The movement of "false antennae" in butterflies with "false head" wing patterns

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Abstract In many butterfly species of the family Lycaenidae, the morphology and color pattern of the hind wings, together with certain behaviors, suggests the presence of a false head (FH) at the posterior end of the perching individual. This FH is considered an adaptation to escape from visually oriented predators. A frequent component of the FH are the tails that presumably resemble the antennae, and the typical hind wings back-and-forth movement along the sagittal plane (HWM) performed while perching apparently move the tails in a way that mimics antennal movement. By exposing 33 individuals from 18 species of Lycaenidae to a stuffed insectivorous bird, we tested two alternative hypotheses regarding HWM. The first hypothesis proposes that, when the butterfly is observed at close range, the HWM distorts the shape of the false head thus reducing its deceiving effect and, therefore, selection will favor butterflies that stop moving their wings when a predator is close by; the second hypothesis says that an increase in the frequency of HWM improves its deflective effect when the butterfly confronts a predator at close range. Our results tend to support the second hypothesis because half of the butterflies started to move their hind wings or increased the rate of HWM when exposed to the stuffed bird; however a substantial proportion of butterflies (30%) stopped moving their hind wings or decreased the rate of HWM as expected from the first hypothesis. Our observations also showed that there is great variation in the rates of HWM, and demonstrated the existence of alternative ways of producing "vivid" movement of the hind wing tails (the "false antennae") in the absence of HWM [*Current Zoology* 61 (4): 758–764, 2015].

Keywords Butterflies, Lycaenidae, Predator deception, Anti-predator behavior, Wing morphology

Behaviors, morphologies and chemicals employed by animals to deceive their predators provide fascinating examples of adaptive evolution (Wickler, 1968; Eisner, 2003; Ruxton et al., 2004). In several butterfly species, especially within the Theclinae subfamily (Lycaenidae), the morphology and color pattern of the hind wings, together with certain behaviors, suggest to the human eye the existence of a head at the posterior end of the perching butterfly (Fig. 1A) (Wickler, 1968; Robbins, 1980 and references therein). Most authors consider that these so-called "false heads" (FHs hereafter) are adaptations that deflect predator attacks towards body parts that are less vulnerable, either because they can be (partially) lost without having (very) negative effects (Wickler, 1968; Robbins, 1980 and references therein) or because they allow the butterfly to detect the potential predator and escape before being damaged (Cordero, 2001). Other authors proposed instead that the FH could prevent attacks by faking a threat for the predator (such as an open mouth when observed from behind; Krizek, 1998), while other researchers suggest that the appearance of having two heads confuses predators (references in Robbins, 1980; Wourms and Wasserman, 1985). Available direct evidence is scant and tends to support the hypothesis that FHs deflect attacks towards the rear end of the butterfly (i.e. towards the FH) (Van Someren, 1922; Sourakov, 2013). One experimental study indicates that the FH confuses avian predators during prey handling (Wourms and Wasserman, 1985), although this study was conducted by adding artificial FH components to butterflies of a species (*Pieris rapae*, Pieridae) unrelated to FH lycaenids. It is also possible that in some species the FH decreases predation via more than one of the mechanisms proposed (for example, depending on the species of predator or the specific circumstances of the interaction).

Robbins (1980) discussed the different color, morphology and behavior traits composing the FH (see also Cordero, 2001). The thin tails present in the anal angle of the hind wings of many lycaenids are considered to resemble the antennae, and several authors have noted that these butterflies perch with the wings closed and frequently move the hind wings back and forth along the sagittal plane, thus moving the tails in a way similar to that of antennae (Wickler, 1968; Owen, 1971; Robbins, 1980, 1981, 1985; Cooper, 1998; Krizek, 1998; Stevens, 2005; Sourakov, 2013). Furthermore, in lycaenids both hind wings move simultaneously and asynchronously (i.e. while one wing moves forward the other moves backwards) and, since in many species the tails of each hind wing cross with each other, the "false antennae" of each hind wing not only move up and down in an alternate way, but they also "flicker" presumably increasing the resemblance to the movement of real antennae (Robbins, 1980, 1985).

