

Masking Behavior by *Mepraia spinolai* (Hemiptera: Reduviidae): Anti-predator Defense and Life History Trade-offs

Patricia A. Ramírez · Andrea González · Carezza Botto-Mahan

Revised: 1 December 2012 / Accepted: 6 December 2012 /
Published online: 8 January 2013
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Abstract Masking, a type of camouflage, has been argued to function as an anti-predator mechanism helping to avoid detection or recognition by a prey or predator. However, research focused on the effects of masking on life history traits is scarce. We evaluated under laboratory conditions whether developmental time and survivorship in the absence of predators, and the probability to be predated by a potential predator are affected when the blood-feeding triatomine *Mepraia spinolai* masks with sand particles. Theoretically, it is expected to find a positive anti-predator effect of masking and the presence of trade-offs between development time and survival. We assigned *M. spinolai* nymphs to a masked or non-masked treatment and subjected them to a lizard, a potential predator. Results show masked nymphs reach the fifth instar faster and survive longer than non-masked nymphs, which is inconsistent with the trade-offs hypothesis we expected to find. In predation experiments, higher number of masked nymphs detected lizards before lizards detected them compared to non-masked nymphs. We suggest that masking may be an adaptation to the extreme climatic conditions the nymphs must face, and seems to render selective advantages to *M. spinolai* nymphs even in the absence of selective forces.

Keywords Masking · life history traits · trade-offs · predation · triatominae · Chagas disease

Introduction

Masking, a type of camouflage consisting on the decoration of the body with foreign material, allows animals to resemble its background and thus offers protection against

P. A. Ramírez · A. González · C. Botto-Mahan (✉)
Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile, P.O.Box 653,
Casilla, Santiago, Chile
e-mail: cbotto@uchile.cl

C. Botto-Mahan
e-mail: carezzabotto@gmail.com

visually oriented predators, interfering with detection and identification as a prey (Brandt and Mahsber 2002; Ruxton et al. 2004; Jackson and Pollard 2007). However, given the animal's resemblance to their natural environment, the benefit can be twofold because animals might also have an advantage in stalking its own prey (McMahan 1982, 1983; Brandt and Mahsberg 2002; Théry and Casas 2002; Weirauch 2006; Zeledón et al. 1969). This phenomenon occurs in several groups, for example, aquatic invertebrates such as decorator crabs (Decapoda: Majidae) (Wickstein 1980) and sea urchins (Camarodonta: Parachinidae) (Richner and Milinski 2000), and some terrestrial insects such as caddisfly larvae (Trichoptera: Limnephilidae) (Otto and Svensson 1980) and lacewing larvae (Neuroptera: Chrysopidae) (Eisner et al. 2002).

Masking also occurs in immature stages of several members of Reduviidae family (Hemiptera) by means of active accumulation of dead remains of the prey, soil particles and debris on their bodies (Zeledón et al. 1973; Haridass et al. 1987; Weirauch 2006). Several triatominae species from the genus *Triatoma*, *Panstrongylus* and *Mepraia*, actively cover their bodies throwing dirt grains onto their dorsum. Kissing bugs use the third leg as a shovel to cover themselves within a short time, by curving the tarsal segment of the leg toward the side of the body (Zeledón et al. 1969, 1973). Specific body structures, i.e., anchor setae and trichomas, assist in fastening the camouflaging material, assuring the attachment of particles by their mechanical properties and the secretion of a sticky substance, respectively (Haridass et al. 1987; Weirauch 2006). After each molt, this “soil” cover is shed with the exuviae and replaced by a new cover.

