees make speedy decisions to avoid potentially dangerous foraging patches (Chittka et al. 2009). Spiders may make a decision early that weaver ants are a potential threat, but this may not be the case with their mimics. Alternatively, weaver ant mimics were looked for a longer time as compared to their model ants, because of a 'mixed message'—they have an ant-like body, but salticid eyes. Mimics are still potential prey; and non-mimetic jumping spiders will benefit by correctly categorizing them as prey.

There are over 6000 species of jumping spiders (World Spider Catalogue 2020) and many tropical species share habitats with different kinds of ants and other insects. Clearly it is advantageous to stay away from the most aggressive of ants, rather than to avoid all of them and their mimics. How a spider perceives some ants as potentially dangerous, and others as less so is governed by a dynamic interaction of sensory modalities and contexts. Microhabitat differences, relative abundance of various species of ants, and their foraging patterns could also contribute to predatory decisions of jumping spiders (Powell et al. 2019). Although studies have examined how a predator responds to a single model and a mimic (Huang et al. 2011), few have examined how predators perceive multiple species of model ants and their mimics (Nelson et al. 2020). Chances of encountering multiple ants, and mimics all in a relatively short stretch of time and space is fairly common in the tropics. Studies, such as ours go a step closer to understanding predator responses towards multiple model and mimetic species.

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Author contributions CC, SV, PB, and DU were involved in project design, data collection and analysis. PB, SV, and DU wrote the paper.

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