According to Cooper (1998), deflection displays can be either "anticipatory" or "reactive". "Anticipatory deflection" is displayed when no predator has been detected and is presumably aimed at deceiving ambush predators, while "reactive deflection" displays are "performed when a prey is confronted by a predator at close quarters" (Cooper, 1998, p. 598). Although Cooper (1998) mentions that the movement of the hind wings resulting in the movement of false antennae (HWM hereafter) observed in lycaenid butterflies is one of the few known examples of "anticipatory deflection", Krizek (1998) and Sourakov (2013) reported that *Arawacus* sp. and *Calycopis cecrops* increase the frequency of HWMs when "threatened" (by a human in the first case and by a salticid spider or a human in the last species), and *Arawacus* even turns its FH to the approaching "threat" (the camera lens of G. Krizek). These observations suggest that the HWM of Lycaenidae with FH is a deflective behavior with elements of both anticipatory and reactive displays. Thus, this hypothesis predicts that HWM is induced or increases in frequency when a predator approaches or is detected when it is already close. However, the fact that, at least to the human eye, FHs better resemble the real heads of butterflies when they are observed from the side led us to suggest that, at least at close distance, the asynchronous HWM also produces a distortion of the shape of the FH (compare Fig. 1A and 1B) that could allow the predator determining where the real head is. Thus, although the HWM increases the "realism" of the FH when observed from a certain distance, the idea that the HWM producing the

movement of the false antennae also distorts the FH predicts that when the predator is close it is better to decrease the frequency of HWM or even stop moving the hind wings to prevent the distortion of the FH. Here we report the results of a field experiment in which we tested these contrasting predictions in several Lycaenidae species exhibiting different degrees of development of the FH (Robbins, 1981).

Riley and Loxdale (1988) suggested that in *Arawacus aetolus* the twisting of the hind wing tails along their longer axis is enough to produce a realistic movement of the false antennae when they are exposed to air currents. This observation led us to consider the possible existence of alternative ways of moving the false antennae that do not require the HWM that distorts the FH. For this reason, during our field study, we made detailed observations of the FH area whenever possible, in an attempt to discover alternative ways of moving the false antennae, including that proposed by Riley and Loxdale (1988).

1　Materials and Methods

Our field work was conducted in a plantation of the fruit-producing rambutan tree (*Nephelium lappaceum*,
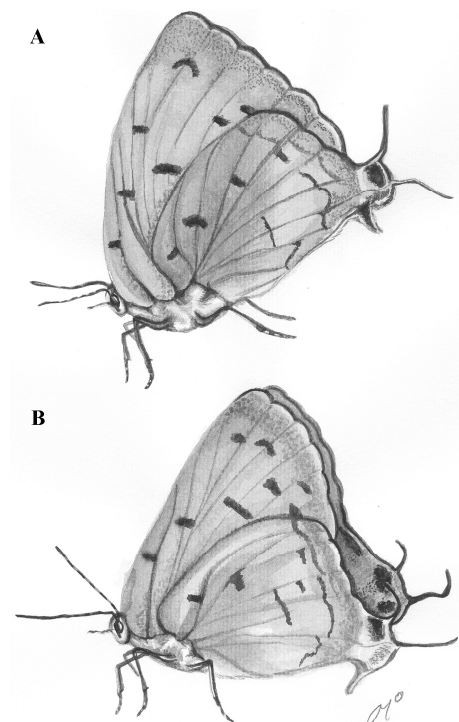
Fig. 1　An example of a lycaenid butterfly with "false head" depicted at two different moments during a bout of hind wings back-and-forth movements

The butterfly shown is *Pseudolycaena damo*; notice the "distortion" of the false head outline at the anal end of the hind wings in B. Drawings by Alejandra Aguilar Caballero.

Sapindacea) belonging to the Hagia Sofía Ranch, located in the municipality of Santa María Huatulco, Oaxaca, México. We performed experimental trials and observations in five consecutive days, late in the flowering season (second half of May), usually under sunny and warm conditions. Previous field work by the second author shows that the flowers of rambutan attract numerous species of foraging Lycaenidae, although the numbers of individuals of each species are usually low. The height of most trees in this plantation is relatively low (2–5 m) and this, together with the slight inclination of the terrain, allowed us to observe and film perching and foraging butterflies, sometimes at very close range.