It has been suggested that kissing bug masking behavior may be the result of a selective pressure to escape from predators such as spiders, lizards, and toads (Zeledón et al. 1973; Stevens and Marilaita 2009), and several members of the Reduviidae family have adopted masking as an antipredator strategy to minimize the probability of detection (Haridass et al. 1987). However, studies focused on the effect of masking on predation are scarce, or have been regarded as intuitively obvious and, therefore, have not been formally tested (Ruxton et al. 2004; Stevens and Merilaita 2009). Ambrose (1986) used nymphs of the assassin bug *Acanthaspis siva* that covers its body with arenaceous material to test the anti-cannibalism function of its covers. The author found that masked bugs suffered less cannibalism from their co-instars than naked bugs. Brandt and Mashberg (2002) carried out experiments using *Acanthaspis sp.* and *Paredocla sp.*, reduviid species that uses dust particles and prey's remains as a mask, and three different types of predators chosen for their different sensory systems for prey detection. Jackson and Pollard (2007) extended Brandt and Mashberg study by using three salticid species (Araneae: Salticidae) as main predators. Both studies show that predators fail to identify masked bugs as prey and that masked bugs were significantly more likely to survive than denuded bugs.

Trade-offs have been pointed out to be major drivers in life-history theory (Stearns 1989). This relates to the idea that there is a compromise between improving some fitness related character with a detrimental change in another fitness related character (Reznick 1985; Stearns 1989). The investment in this anti-predator defense may be costly to the organism and, therefore, negatively affect energy allocation for life history traits such as growth and reproduction (Hultgren and Stachowicz 2008). Few studies have addressed the effect of camouflage on life history traits. For example, trade-offs have been found in the case of melanisation for three Lepidopteran species: melanism is shown to be related with a slower development, smaller body size, lower

mating rate and lower fecundity in the cotton bollworm *Helicoverpa armigera*. However, longer life span of the melanic female moths was also found for this species (Weihua et al. 2008). For the Peacock butterfly *Inachis io*, dark relative to pale pupae exhibit longer development time and smaller adult size. Similarly, longer development time for instars 1–4 was found for the Map butterfly *Araschnia levana*, but shorter fifth instar periods and larger body size adults relative to pale larvae (Winding 1999). However, there is scarce information about trade-offs in behavioral masking. In an aquatic invertebrate, negative correlations were found between body size and masked individuals in the decorating crab *Oregonia gracilis* (Majidae) suggesting some cost in this type of behavior (Berke and Woodin 2008).

Currently, the consequences of masking on life-history traits such as developmental time and survivorship in Reduviidae are unknown. In this study, we evaluate under laboratory conditions whether developmental time and survivorship in the absence of predators, and the probability to be predated by a potential predator are affected when the blood-feeding triatomine *Mepraia spinolai* masks in the presence of a suitable substrate. We expect to find a positive anti-predator effect of masking and the presence of trade-offs between development time and survival with the masking behavior in the absence of selection forces (i.e., without predators).

M. spinolai is a sylvatic species, occasionally found in human dwellings, that transmits *Trypanosoma cruzi*, the causative agent of Chagas disease, in arid and semiarid Chile (Lent et al. 1994; Botto-Mahan et al. 2005). This strictly hematophagous and diurnal insect is found between 18° and 34° S, and its main habitat includes nests of wild homiothermal animals, rock crevices, stone walls and caves (Lent and Wygodzinsky 1979). *M. spinolai* requires blood of vertebrates to complete its life cycle that includes egg, five instar nymphs, and adult (Sagua et al. 2000; Botto-Mahan et al. 2006). Often one full engorgement is sufficient for molting from one instar nymph to the next (Kollien and Schaub 2000). First to fifth instar nymphs mask by throwing dirt grains, sand, dust or fine soil onto their dorsum (Fig. 1). In the absence of this mask cover, they are dark reddish-colored (Fig. 2). The overall color of adult males and females is black with red markings on the abdomen (Lent and Wygodzinsky 1979), and the camouflaging behavior is absent. It has been documented that lizards of the genus *Liolaemus* consume insects of the Hemiptera Order (Vidal and Labra 2008).

