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ANTI-APOSTATIC FEEDING BEHAVIOR IN TWO SPECIES OF ASSASSIN BUG, THE WHITE-SPOTTED ASSASSIN BUG PLATYMERIS BIGUTTATUS AND RED-SPOTTED ASSASSIN BUG PLATYMERIS RHADAMANTHUS (HEMIPTERA: REDUVIIDAE)

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Abstract.–Predator-prey relationships are a driving force when examining community ecology. One question in predator-prey interactions is how a predator may respond to novel prey phenotypes, a form of frequency dependent prey selection. A predator may selectively target or avoid the novel prey, a behavior referred to as anti-apostatic or apostatic selection respectively. We examined apostatic prey selection by observing feeding behavior in two species of assassin bugs (Hemiptera: Reduviidae), the white-spotted assassin bug (*Platymeris biguttatus*) and the red-spotted assassin bug (*Platymeris rhadamanthus*) which were fed unmodified and modified (novel) phenotypes of Turkistan cockroaches, *Blatta lateralis* (Blattodea: Blattidae). The two species of assassin bugs represent either generalist (*P. biguttatus*) or specific feeders (*P. rhadamanthus*). We hypothesized that the generalist feeder would engage in anti-apostatic feeding while the specific feeder would engage in apostatic feeding. Our results indicated that there was no difference in feeding behavior between the two species, however an overall trend of apostatic feeding was observed in response to two of the four novel prey phenotypes. Factors beyond prey phenotype may also be influencing feeding choice in these insects. While the two predator species did not exhibit different feeding behaviors, the observation of apostatic feeding in this genus suggest an overall trend of utilizing specific prey images in feeding.

Keywords: apostatic feeding, predator/prey interactions, feeding strategy, generalist, specialist

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Predator-prey relationships are an essential and long-studied component of community ecology, playing a crucial role in determining abundance, diversity, and distribution in most species. In addition, such relationships can drive evolutionary change in both prey and predator

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species, often referred to as an evolutionary arms race. Many previous studies have examined individual relationships between predators and their prey, focusing on long term ecological stability, cyclical boom or bust periods, unstable interactions that lead to the local extinction of one or both species, frequency dependent predation, and frequency independent predation (Greenwood & Elton 1979, Gendron 1987, West 1986, Hughes & Croy 1993, Lindstrom & Hornfeldt 1994, Eubanks & Denno 2000, Ramos-Jiliberto 2003, Sundell et al. 2004, Miner et al. 2005, Henden et al. 2010). Fewer studies have examined the frequency dependent feeding behavior referred to as apostatic prey selection. Apostatic prey selection is a form of non-random prey selection, in which the feeding behavior of the predator changes in relation to the presence of an uncommon or novel prey type (Allen & Greenwood 1988). In apostatic selection, a predator will avoid novel prey phenotypes relative to common prey, while in anti-apostatic selection a predator will preferentially prey upon novel prey phenotypes (Clarke 1962, Allen 1974, Allen & Greenwood 1988, Allen & Weale 2005, Surmacki et al. 2013).

In addition to prey choice behavior, predators may be classified as generalist or specialist predators by observing behavior relating to prey choice. Generalist predators utilize more than one type of prey item as a food source, potentially due to utilizing multiple prey images rather than a single defined prey image. In contrast, specialist or specific predators may have a preferred or predefined prey species and will preferentially or exclusively feed on a single or limited prey items (Snyder & Ives 2001). It is hypothesized that this difference may be due to the utilization of a specific prey image (Snyder & Ives 2001). Specific predators are different from similarly named specialist predators – a specialist predator is ecologically, behaviorally, or biologically adapted to feed on a specific prey type (Hanski et al. 1991, Van Tienderen 1991) while specific predators may show a preference for a prey type but are capable of preying on other food items. Specific predation may also be the result of seasonality in prey abundance. In this study we focused on specific predators which may be capable of feeding on other food items but preferentially choose to prey on a specific prey item.

