Two-headed butterfly vs. mantis: do false antennae matter?

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The colour patterns and morphological peculiarities of the hindwings of several butterfly species result in the appearance of a head at the rear end of the insect's body. Although some experimental evidence supports the hypothesis that the "false head" deflects predator attacks towards the rear end of the butterfly, more research is needed to determine the role of the different components of the "false head". We explored the role of hindwing tails (presumably mimicking antennae) in predator deception in the "false head" butterfly Callophrys xami. We exposed butterflies with intact wings and with hindwing tails experimentally ablated to female mantises (Stagmomantis limbata). We found no differences in the number of butterflies being attacked and the number of butterflies escaping predation between both groups. However, our behavioural observations indicate that other aspects of the "false head" help C. xami survive some mantis attacks, supporting the notion that they are adaptations against predators.

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14 **ABSTRACT**

15 The colour patterns and morphological peculiarities of the hindwings of several butterfly species

16 result in the appearance of a head at the rear end of the insect's body. Although some

17 experimental evidence supports the hypothesis that the "false head" deflects predator attacks

18 towards the rear end of the butterfly, more research is needed to determine the role of the

19 different components of the "false head". We explored the role of hindwing tails (presumably

20 mimicking antennae) in predator deception in the "false head" butterfly *Callophrys xami*. We

21 exposed butterflies with intact wings and with hindwing tails experimentally ablated to female

22 mantises (*Stagmomantis limbata*). We found no differences in the number of butterflies being

23 attacked and the number of butterflies escaping predation between both groups. However, our

24 behavioural observations indicate that other aspects of the "false head" help *C. xami* survive

25 some mantis attacks, supporting the notion that they are adaptations against predators.

26

27 **INTRODUCTION**

28 Butterfly wings are canvases on which evolution designs solutions to the problems posed by

29 thermoregulation, sexual selection and predation (*Monteiro & Prudic, 2010*; *Kemp & Rutowski,*

30 *2011*). These adaptations frequently involve compromises between selective pressures when

31 optimal trait values differ between functions (*Ellers & Boggs, 2003*), although sometimes they

32 coincide (*Finkbeiner et al., 2014*). Several butterfly species exhibit colour patterns and

33 morphological peculiarities in their hindwings that suggest, at least to the human eye, that a

34 butterfly resting with its wings closed possess a second head at the rear end of its body (*Robbins,*

35 *1980*; *Cordero, 2001*). This appearance is enhanced by peculiar behaviours, such as the back and

36 forth movements of the closed hindwings that presumably permit the "false antennae"—the

37 "tails" frequently present in the border of the anal angle of the hindwings (Fig. 1a)—mimic the

38 movements of real antennae (*Robbins, 1980*; *López-Palafox et al., 2015*). False head butterflies

39 are especially common among the subfamily Theclinae (Lycaenidae). Several specific

40 hypotheses on the function of the "false head" have been advanced; all of them consider visually

41 oriented predators as the main selective pressure, and avoidance or deflection of attacks as the

42 main advantage (*Robbins, 1980*; *Cordero, 2001*). Although false head butterflies are textbook

43 examples of anti-predator adaptations (e.g. *Wickler, 1968*; *Ruxton et al., 2004*), to the best of our

44 knowledge, there are only two published experimental studies testing the effect of false heads on

45 probability of predation in live butterflies.

46   *Sourakov (2013)* exposed two *Calycopis cecrops* (Lycaenidae) butterflies, a species with

47 false head, and thirteen individuals from eleven species of butterflies and moths without false

48 heads, to one individual predatory salticid spider (*Phidippus pulcherrimus*). The spider

49 repeatedly failed to trap the lycaenid butterflies because it directed all its attacks towards the

50 false head, but captured all individuals from the other species, mostly (11 out of 13 cases) in the

51 first or second attack. *Wourms & Wasserman (1985)* added artificial "false heads" to *Pieris*

52 *rapae* (Pieridae) butterflies by attaching tails ("false antennae") and painting spots ("false eyes")

53 on the anal angle of the hindwings, as well as by painting lines converging on the anal angle,

54 three of the main components of false heads identified by *Robbins (1980). Wourms &*

55 *Wasserman (1985)* compared predation rates by Blue Jays (*Cyanocitta cristata*) between intact

56 butterflies and butterflies with false heads added. All control and experimental butterflies

57 attacked were caught, but the percentage of butterflies escaping during handling was twice as

58 large in the treatment with artificial false heads as in the control group (16 out of 60 *vs*. 10 out of

59 79, respectively). The authors mention that butterflies escaped due to "mishandlings" by the

60   birds, i.e. due to errors resulting from misdirected strikes while handling captured prey (*Wourms*

61   *& Wasserman, 1985*). Thus, the experimental research available supports the idea that false

62   heads help butterflies to deflect attacks away from their less vulnerable end (*Wourms &*

63   *Wasserman, 1985*; *Sourakov, 2013*).