Methods

Life History Trait Experiments

M. spinolai eggs were obtained from laboratory matings between adults collected on rocky hillsides at the Reserva Nacional Las Chinchillas (31°30' S, 71°06' W, Chile; Botto-Mahan et al. 2002). The climate is of a semiarid Mediterranean type with most rainfall concentrated in the winter season. Mean annual precipitation is 185.0 mm with large variation between years and frequent droughts (di Castri and Hajek 1976). Eggs were daily isolated from the mating jars, cleaned and placed in sterile plastic containers. Once the first-instar nymphs emerged, a random assignment to housed without sand (i.e., non-masked; $N=58$) or with a layer of fine sand as substrate (i.e., masked; $N=60$) was



Fig. 1 Masked *Mepraia spinolai* in the field

performed. The sand used in the treatment was obtained from the insect-collecting place previously mentioned. Nymphs were kept in groups of 20 individuals (three groups per treatment) housed in cylindrical plastic containers (6.2 cm w × 7.0 cm h) with a tulle-mesh cap to allow ventilation and a folded piece of paper as refuge. All insects were reared under optimal growing conditions in a climatic chamber at 27° C, 65–70 % relative humidity, 14:10 light:dark photoperiod (Ehrenfeld et al. 1998) in the absence of predators. Nymphs were fed 1 week after eclosion, using laboratory mice (C₃H strain) obtained from a biotherium (Universidad de Chile, Santiago, Chile). After each molt, nymphs were starved for 2 weeks and then fed on mice, a passive blood donor, up to three times until they molted to the fifth instar stage. First-instar nymphs were weighed before and after the first feeding event in an analytic scale (precision 0.1 mg), to ensure similar initial conditions between control and camouflaged nymphs. Feeding experiments were conducted with permission of the Ethical Committee of the Faculty of Science, University of Chile.

Predation Experiments

A total of 28 control and 26 camouflaged fifth-instar nymphs were subjected to a potential predator, the lizard *Liolaemus platei* (Squamata: Tropiduridae), interested in



Fig. 2 Non-masked fourth instar *Mepraia spinolai* nymph

attacking and feeding on *M. spinolai*. This lizard is frequently found in the study area and some remains of *M. spinolai* body parts, such as legs, have been found in its stomach content (Dr. M. Lamborot, unpublished data). Six adult lizards (mean weight \pm SE: 4.62 ± 0.33 g) naturally coexisting with *M. spinolai* populations in the field were used for the trials. Four lizards were marked with a small thin line using a non-toxic marker and the other two had distinctive natural markings that were used for recognition as different individuals. All lizards were housed together in a glass terrarium ($50 \text{ cm l} \times 30 \text{ cm w} \times 25 \text{ cm h}$), with a layer of sand, a medium-size rock, dry branches, a cardboard cylinder, and a Petri dish with fresh water provided ad libitum. At arrival, lizards were fed with two mealworm larvae each (mean weight \pm SE: 0.12 ± 0.013 g) and kept at a normal room temperature ($25\text{--}28$ °C), 12:12 light:dark photoperiod, and additional direct bulb light from 07:00 to 10:00. Experiments started 9 days after the first feeding, time during which no additional food was provided. Two weeks after the beginning of the experiments, all lizards were fed again as previously described. This feeding procedure was followed until all *M. spinolai* individuals were tested.

Predation trials took place on an experimental arena (a glass terrarium of $44 \text{ cm l} \times 31 \text{ cm w} \times 32 \text{ cm h}$) between 10:00 and 18:00 in a noiseless room. The base of the terrarium was covered with gray rough cardboard resembling the natural soil color of the collecting field site, and the terrarium walls were translucent to conceal the observer. Sand was not used as a substrate to avoid camouflaging by control nymphs. Lizards were placed on the arena 5 min before the experiments started, as a habituation time. The lizard was placed in the center of the arena and a randomly assigned nymph (masked or non-masked) was aleatory placed at one of the corners of the terrarium. Nymphs and lizards were covered with dark plastic containers in order to avoid earlier detection. Behavioral experiments started once the dark containers were removed and ended when the lizard bit the nymph or after 30 min of observation without interaction. For each individual lizard between six and nine paired experiments were carried out, and only by random all lizards were paired with masked and non-masked nymphs without a specific sequence. A particular combination of a nymph-lizard was used only once. Time elapsed for the nymph and lizard to detect each other, and the number of approaches and attacks to each other were quantified. Specifically, a nymph detected a lizard when the former moved its antennae towards the lizard and maintained a frozen posture facing the predator, and a lizard detected a nymph when the former looked at the nymph and kept visual contact without moving its head. The arena was cleaned of any remains before a new pair nymph-lizard was introduced into the terrarium again.