Apostatic predation behavior may involve a predator utilizing a specific prey image, as is seen in specific predators. We predict that when comparing apostatic predation between generalist and specific predators, generalist predators will display increased random prey selection or increased anti-apostatic predation. We further predict specific predators will exhibit increased apostatic predation. To examine this experimentally, two closely related species of predators should be studied, one of which is considered a generalist predator while the other is considered a specific predator. Related species that match these differential requirements for feeding preferences can be found in the group of insects collectively known as the assassin bugs. Members of the assassin bug group are in the family Reduviidae (Hemiptera). Reduviid species exhibit a wide range of feeding behaviors, including blood feeders (Triatominae), spider feeders (Emesinae), ant feeders (Holoptilinae), termite feeders (Salyavatine), and sticky trap bugs (Harpactorinae) (Weirauch & Munro 2009). Two species of closely related African assassin bugs, the white-spotted assassin bug (*Platymeris biguttatus*) and the red-spotted assassin bug (*Platymeris rhadamanthus*) show a difference in prey preferences in natural environments. There is little published data on the ecology or feeding behavior of *P. biguttatus*. They are colloquially thought of as generalist feeders. One published study indicated that *P. biguttatus* that were fed a variety of insects (mealworms, cockroaches, and crickets) grew faster and lived longer than when fed just one species of feeder insect (Holmes 2020). On the other hand, *P. rhadamanthus* are specific feeders, exclusively feeding on rhinoceros beetles in the wild (Ambrose 2000).

We hypothesized that both species of reduviid would exhibit non-random feeding in response to novel prey phenotypes, predicting either apostatic or anti-apostatic feeding behavior in the two species. To test this hypothesis, we introduced novel prey phenotypes and observed predation rates compared to the normal prey phenotype. We predicted that the selection rate of an introduced novel prey phenotype would differ from random selection probability. We further hypothesized that the red-spotted and white-spotted assassin bugs would exhibit different feeding responses to introduced novel prey phenotypes due to differential feeding behavior exhibited in the wild. We predicted that the white-spotted assassin bug (*P. biguttatus)*, a generalist feeder, would exhibit anti-apostatic feeding while the red-spotted assassin bug (*P. rhadamanthus)*, a specialist feeder, would exhibit apostatic feeding behavior.

MATERIALS & METHODS

Study species.—Thirty white-spotted assassin bugs, *Platymeris biguttatus*, and thirty red-spotted assassin bugs, *P. rhadamanthus* (Hemiptera: Reduviidae) were obtained from captive bred colonies from California as immatures and raised to adulthood while housed in an environmental chamber prior to the start of the experiment. Both species were placed into separate screen-covered 76 by 30 by 30 cm glass-sided tanks upon arrival. A layer of vermiculite ca. 10 mm thick served as substrate. Distilled water was offered *ad libitum* via a petri dish. Each cage contained a 25 cm by 11 cm folded cardboard tent to act as cover for the insects. Both species were fed a variety of small, medium, and large Turkistan cockroaches, *Blatta lateralis* (Blattodea: Blattidae) during both colony maintenance and the experiment. The tanks were kept in an environmental chamber and maintained at a constant relative humidity between 75% and 86%, at a temperature of 26–27.5°C, on a 12:12 light: dark cycle. Tanks were misted once per week with deionized water.

Experimental design.—Experimental tanks for the reduviids used in this study were maintained in the same environmental chamber that was used for housing the laboratory colonies from which the test subjects were derived. Due to space and time limitations, rather than test feeding behavior individually, each cage contained four assassin bugs, either *P. biguttatus* or *P. rhadamanthus*, with three replicates of each cage. Due to resource limitations, assassin bugs could not be housed individually.

Every four days, each cage of reduviids was provided with five Turkistan cockroaches measuring between 1.27 and 1.54 cm in length. The feedings were divided into one of four treatments. For each feeding, one of the five cockroaches in each feeding was painted either a pink, yellow, or green color using ICING brand nail polish colors Groovin Green©, Bikini Babe© (pink), or Suns Up© (yellow). A fourth treatment consisted of using clear nail polish. This control was chemically like a nail polish treatment, while visually would be like the untreated cockroaches. The untreated cockroaches acted as a normal phenotype compared to which the novel treated phenotypes differed. A chill plate was used to immobilize the five cockroaches for marking. Cages were randomly assigned a treatment prior to each feeding. The sequence of distributing the phenotypes among the six cages was randomized to ensure there was no pattern which might influence prey selection. After a period of 24 hr, any remaining cockroaches and remnants of consumed cockroaches were removed from each cage. The number and phenotype of consumed and unconsumed cockroaches was recorded. Unconsumed cockroaches were discarded and not used in subsequent trials. These trials continued until there was a minimum of six replicates of each feeding event for each treatment type per cage.