64   However, these experimental studies have some limitations. *Sourakov's (2013)* sample

65   size was very small and the control group differed in a number of morphological and behavioural

66   aspects besides the absence of a false head. *Wourms & Wasserman (1985)* recognized that the

67   wing shape of *P. rapae* is different from that of "false-head" Lycaenidae and that some of the

68   behaviours associated with the functioning of false heads are absent in this species. Furthermore,

69   although these studies support the deflecting function of false heads, visually guided predators of

70   butterflies exhibit a variety of sensory capabilities and employ different hunting strategies, and it

71   is not clear if false heads are useful against all them.

72   Salticid spiders and birds are active hunters that are probably able to use fine details to

73   identify and attack butterflies, while sit-and-wait predators, such as mantises, appear to recognize

74   prey by assessing a number of general features in objects found in the environment (*Kral, 2012;*

75   *Prete et al., 2013*). According to behavioural and electrophysiological studies (reviewed in *Prete*

76   *at al., 2013*), the main features used by mantises include the size of the object, contrast with the

77   background, leading edge length, speed and movement pattern. Thus, considering the last two

78   features, we hypothesize that the movement of false antennae (i.e., the "tails" present in the

79   border of the anal angle of the hindwings) deflects mantis attacks to a less vulnerable area and

80   increases the probability of escape. We tested this idea by measuring the effects of

81   experimentally ablating the hindwing tails of the false head butterfly *Callophrys xami*

82   (Lycaenidae: Techlinae) (Fig. 1) on the probability of exhibiting hindwing back-and-forth

83   movement, and on the probability of being attacked and captured by female mantises

84   (*Stagmomantis limbata*).

85

86   **MATERIALS AND METHODS**

87   Experimental butterflies were raised from eggs laid by three females collected in the Pedregal de

88   San Ángel Ecological Reserve (PSAER) of the Universidad Nacional Autónoma de México

89   (UNAM), located in the main campus of the UNAM in the South of Mexico City. *Callophrys*

90   *xami* is a multivoltine "false head" butterfly whose main food plant in the collection site is

91   *Echeveria gibbiflora* DC (Crassulaceae). Rearing methods followed *Jiménez & Soberón (1988-*

92   *1989)*.

93   The predators used in the experiment were adult females (males did not attack butterflies

94   in pilot tests) of the mantis *Stagmomantis limbata*, a species living in the PSAER and, therefore,

95   a potential natural predator of *C. xami*. Some of the females were the offspring of a female

96   collected in the PSAER, whose nymphs were maintained individually in ½ L plastic containers

97   until the fourth instar and afterwards in 1 L containers. Nymphs from instars 1 to 3 were fed

98   *Drosophila nubin* ad libitum every other day, and afterwards with *Achaeta domesticus* crickets.

99   The rest of the female mantises used were donated as adults by the Unidad de Manejo Ambiental

100 Yolkatsin (México), where a colony of mantises raised in captivity has been maintained during

101 several generations. These mantises were also fed *Drosophila* from instar 1 to 3, and *A.*

102 *domesticus* afterwards. Thus, before our experiment, none of the mantises had been in contact

103 with butterflies. All insects were maintained at ambient temperature under a 12 h dark–12 h light

104 photoperiod in the insectary of the Instituto de Ecología (UNAM) located besides the PSAER.

105   The butterflies were randomly assigned to a treatment group: in the experimental group

106   the hindwing tails were ablated (Fig. 1b), whereas in the control group the wings remained intact

107   (Fig. 1a). Hindwing tails ablation was achieved by first introducing the butterflies in a -20°C

108   freezer until they were immobile (between 2 and 5 min), then the tails were cut out with micro-

109   scissors (Iris Scissors, Bioquip™). Manipulation of each butterfly lasted approximately 2 min.

110   Control individuals were also introduced in the freezer and manipulated for a similar amount of

111   time as experimental butterflies. Twenty-six butterflies of both sexes were attacked thus

112   producing experimental data (14 males: 8 control, 6 experimental; 12 females: 6 control, 6

113   experimental; see Appendix).