Choice Experiments

Although lizards were kept unfed for 9 days before predation experiments were conducted, choice experiments were performed in order to assess the lizard's responsiveness to different stimuli and to establish its need for food. These tests were carried out with a randomly selected lizard after it was used in predation tests. For these experiments, mealworms and masked nymphs were used as potential prey because under field conditions, *L. platei* are known to feed on mealworms (Vidal and Labra 2008) and *M. spinolai* masked nymphs are the only nymphs found in *L. platei* natural habitat. A total of 19 choice experiments were carried out using a mealworm larva

and a masked nymph as two potential prey for a lizard. The same arena under the same experimental conditions was used as in the predation experiment (see above), but in this case the mealworm larva and the nymph were placed together at a randomly selected corner, keeping the lizard at the center of the arena. The lizard could either eat the mealworm or the nymph, and that feeding choice was recorded. After these experiments were concluded, all lizards were released at the same place where they were caught in the field.

Data Analyses

The weight of first instar nymphs from control and treatment was compared by a one-way ANOVA. Comparisons of developmental time (i.e., number of days elapsed from feeding as first instar until second instar nymph emergence, and so on) between masked and non-masked nymphs were analyzed, by stage, using a two-factor nested ANOVA, where the main effects were the treatment (masked or non-masked) and the replicates (plastic containers) nested within the treatment. Data were previously log-transformed to satisfy ANOVA assumptions (Sokal and Rohlf 1995). To determine whether nymph survivorship (i.e., proportion of nymphs alive at the fifth stage) was affected by the presence of sand on their bodies, a univariate Kaplan-Meier survival analysis was performed, including all the masked and non-masked nymphs, and computed the Wilcoxon chi-squares statistics to test homogeneity of the estimated survival function between groups (STATISTICA, StatSoft, Inc., version 7, 2004).

In the Predation experiments, detection time was established as the time elapsed from the start of the experiment until lizard detection by the nymph, and vice versa. Detection time was analyzed by a one-way ANOVA after log-transformation (Sokal and Rohlf 1995). The number of approaches from the lizard to the nymph was analyzed with a Chi-square contingency table. Lizard attacks to the nymph (e.g., bite) were analyzed with the Fisher's exact test. In the Choice experiments, lizard's food preference was analyzed by a Chi-square contingency table (Sokal and Rohlf 1995).

Results

Life History Trait Experiments

First-instar nymphs from both treatments did not differ in their weights after the first blood feeding (mean body weight \pm SE (mg): non-masked = 11.13 ± 0.59 , masked = 10.87 ± 0.60 ; $F_{1,117} = 0.092$, $P = 0.76$), showing that the initial conditions were the same for both groups. A total of 47.46 % and 55.0 % of the individuals from the non-masked and masked groups reached the fifth-nymphal stage, respectively. Statistical analysis revealed a significant effect of masking on survivorship ($Z = 2.02$, $P = 0.043$; Fig. 3). Survival was 12.5 % higher in the masked nymphs than in the non-masked ones. Molting probability from instar I to II was significantly higher in the masked group compared to the non-masked ($\chi^2 = 5.07$, $df = 1$, $P = 0.024$) and a borderline significance was found in the transition from III to IV stage ($\chi^2 = 3.29$, $df = 1$, $P = 0.070$). We did not detect statistically significant differences between the groups in the transitions II to III and IV to V ($\chi^2 = 0.04$, $df = 1$, $P = 0.84$; $\chi^2 = 1.64$, $df = 1$, $P = 0.20$, respectively; Table 1).