Statistical methods.—Each cage with four reduviids was considered a single experimental unit, eliminating the need to develop a "per reduviid" feeding estimate. An average feeding rate of the reduviids on cockroaches was calculated (total eaten/total provided). From this rate, a binomial expansion was calculated, indicating expected probability for all feeding (feeding on zero of the five cockroaches, feeding on one of the five cockroaches, etc.). Pearson's chi-squared analyses were then be used to determine if the observed frequency of feeding matched the predicted frequency of feeding for each species to determine if overall feeding behavior was random (matching the binomial distribution) or not.

A second analysis tested the randomness of selecting treated prey versus non-treated prey, using the probability of randomly selecting a treated cockroach out of each feeding outcome (i.e., if two cockroaches are consumed, what is the random probability that the treated cockroach was consumed). Chi-squared analyses were used to determine if each species predation of treated prey was different from expected (assuming a random distribution).

The final analysis used a Pearson's chi-squared test to determine if the predation rates of the different treatments (clear, green, pink, yellow) were different from each other for each species. If treatments were not responded to differently, there should be no difference in the number of each treatment consumed.

All statistical analyses were conducted using JMP version 15 (SAS Institute, Cary, NC).

RESULTS & DISCUSSION

In 169 trials, a total of 423 reduviids were consumed out of the 845 total potential prey items provided, resulting in an overall frequency of predation of 50.06%. This frequency was used to calculate an expected frequency of predation with a binomial expansion (the expected probability of feeding on zero out of five prey items, one out of five prey items, etc.) if feeding behavior were considered random. This was calculated for each species (Table 1, Figure 1), analyzing if the experimental unit (cage) fed on between zero and five reduviids based using a random binomial distribution model. This analysis was testing the overall frequency of predation, not if the novel prey was or was not consumed. Our results indicated that neither *P. biguttatus* nor *P. rhadamanthus* differed significantly from random feeding probabilities, indicating that there was no overall selection difference in the number of prey selected by the predators from a random distribution.

Using this binomial expansion, we calculated the random probability of the treated prey being eaten (where one out of five, or 20%, of the provided prey items were treated with the nail polish) for each potential outcome where at least one prey item was consumed, then added those values to estimate the expected number of treated prey nsumed. Using the predicted values from the binomial expansion rather than the actual observed feeding rates would have increased the potential error relative to what was observed. While there was no

Table 1. Using a binomial expansion based on an expected probability of feeding of 50.6161%, we estimated the expected feeding events for each species and compared those to the observed. Results indicated that neither *P. biguttatus* nor *P. rhadamanthus* deviated significantly from random feeding behavior (not considering consumption of treated prey). n is the total number (feeding on treated prey); Exp n and Obs n is the expected sample number and observed number, respectively.

Species	n	Treatment	Exp n	Obs n	χ^2	*df*	*P*
P. bigutattus	66	Clear	16.5	18	0.667	3	0.881
		Green	16.5	14			
		Pink	16.5	16			
		Yellow	16.5	18			
P. rhadamanthus	56	Clear	14	19	2.7143	3	0.4378