114   Twenty-four female mantises were used, but five never attacked. Twelve mantises that

115   attacked were used just once (six with experimental and six with control butterflies) and seven

116   were used twice (five first with a control and then with an experimental butterfly, and two first

117   with an experimental and then with a control butterfly). Mantises used twice had a time interval

118   between trials of at least two weeks thus reducing possible learning effects. The fact that only

119   two of the seven mantises captured both butterflies and that other four captured the first but

120   failed capturing the second butterfly, suggests learning had no effect on our results. To increase

121   the probability of attack, mantises were starved three days before being exposed to a butterfly.

122   Butterflies were individually exposed to one mantis in a glass chamber measuring 29.5

123   cm × 25 cm × 9.5 cm (length × height × width), with one of the two largest (29.5 cm × 25cm)

124   sides covered with white Styrofoam. A Sony Handycam HDR-SR1was used to film most of the

125   trials (23 out of 26). The room where the experiments were carried out was illuminated with two

126   30W white fluorescent tubes (Philips™ Slim line LDD F48T8/TL865) located at a diagonal

127   distance from the chamber (i.e., they were not directly above it) of 2.5 m and 3.6 m, respectively.

128   The mantis was introduced to the experimental chamber two hours before each trial. Afterwards,

129   the butterfly was gently introduced in the chamber in a position as far as possible from the

130   mantis. A trial was discarded if the mantis failed to attack the butterfly within 5 min. If the

131   mantis attacked within five minutes after the introduction of the butterfly, we recorded the result

132   (i.e. butterfly captured or escaped) and finished the trial. We allowed just one attack.

133

134   **RESULTS**

135   We staged 22 control and 22 experimental interactions between a mantis and a butterfly.

136   Twenty-six butterflies (59.1%) were attacked. The butterflies were attacked when they were

137   walking, perching after walking or after landing; in one case the butterfly was detected after

138   stepping on one leg of the mantis. The number of butterflies attacked (Fig. 2a) was statistically

139   independent of the presence of hindwing tails (Chi squared = 0.38, P = 0.54, $gl.$ = 1). The

140   number of attacked butterflies displaying hindwing movements (that presumably allow the

141   hindwing tails to mimic the movement of antennae) during the interaction with a mantis (Fig. 2b)

142   was statistically independent of the presence of hindwing tails (Fisher's exact test, P = 0.27).

143   The number of butterflies surviving the attack (Fig. 2c) was statistically independent of

144   the presence of hindwing tails (Fisher's exact test, P = 0.70). Attacks directed to the rear end of

145   the butterfly resulted in less captures than those directed to other body parts (lateral and frontal

146   attacks): five out of six butterflies escaped when attacked in the rear end, in contrast to four out

147   of 17 attacks directed to other parts (Fisher's exact test, P = 0.018). (We have not videos of three

148   interactions, one of them of a control butterfly that escaped.) However, two of the five failed

149   attacks directed to the rear end involved butterflies with their hindwing tails ablated.

150   Furthermore, only in one case the mantis directed the attack towards the "false head" despite the

151 real head of the (control) butterfly was closer to the head and front legs of the mantis (see

152 interaction between butterfly 127 and mantis 17 in seconds 27 to 43 of Video). In the other four

153 failed attacks, the rear end of the butterfly was closer to the head and front legs of the mantis (see

154 Video).

155

156 **DISCUSSION**

157 In false head butterflies, the tails present in the anal angle of the hindwings are considered to

158 mimic the antennae of the real head, a hypothesis consistent with the peculiar back-and-forth

159 movements of the closed hindwings that apparently aid mimicking the movement of the real

160 antennae (*Robbins, 1980*; *López-Palafox et al., 2015*). This idea led us to predict that the success

161 in escaping a mantis attack would decrease in butterflies with "false antennae" experimentally

162 ablated. Nevertheless, our experiment failed to reveal an advantage of possessing hindwings

163 tails. The presence of hindwings tails in perching *C. xami* butterflies had no statistically

164 significant effect on the probability of surviving an attack from a mantis that is possibly a natural

165 predator.

166   Furthermore, although the absolute difference in the proportion of butterflies escaping an

167 attack was in the predicted direction (Fig. 2), direct evidence of improved deception due to the

168 presence of false antennae is weak. In one case, the mantis was apparently deceived into

169 attacking the rear end (false head) of a butterfly with false antennae, judging from the fact that

170 the mantis' head and front legs were closer to the real head (see interaction between butterfly 127

171 and mantis 17 in seconds 27 to 43 of Video). However, in the other four failed attacks directed to

172 the rear end, the back of the butterfly was closer to the front legs of the mantis, suggesting that

173 the mantis was not deceived into attacking that part. Furthermore, two of these four failed attacks

174 involved butterflies with hindwing tails ablated.