We made behavioral observations directly or with the help of binoculars, and we recorded all our observations using a digital voice recorder (*Sony* ICD-PX333); we filmed some of our experimental trials (see next paragraph) and observations with either a digital camera (*Sony* Handycam HDR-SR1) or an iPod touch (*Apple* Inc.). All butterflies were identified by one of us (ALM) or collected to be compared with museum specimens when its identity was not clear.

To assess the effect of a close-range encounter with a predator on HWM we performed a field experiment in which we exposed foraging butterflies of a variety of Lycaenidae species to a stuffed insectivorous bird belonging to a species present in the area (*Myiarchus tuberculifer*, Tyrannidae), although the specimen was collected in a different locality; the bird was in a position simulating an approaching predator. Every time we found a butterfly on an inflorescence that permitted observation with the naked eye or with binoculars, one of us (TGLP) counted the number of times the butterfly moved its hind wings back and forth along the sagittal plane during a period of at least four and a half minutes (median [$Q_{25\%}$–$Q_{75\%}$] in minutes:seconds: 5:40 [5:14–6:16]), the only exception was an individual observed for 2 min and 38 sec, and the longest observation period was 7 min and 40 sec. One movement was counted when one complete sequence of back-and-forth movements by one hind wing was completed. Observation time in this initial period varied for different reasons such as wind conditions, which could increase the probability that the butterfly flew away or remained motionless. After the initial observation period, one of us (CC or ALM) carefully brought the stuffed bird, mounted on the 1 m long handle of an entomological net, to a distance of ≈ 10-20 cm from the butterfly. We brought the stuffed bird close to the butterfly trying to prevent

the butterfly from observing the bird before it was very close (≤ 50 cm); for this end we usually put the bird below the butterfly and moved it up slowly, using the leaves and inflorescences of the tree to hide the bird from the butterfly. While we brought the bird near the butterfly, the same person that counted the number of hind wing movements (TGLP) observed the butterfly and recorded its behavior, either with the voice recorder or the digital camera; the observation period of the butterfly exposed to the bird varied between six seconds and five min and 22 sec (median [$Q_{25\%}$–$Q_{75\%}$] in minutes:seconds: 1:13 [1:00–1:55]) depending on the behavior of the butterfly (for example, the butterfly could fly away during the experimental trial).

We present our experimental results following Robbins' (1981) ranking of Lycaenidae species according to the number of FH components possessed. Robbins considered two wing color and two wing morphology FH components in his classification which are roughly the following: (a) presence of two or more lines converging to the caudal angle of the hind wings, (b) presence of one or more spots of contrasting color in the anal angle of the hind wings ("eyespots") (Fig. 1A), (c) modification of the contour of the anal angle of the hind wings that presumably mimics the shape of a head (Fig. 1A), and (d) presence of tails in the anal angle of the hind wings ("false antennae") (Fig. 1A). Species with zero or one of these component are placed in rank 4, species with two in rank 3, species with three in rank 2, and those with all four components in rank 1. Obviously, species in rank 1 are the ones with the most developed FH.

2   Results

We conducted experiments using 33 butterflies belonging to 18 species of Lycaenidae (Table 1). In 10 species we studied just one individual, in five two individuals, in two three individuals, and in one seven individuals (Table 1). Although we observed two individuals of a species belonging to Robbins' (1981) rank 1 *Laothus erybathis*, we could not perform experimental assays with them because they flew away before being exposed to the stuffed bird. Thus, we performed experiments in two rank 2 species, fifteen rank 3, and one rank 4 (Table 1).

2.1   Variability in the frequency of back-and forth movement of hind wings

Three species in which we observed just one individual did not show HWMs either before being exposed or while they were exposed to the bird (Table 1). Overall,

Table 1 Effect of exposure to a stuffed insectivorous bird on the rate of hind wing movement of 18 species of Lycaenidae butterflies differing in the number of false head components