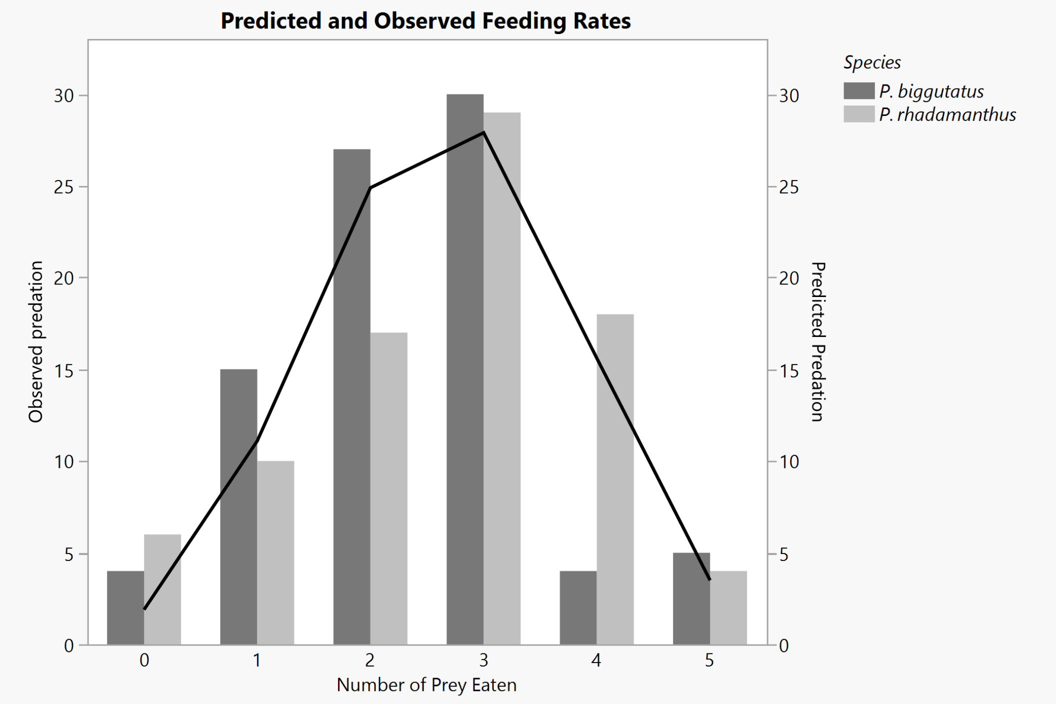


Figure 1. Expected and observed frequencies of feeding for each possible feeding outcome (consuming zero prey items, one prey item, etc., up to 5 prey items). The line represents the expected feeding rates based on a random binomial distribution. The bars represent the observed feeding rates for each of the two species. There was no significant difference between the observed and expected frequencies of predation.

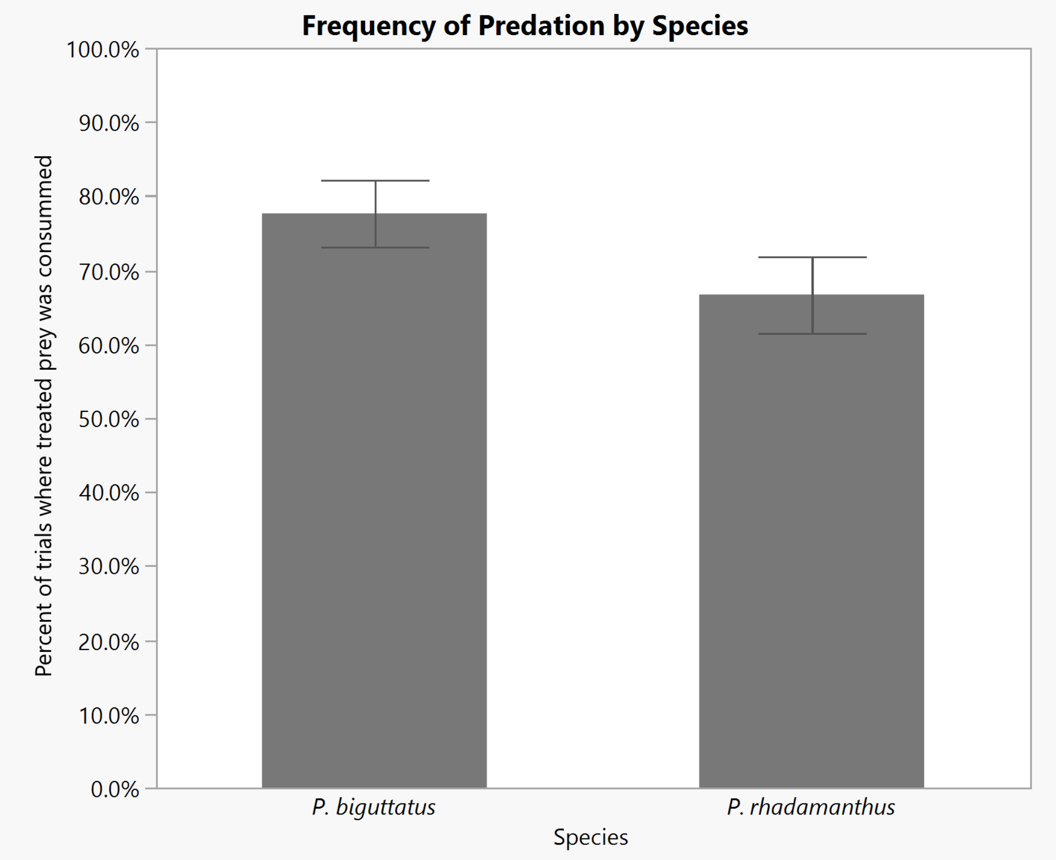
statistical difference between the expected and observed feeding rates (Table 1), the feeding rates were different from the expected value. To calculate the expected rates of feeding on treated prey, we multiplied the observed number of times any prey would have been eaten (for example, the number of times two out of the five prey items were consumed) by the probability that one of those consumed prey items would be treated with the nail polish. Overall, the reduviids were observed feeding on the treated prey item 122 times (out of 169 trials, including trials where no prey at all were eaten). If selection of treated prey were random, we should have observed that the treated prey was consumed only 96 or 97 times, suggesting an overall selection bias for treated cockroaches (anti-apostatic behavior). A Pearson chi-squared test indicated that both *P. biguttatus* (chi-squared = 31.9223, df = 1, p <0.0001) and *P. rhadamanthus* (chi-squared = 13.1724, df = 1, p = 0.0003) preyed on the treated prey item more frequently than expected (Table 2), suggesting anti-apostatic feeding behavior for both species (Figure 2).