175   There are several possible explanations for our results. First, hindwing tails could perform

176 no function in this species, but being present because they were inherited from their phylogenetic

177 ancestors. We cannot discard this possibility, but phylogenetic inertia seems unlikely considering

178 that in Theclinae (the diverse subfamily including *C. xami*) false head components evolve rapidly

179 (*Robbins, 1981*). Second, hindwing tails could be involved in a different function, such as in

180 courtship behaviour or flight manoeuvrability. These alternatives deserve further study. Finally,

181 hindwing tails could improve the deceiving effect of "false heads" (i.e. act as "false antennae")

182 against predators different from mantises, such as birds that detect their prey by using fine details

183 of the wings and actively, and rapidly, approach it from a relatively long distance. In contrast,

184 against a mantis, a predator that relies on crypsis and has a sit-and-wait strategy that allows more

185 time to observe the prey at close range, hindwing tails could be useless. In fact, our observations

186 suggest that *S. limbata* cryptic appearance and behaviour is quite successful against *C. xami*

187 since in many cases the attacked butterflies approached the mantis (in one case was the butterfly

188 was detected because stepped over a mantis leg). Furthermore, the back and forth movements of

189 the closed hindwings, that presumably permit the "false antennae" mimic the movements of real

190 antennae (*Robbins, 1980*; *López-Palafox et al., 2015*), possibly have a negative effect because

191 they attract the attention of the mantis (*Prete et al., 2013*).

192   Although our observations show that in many cases mantises did not direct their attacks

193 towards the "false head", and that many attacks resulted in successful capture of butterflies (16

194 out of 26 in our experiment), our study also indicates that at least some aspects of the "false

195 head" help *C. xami* survive some mantis attacks, supporting the notion that they are adaptations

196   against predators (*Robbins, 1980*; *Cordero, 2001*; *Sourakov, 2013*). Five out of six butterflies

197   that were attacked in the "false head" zone were able to escape. In two of these cases (one

198   control and one with hindwing tails ablated), the mantis teared small pieces of wing from the

199   false head area (see interactions between butterfly 92 and mantis 16 in seconds 21 to 28, and

200   between butterfly 129 and mantis X in seconds 59 to 62 of Video), an observation consistent

201   with the idea that the "false head" area breaks-off easily (*Robbins, 1980*). Thus, our observations

202   indicate that escaping from an attacking mantis depends on several factors, such as the ability to

203   take flight rapidly (see Video) and the specific part of the wings grabbed by the mantis.

204

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212

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254   handling than during the initial strike of an avian predator. *Evolution* **39**:845-851. DOI:

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Figure 1 *Callophrys xami* **(a) with hindwing tails intact (control) and (b) with hindwing tails**

experimentally ablated (dead experimental specimen with broken antennae). Photographs

by Raúl Iván Martínez.