Species	Robbins' rank[1]	# Hind wing movements per min before being exposed to bird[2]	# Hind wing movements per min during exposition to bird[3]	Trend[4]
Atlides halesus	2	[65] / [6:07] = 10.7	[4] / [0:07] = 33.3	↑
Pseudolycaena damo	2	[43] / [5:40] = 7.5	[43] / [3:45] = 11.5	↑
P. damo		[0] / [6:42] = 0.0	[5] / [1:17] = 3.8	▲
P. damo		[2] / [6:15] = 0.3	[0] / [1:48] = 0.0	▼
P. damo		[1] / [4:30] = 0.2	[0] / [2:25] = 0.0	▼
P. damo		[10] / [4:56] = 2.0	[3] / [0:41] = 4.3	↑
P. damo		[9] / [5:21] = 1.7	[5] / [1:03] = 4.8	↑
P. damo		[19] / [5:14] = 3.7	[28] / [1:08] = 25.4	↑
Calycopis isobeon	3	[4] / [5:42] = 0.7	[52] / [5:22] = 9.6	↑
Electrostrymon joya	3	[22] / [6:07] = 3.6	[22] / [1:52] = 11.6	↑
Electrostrymon mathewi	3	[0] / [6:16] = 0.0	[18] / [1:15] = 14.4	▲
Ministrymon arola	3	[20] / [6:14] = 3.2	[31] / [3:25] = 9.1	↑
M. arola		[2] / [5:06] = 0.4	[0] / [0:06] = 0.0	▼
Ministrymon azia	3	[54] / [6:12] = 8.7	[0] / [2:09] = 0.0	▼
M. azia		[0] / [5:20] = 0.0	[8] / [2:26] = 3.3	▲
M. azia		[4] / [4:30] = 0.9	[3] / [1:55] = 1.6	↑
Ministrymon clytie	3	[1] / [5:14] = 0.2	[0] / [0:25] = 0.0	▼
Ocaria ocrisia	3	[0] / [5:30] = 0.0	[0] / [2:35] = 0.0	=
Parrhasius polibetes	3	[0] / [7:27] = 0.0	[1] / [3:36] = 0.28	▲
Rekoa marius	3	[13] / [5:31] =　2.4	[3] / [1:00] = 3.0	↑
R. marius		[12] / [5:33] = 2.2	[10] / [1:05] = 9.1	↑
Rekoa meton	3	[0] / [6:00] = 0.0	[0] / [1:34] = 0.0	=
Rekoa palegon	3	[27] / [6:47] = 4.0	[2] / [1:06] = 1.8	↓
R. palegon		[0] / [2:38] = 0.0	[0] / [1:24] = 0.0	=
R. palegon		[0] / [5:40] = 0.0	[0] / [1:13] = 0.0	=
Rekoa stagira	3	[5] / [5:10] = 1.0	[0] / [0:45] = 0.0	▼
R. stagira		[2] / [6:42] = 0.3	[2] / [0:42] = 2.9	↑
Strymon mulucha	3	[0] / [5:00] = 0.0	[0] / [1:00] = 0.0	=
Strymon rufofusca	3	[2] / [6:52] = 0.3	[0] / [1:08] = 0.0	▼
Strymon yojoa	3	[85] / [6:31] = 13.1	[2] / [0:55] = 2.2	↓
S. yojoa		[0] / [6:46] = 0.0	[0] / [1:03] = 0.0	=
Strymon cestri	4	[5] / [7:40] = 0.6	[22] / [1:26] = 15.7	↑
S. cestri		[34] / [5:20] = 6.4	[0] / [0:45] = 0.0	▼

[1] Species rank according to the number of false head components present in the hind wings (Robbins, 1981). Rank 2: 3 components, Rank 3: 2 components, and Rank 4: 1 or 0 components. [2] [Number of hind wing movements recorded before exposing the butterfly to the stuffed bird] / [Amount of time the butterfly was observed before being exposed to the stuffed bird] = Number of hind wing movements per minute before being exposed to the stuffed bird; time is given as minutes:seconds. [3] [Number of hind wing movements recorded while the butterfly was exposed to the stuffed bird] / [Amount of time the butterfly was observed while it was exposed to the stuffed bird] = Number of hind wing movements per minute during exposition to the stuffed bird; time is given as minutes:seconds. [4] ▲: the butterfly started moving its hind wings when exposed to the bird; ↑: the frequency of hind wing movements increased when the butterfly was exposed to the bird; ▼: the butterfly stopped moving its hind wings when exposed to the bird; ↓: the frequency of hind wing movements decreased when the butterfly was exposed to the bird; =: frequency of hind wing movements remained the same when the butterfly was exposed to the bird.