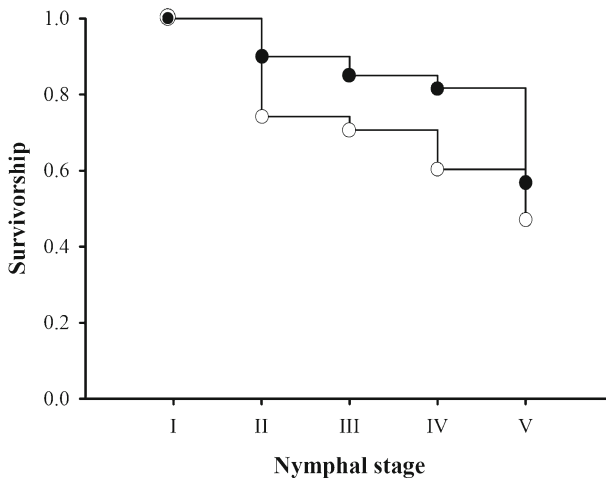


Fig. 3 Survivorship curve of *M. spinolai* nymphs from masked (filled circles) and non-masked (open circles) groups for each nymphal stage. Masked nymphs showed a higher overall survival probability than non-masked nymphs

Regarding developmental time, our results showed statistically significant differences between masked and non-masked nymphs in all of the nymphal stages (Transition I-II: $F_{1,93}=7.60$, $P=0.007$; II-III: $F_{1,89}=4.20$, $P=0.043$; III-IV: $F_{1,80}=14.74$, $P<0.001$; IV-V: $F_{1,55}=5.06$, $P=0.028$; Table 2), indicating that nymphs with dirt grains on their bodies reach the next developmental stage faster than those free of dirt grains.

Predation Experiments

A total of fifty-one predator/prey experiments were performed, however, three of them were not included in the analyses because both the lizard and the nymph stayed motionless during the entire experiment. A lower number of lizards detected the masked nymphs before the nymphs detected them compared to non-masked nymphs ($\chi^2=5.08$, $df=1$, $P=0.024$; Table 2). Even though we recorded a higher detection time on the masked group, no statistically significant differences were found in the time needed for lizards to detect non-masked and masked nymphs (Mean \pm SE (sec): non-

Table 1 Molting probability and developmental time of *Mepraia spinolai* from each transition from one nymphal stage to the next

Transition	Molting probability (%)		Mean developmental time (days \pm SE)	
	NM	M	NM	M
I-II	74.14	90.00	15.73 \pm 0.6	14.60 \pm 0.2
II-III	95.35	94.44	16.84 \pm 0.3	16.36 \pm 0.2
III-IV	85.37	96.08	22.95 \pm 0.8	20.02 \pm 0.5
IV-V	80.00	67.35	48.80 \pm 7.7	36.65 \pm 3.9

M masked group ($N=60$); NM non-masked group ($N=58$)

Table 2 Percentage of events in which the kissing bug *Mepraia spinolai* detected the lizard *Liolaemus platei* before/after the lizard detected them. Percentage of contacts between *M. spinolai*-*L. platei*

Treatment	Detection		Contacts	
	Before	After	Contact	No contact
Control	50 % (11)	50 % (11)	63.6 % (14)	36.4 % (8)
Camouflaged	80.8 % (21)	19.2 % (5)	53.8 % (14)	46.2 % (12)

Number of events and contacts are shown in brackets

masked: 201.45 ± 42.65 ; masked: 222.77 ± 45.64 ; one-way ANOVA: $F_{1,46} = 0.25$, $df = 1$, $P = 0.62$). Similarly, no differences were found in the number of approaches toward the nymphs, irrespectively of their treatment condition ($\chi^2 = 0.13$, $df = 1$, $P = 0.71$; Table 3). The number of lizard attacks toward non-masked and masked nymphs did not significantly differ (Fisher’s exact test: $P = 0.20$; Table 3).

Choice Experiments

When a nymph and a mealworm were offered to a lizard, mealworm larvae were selected in 11 out of 19 events, in eight events lizards showed no interest for either of them, and nymphs were never chosen ($\chi^2 = 15.48$, $df = 1$, $P < 0.001$). This reflects that experiments took place at a stress free environment for the lizards and that they were hungry enough to pursue an edible item.