These data were further analyzed for each species, looking at the specific response to each treatment (clear, pink, green, or yellow nail polish). If there were no preference in selection of a specific prey treatment, then each treated prey item would expect to be eaten with the same frequency. Table 3 presents the chi-squared analysis of the feeding responses by species. For both species, there was no difference in the response to individual prey treatment, indicating the reduviids

Table 2. Chi-squared analysis of expected frequency of feeding on treated prey items, assuming a random probability. The expected probability of feeding on the treated prey when there was no predation observed is zero, so those data were excluded from the analysis. These results indicate that *P. biguttatus* fed on the treated prey more frequently than expected, while *P. rhadamanthus* did not.

Species	n	Exp Frequency	Exp n	Obs n	χ^2	*df*	*P*
P. bigutattus	85	50.6161%	43.024	66	27.164	1	<0.0001
P. rhadamanthus	84	50.6161%	42.518	56	10.038	1	0.0015

Figure 2. Frequency of predation by the two reduviid species, *P. biguttatus* and *P. rhadamanthus*. Error bars represent one standard error. There was no significant difference between the two species in the frequency in which they consumed treated cockroaches, although there was a slightly higher probability that *P. biguttatus* consumed the treated food. Both species fed on treated prey more than would be expected based purely on random probability.



either did not detect a difference between the treatments or did not respond differently to the treatments (Figure 3). While not a statistically significant difference, the colored treatments (pink, green, yellow) were consumed less frequently by *P. rhadamanthus* than by *P. biguttatus*.

Our data supports the idea that prey consumption (in terms of number of prey items) is a random process, with the number of prey items (out of five) being consumed not being significantly different than what would be expected using the overall predation rate and a

Table 3. Feeding response to each of the treatment. Looking only at the times a treatment was consumed, a chi-squared analysis was used to determine if the frequency of predation differed from random selection. Results suggest that none of the treated prey items were selected more or less frequently than would be expected at random.

Species	n	Treatment	Exp n	Obs n	χ^2	*df*	*P*
P. bigutattus	66	Clear	16.5	18	0.667	3	0.881
		Green	16.5	14			
		Pink	16.5	16			
		Yellow	16.5	18			
P. bigutattus	56	Clear	14	19	2.7143	3	0.4378
		Green	14	11			
		Pink	14	12			
		Yellow	14	14			

binomial distribution (Table 1). That the p-value for both species was close to significant suggests there may be some feeding characteristic that should be explored that may result in non-random feeding (regardless of whether there are novel prey or not).