we observed only six experimental individuals (18% of the total) that never moved their hind wings (Table 1). The 15 species in which at least one individual showed HWM varied widely in the frequency of movements, from zero in at least one individual from 11 species, to 33.3 movements per minute when *Atlides halesus* was exposed to the bird (Table 1); in fact, within the species with more individual observations *Pseudolycaena damo*

variation was considerable, ranging from no movements in some individuals (either before being exposed or while they were exposed to the bird) to 25.4 movements per minute in an individual while exposed to the bird. The two individuals from the rank 1 species that we observed *L. erybathis* moved their hind wings 21 times in 7 minutes and 34 seconds (2.8 movements per minute), and 92 times in 4 minutes and 37 seconds (20 movements per minute). We found a positive correlation between the rate of HWM before and during exposure to the stuffed bird (Spearman $r = 0.42$, $P = 0.016$, $n = 33$; Fig. 2).

2.2   Effect of predation risk on the back-and forth movement of hind wings

Overall, the median rate of HWM during exposition to the bird was thrice the rate observed before exposing the butterflies to the bird (median $[Q_{25\%}–Q_{75\%}]$: 1.8 [0–9.1] *vs*. 0.6 [0–3.2]; Wilcoxon Matched Pairs Test: $Z = 2.19$, $P = 0.029$, $n = 33$). However, although half of the individuals ($n = 17$) started to move their hind wings or increased their rate of HWM when exposed to the bird, we observed 10 butterflies (30%) that stopped moving their hind wings or decreased their rate of HWM when the bird was near (Table 1).

We explored the possible relationship between the "complexity" of the FH and the effect of exposure to the bird on HWM rate, by using the ranking proposed by Robbins (1981; see last paragraph of section 2) and analyzing the effect of exposure to the bird separately for rank 2 butterflies (those with the more complete FH in our sample) and for rank 3 plus rank 4 butterflies. We found that rank 2 butterflies increased their rate of HWM in presence of the bird (median $[Q_{25\%}–Q_{75\%}]$: 1.85
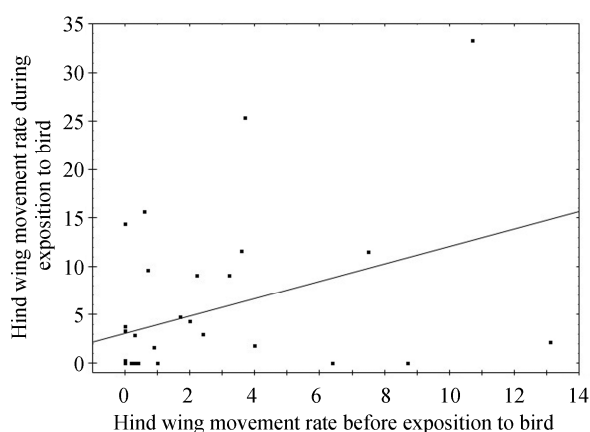
Fig. 2   Relationship between the rates of hind wing movement before being exposed and during exposition to a stuffed insectivorous bird of a sample of Lycaenid butterflies
Hind wing movement rate is number of times a butterfly moved its hind wings back-and-forth per minute. The correlation between the two variables was significant: Spearman $r = 0.42$, $P = 0.016$, $n = 33$.

[0.28–4.65] *vs*. 4.55 [2.85–14.98]; Wilcoxon Matched Pairs Test: $Z = 2.1$, $P = 0.036$, $n = 8$), while rank 3+4 butterflies did not modify their relatively low rate of HWM (0.40 [0.00–2.40] *vs*. 0.30 [0.00–3.30]; Wilcoxon Matched Pairs Test: $Z = 1.15$, $P = 0.25$, $n = 25$). However, when we compared the proportion of butterflies that increased the frequency of HWM in presence of the bird, we did not find a significant difference between rank 2 species (6 out of 8 butterflies) and rank 3+4 species (11 out of 25 individuals) (Fisher's exact test: $P = 0.13$); when we excluded six individuals that did not move their hind wings from the rank 3+4 group the proportions were even more similar ($P = 0.35$).

2.3   Alternative ways of moving false antennae

We observed some butterflies close enough to confirm that at least some species are able to move their false antennae without conspicuously moving their hind wings. We observed two different behaviors, one of which is a variant of the typical HWM. In many lycaenids, while the butterfly is perching or walking, the tails of the FH are crossed and due to this configuration the tails move up and down and laterally during HWM (Robbins, 1980).