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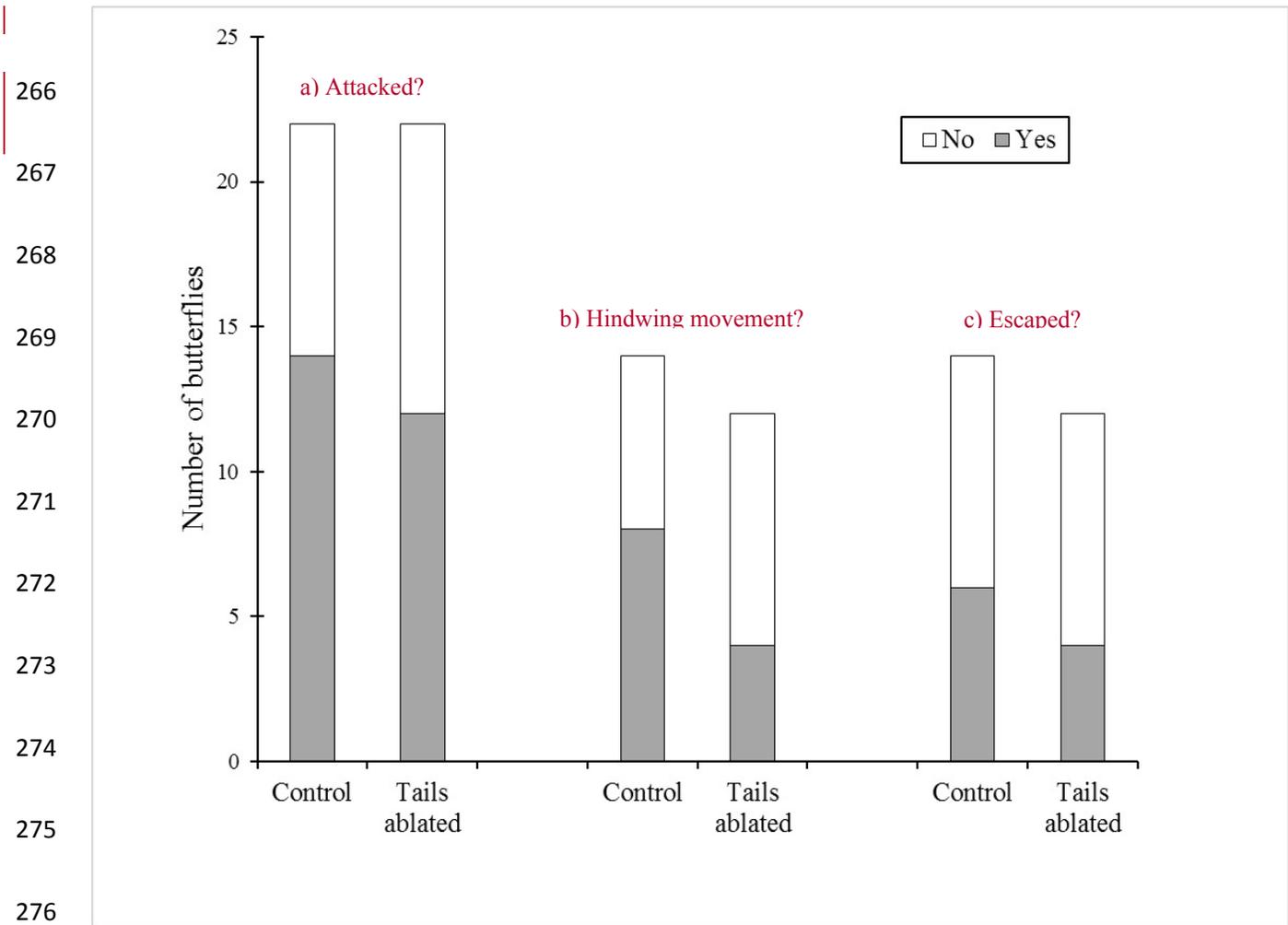
Figure 2 Experimental ablation of hindwing tails ("false antennae") in the "false head"

butterfly *Callophrys xami* and its effect on interactions with female mantis (*Stagmomantis*

***limbata*).** Control butterflies were manipulated in the same way as experimental butterflies but

their hindwing tails were not ablated. (a) Number of butterflies attacked (gray) or ignored

(white). (b) Number of butterflies that performed hindwing movements (gray) or not (white)

before being attacked. (c) Number of butterflies escaping (gray) or being captured (white). None

of the differences between control and experimental groups were statistically significant (see

text).

287 **APPENDIX**

288 **Raw data from the experiment on the effect of ablation of butterfly (*Callophrys xami*)**

289 **hindwing tails ("false antennae") on hindwing movement (HWM) and capture by female**

290 **mantis (*Stagmomantis limbata*).** Control butterflies were manipulated in the same way as

291 experimental butterflies but their hindwing tails were not ablated.

Treatment	Mantis code	Butterfly [a]	HWM	Result
Control	4	37-F	No	Captured [b]
Control	11	14-M	No	Captured
Control	T	106-F	No	Captured
Control	X	117-F	No	Captured
Control	1	1-M	Yes	Captured
Control	11	126-M	Yes	Captured
Control	15	90-F	Yes	Captured
Control	Z	78-F	Yes	Captured [b]
Control	5	39-M	No	Escaped
Control	13	94-M	No	Escaped
Control	1	38-M	Yes	Escaped [b]
Control	12	86-M	Yes	Escaped
Control	16	92-M	Yes	Escaped
Control	17	127-F	Yes	Escaped
Tails ablated	14	70-M	No	Captured
Tails ablated	14	102-F	No	Captured
Tails ablated	1E	68-M	No	Captured
Tails ablated	2E	60-M	No	Captured
Tails ablated	A	101-F	No	Captured
Tails ablated	T	128-F	No	Captured
Tails ablated	7	33-F	Yes	Captured
Tails ablated	15	119-M	Yes	Captured
Tails ablated	10	8-M	No	Escaped
Tails ablated	6	42-F	No	Escaped
Tails ablated	5	18-M	Yes	Escaped
Tails ablated	X	129-F	Yes	Escaped

292   [a] M: male, F: female. [b] Interaction not recorded in video.