Both species exhibited anti-apostatic feeding behavior (Table 2), although the degree of response was greater for *P. biguttatus*. We predicted that *P. rhadamanthus* would exhibit apostatic feeding behavior, which was not observed, although the feeding behavior observed showed decreased anti-apostatic tendencies than in *P. biguttatus* as indicated by the larger difference from expected predation rate on treated prey.

The reduviids used in this study were purchased from commercial colony-raised populations (not collected from the wild) that utilized Turkistan cockroaches and other cockroach species as feeders. Prior to the initiation of the experiment, both species were fed on non-treated cockroaches. This may have influenced the results, as the reduviids may have become acclimated to these prey items over time regardless of their generalist or specific feeding behavior in natural settings. In addition, it is critical to recognize that the natural prey of the red-spotted assassin bug is a rhinoceros beetle, so both species were being fed a

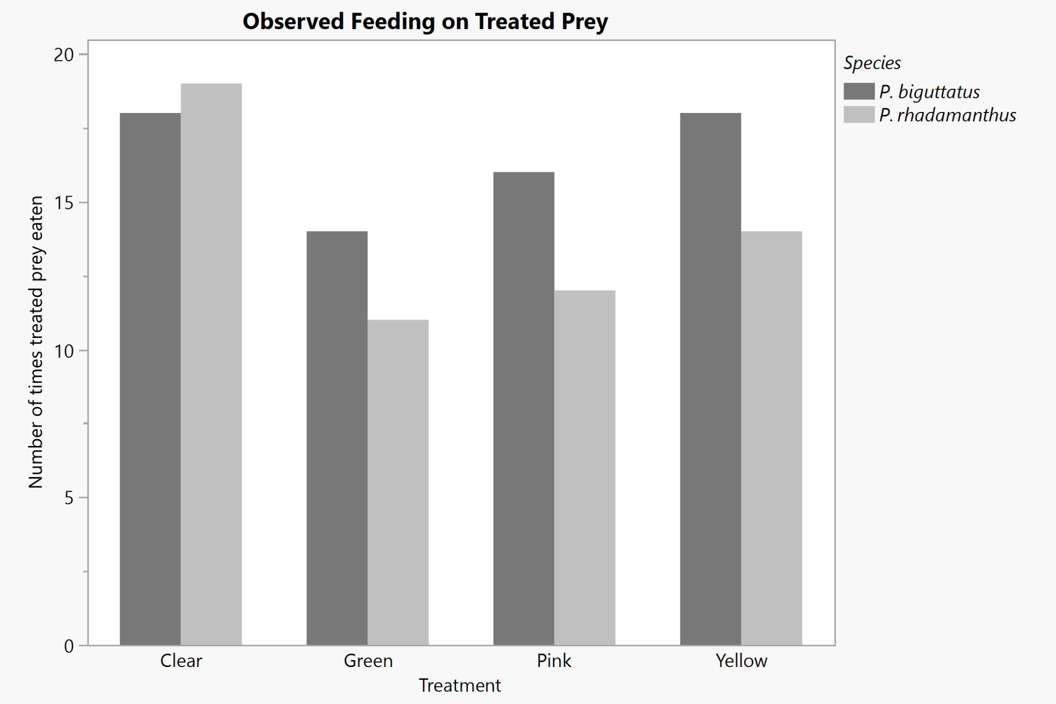


Figure 3. Observed frequency of predation for each of the treated prey. There was no significant difference between the individual treatments, although the number of times *P. rhadamanthus* fed on colored prey (pink, green, yellow) was less than was observed in *P. biguttatus*.

novel prey relative to their wild prey items throughout the entire experiment. It is possible that the overall observed anti-apostatic feeding behavior may have been influenced by these practices. However, with the treatments there was still an observed significant difference in feeding behavior, suggesting the reduviids were still responding differently to the treated cockroaches. In addition, the generalist species (*P. biguttatus*) did show greater anti-apostatic feeding behavior than the specific feeding (*P. rhadamanthus*).