In some butterflies we observed that the crossing occurs at the base of the tails and a very small hind wing displacement along the sagittal plane, almost imperceptible if it is not observed from a very close distance, results in the false antennae moving quite "vividly". Although we only have one video record of this behavior (in an individual *Allosmaitia strophius*), we observed it in other butterflies during our field study. A second behavior that produces vivid false antennae movement consists in placing the abdomen between the anal angles of the closed hind wings, and then gently moving it up and down and possibly also sideways. We observed this behavior in an unidentified species of *Strymon* and in *Strymon rufofusca*.

3   Discussion

3.1   Variability in the frequency of back and-forth movement of hind wings

The sample of Lycaenidae species that we studied showed wide intra- and interspecific variation in the frequency of HWM. Although we did not observe HWM in three species in which we only studied one individual (Table 1), we suspect that all species perform HWM at least sometimes because in *Rekoa palegon* and *Strymon yojoa* we observed individuals that moved their hind wings and individuals that never moved them (Table 1). Experimental studies are necessary to determine if the

variation we observed results from consistent individual and/or interspecific differences in HWM rate. Even though individual and/or interspecific differences in HWM could explain the positive correlation between the rates of HWM measured before and during exposure to the stuffed bird (Fig. 2), there are alternative explanations for this correlation. Our observations indicate that studying the possible influences of environmental factors (such as temperature) on the frequency of HWM, as well as the possible effects of differences in HWM frequency on the butterflies' ability of to escape from predation, will produce fascinating insights.

3.2 Effect of predation risk on the back and-forth movement of hind wings

Our experimental results are consistent with the hypothesis that, at least in several FH lycaenid butterflies, HWM is a deflecting display because the rate of HWM was higher when the butterflies were exposed to the stuffed bird. Furthermore, our results suggest that the HWM is a deflective display combining elements of reactive and anticipatory displays (*sensu* Cooper, 1998), because exposure to the bird induced the expression of this behavior in butterflies that were not moving their wings ($n = 4$; Table 1) or resulted in an increased frequency of movement in butterflies that were already performing HWM ($n = 13$; Table 1). These results are in agreement with natural history observations in *Arawacus* sp. (Krizek, 1998) and *Calycopis cecrops* (Sourakov, 2013), where the frequency of HWM increased when the butterflies perceived a "threat". Of course, the crucial prediction that increasing the frequency of HWM reduces the probability of being captured needs to be tested; one of the main methodological challenges implied in this test will be to isolate the effect of HWM from other FH components.

On the other hand, we observed 10 butterflies decreasing their rate of HWM during exposure to the bird (Table 1) as expected from the alternative hypothesis that the HWM distorts the FH and selects against moving the hind wings when a predator is close. A possible explanation for our experimental results is that each of the two hypotheses applies to a different subset of species. Nevertheless, six of the 10 butterflies that decreased their rate of HWM in presence of the bird belong to species in which we also observed individuals increasing their rate of HWM when exposed to the bird (Table 1). We did not find support for the idea that the distortion of the FH due to HWM is more evident in species with more "complex" or "complete" FHs (those in Robbins' rank 2 species in our sample) than in butter-

flies with more "simple" or "incomplete" FHs (those in Robbins' ranks 3 and 4) because, contrary to expectations, rank 2 butterflies tended to increase their rate of HWM in presence of the bird, while rank 3+4 butterflies did not modify their relatively low rate of HWM (Table 1). However, this result must be considered with caution because we only studied two rank 2 species.

3.3 Alternative ways of moving false antennae

The existence of alternative ways of moving the false antennae without HWM is consistent with the hypothesis that at close range the HWM is disadvantageous because it distorts the FH shape facilitating the detection of the real head by the predator. However, the use of the alternative ways of moving the false antennae described above is also predicted by other hypotheses; for example, these alternative behaviors could be less energetically expensive than the typical HWM. One interesting hypothesis is that the FH distorting effect of the HWM is relevant only for some types of predators and it is against these predators that the butterflies use the alternative ways of moving the false antennae. It will be interesting to perform experiments similar to ours but with other visually oriented predators that have been considered selective pressures in the evolution of FHs, such as lizards (Van Someren, 1922), salticid spiders (Sourakov, 2013) or mantids (López-Palafox and Cordero, in prep.).

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