Discussion

Masking behavior is known to be a mean of reducing predation risk (Odhiambo 1958; Merilaita 2003; Jackson and Pollard 2007; Stevens and Merilaita 2009) and as such, this anti-predator defense may affect life history traits of an organism as the result of resources allocation trade-offs between these two competing traits (Stearns 1989, 1992; Ruxton et al. 2004; Hultgren and Stachowicz 2008). However, under laboratory conditions, *M. spinolai* masked nymphs had a higher probability to survive than non-masked nymphs and needed less time to reach the next nymphal stage in the

Table 3 Percentage of events in which the lizard *Liolaemus platei* approaches and attacks the nymph *Mepraia spinolai*

Treatment	Approaches		Attacks	
	Approach	Not approach	Attack	Not attack
Control	40.9 % (9)	59.1 % (13)	4.5 % (1)	95.5 % (21)
Camouflaged	46.2 % (12)	53.8 % (14)	15.4 % (4)	84.6 % (22)

Number of events is shown in brackets

absence of predators. Even though molting probability did not show a clear tendency among stages, overall results indicate that masking improves the chances of nymphs to reach the mature and reproductive adult stage. These results are inconsistent with the trade-offs hypothesis we expected to find. Although we cannot rule out other type of costs associated with masking, at this point internal costs imposed by masking can be dismissed. We can also discard a possible stress factor imposed by the absence of masking material given that nymphs only kicked sand onto their dorsum for a few minutes after eclosion. After that, this behavior stopped until the next molt, hence, it is unlikely that this short period of time would have a negative effect on their overall performance. The arid climate of *M. spinolai*'s natural habitat may be an important stressor in terms of its thermoregulation. Therefore, the masking cover may be an adaptation to the extreme climatic conditions the nymphs must face, acting as a thermal insulator and stabilizing its body temperatures. Masking is not a learned behavior for once nymphs emerged from the egg they rapidly start throwing dirt grains onto their dorsum. Moreover, several specialized masking structures are known to assist in the application, fastening, and attachment of the cover (Zeledón et al. 1969; Haridass et al. 1987; Weirauch 2006), which suggests that their bodies may be somehow adjusted for the presence of a sand cover and the absence of it may be acting in deterrence of some physiological components related to the species fitness. However, these potential physiological effects of masking must yet to be formally tested.

Endler (1986) established five distinctive stages in prey recognition, being the first two the detection and identification of an edible organism. Masking, as an anti-predator mechanism, attempts to disrupt those stages (Brandt and Mahsberg 2002; Merilaita 2003). In the predation experiments, there were a significantly higher number of masked nymphs that detected the lizards before the lizards detected them, and even though there were no significant differences in the number of approaches and attacks toward the nymphs, we registered few more approaches and attacks toward the masked nymphs compared to non-masked ones. These results indicate that masking helps *M. spinolai* to avoid early detection by a predator, but given that among free ranging kissing bugs masked nymphs are the most often prey in the lizard's natural habitat, they will probably be recognized as an edible object and therefore lizards will approach to them instead. This is expected as *M. spinolai* masking consists of a sand cover that minimizes the probability of detection by means of loosing contrast against its background (Endler 1978; Haridass et al. 1987) but not necessarily interrupting its recognition as a prey (Stevens and Merilaita 2009). It is likely, then, that the sand cover besides being an adaptation for extreme climatic conditions, is also providing additional advantages in terms of predation given that nymphs gain protection by minimizing detection probabilities.

Although camouflage is a widespread strategy to reduce risk of predation in animals, few studies have focused on kissing bugs predator–prey interactions or on its effect on life history traits. This is the first study that addresses the effect of the masking behavior shown by *Mepraia spinolai* on its life history traits and as an anti-predator mechanism. Here we have shown that masked nymphs had a lower predation risk, and a higher survivorship and lower developmental time in the absence of predators. Therefore, masking seems to render selective advantages to *M. spinolai* nymphs even in the absence of selective forces, which may ultimately assure the reproduction and maintenance of populations under natural conditions.

Acknowledgments We thank Carmen Gloria Ossa for laboratory assistance, and Dr. Rodrigo Zeledón and Dr. Dunston Ambrose for sharing some of their articles difficult to find. Financial support was obtained from FONDECYT 11090086.

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