It is important to consider that artificial settings may influence feeding responses and responses to differences in prey abundance (Relyea 2005). By training the reduviids on the same food types, the species may have both ultimately elicited similar responses when exposed to a novel phenotype of that food type. In addition, training predators to feed on a specific prey item may theoretically train them to exhibit apostatic feeding behavior, although we observed significant anti-apostatic feeding in two of the treatments. This provides further evidence that there may be anti-apostatic feeding tendencies in both species.

Other studies that examine frequency-dependent predatory behavior predominantly in birds (Paulson 1972, Bond & Kamil 1998, Allen & Weale 2005) have been used to explain morphological diversity of insects in locations with abundant predators (Rand 1967). The focus of many of these studies has been to compare predator response to prey selection, but comparing predators that are thought to exhibit different feeding strategies. Marples & Mappes (2011) showed that birds will often attack conspicuous prey but some predators will ignore conspicuous prey, a potential form of apostatic selection, hypothesizing that some predators will ignore novel prey due to familiarization (a tactic related to specific predators). Within insects, studies have examined feeding behavior of beetles on aphids (Lang & Gsödl, 2001), verifying that generalists may exhibit more opportunistic feeding behavior, although that study explored active versus passive choice and did not compare behavior to more specialist feeders. Aditya et al. (2005) demonstrated that water bugs varied feeding behavior based on prey frequency, although this was in response only to frequency, not novel morphology. Other related studies of insect prey choice have focused on quality of the prey (Waldbauer & Friedman 1991) or resistance to predators by the prey (Frago et al. 2017, McLean & Parker 2020).

Our data suggests that white-spotted and red-spotted assassin bugs may not be able to perceive visual differences between the treatments. Little is known about the visual acuity of assassin bugs. Damselflies and dragonflies (Insecta: Odonata) are representatives of one of the few orders upon which extensive research of visual acuity has been conducted. They have been shown to have some of the most specialized visual systems (Bybee et al. 2012), which is understandable given their active predation behavior in both adult and larval stages. Assassin bugs are predators, which suggests they may have developed strong visual acuity. The fact that the clear treatment was consumed at the same rates as the colored treatments suggests that colors were not detected by the reduviids. However, the fact that there was anti-apostatic feeding observed suggests that chemical differences in the treatments may have played a role in prey selection. In addition, the clear treatment may have resulted in a visual difference between treated and untreated animals (such as a glossier exoskeleton on the treated insects) which in turn may have impacted feeding choices.

Predator feeding style may have influenced the results of these experiments. Observations of feeding behavior during the experimental trials suggest that these predators are ambush predators (Potocnjak, pers. obs.). Ambush, or sit-and-wait, predator, do not stalk or actively pursue their prey. No long-term observations of the feeding process occurred during the extended feeding period, however short-term observations suggest that the treatment had no effect due to cockroach mobility or behavior. It is possible that predation behavior was due to random movement of the prey items, rather than selecting targeted prey for consumption. This idea is supported by the finding that the number of prey consumed (between zero and five out of five prey items) was randomly distributed. It seems likely that both treated or untreated cockroaches randomly wandered into the ambush area of the assassin bugs, and prey choice may still have been involved in the assassin bug choosing to ambush a potential prey item.

This study demonstrated an anti-apostatic feeding behavior of two closely related species, the generalist feeder *Platymeris biguttatus* and the specific feeder *P. rhadamanthus*. The generalist feeder did show a slightly higher rate of predation on the novel phenotype (anti-apostatic feeding) relative to the specific feeder (Figure 2). Rather than simply studying the result of predation (prey items fed upon), future studies may benefit by observing the actual feeding behaviors. As assassin bugs utilize ambush predation to acquire prey, examining the specific predatory behavior (average time before striking, stalking behavior, accuracy of strikes, and time between subsequent strikes) may identify differences in feeding behavior between the species.

This study has provided evidence that novel prey phenotypes can influence prey choice within insects, including those that engage in ambush predation tactics. Anti-apostatic feeding was observed overall in response to color treatments in the feeding assassin bugs, suggesting that prey choice is taking place and targeting novel prey phenotypes. The generalist predator exhibited a higher degree of anti-apostatic feeding behavior as compared to the specialist predator. A greater feeding response may be predicted in insects that engage in active hunting behaviors rather than utilized ambush tactics. Avoiding any "training" of predators prior to experimental study may change these results, showing a greater difference in future studies.

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