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Evidence for the Function of the Eye-spots in the Butterfly Genera *Caligo* and *Eryphanis* (Lepidoptera: Nymphalidae: Morphinae: Brassolini)

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ABSTRACT
Direct observations of seven predatory attacks by the geckonid *Thecadactylus rapicauda* on butterflies of the genera *Caligo* and *Eryphanis* are reported. Two hundred and nine individuals of these butterflies were examined and the probable causes of wing damage classified. Of those examined, 57% showed wing damage of which 60% was consistent with attack by *Th. rapicauda.* The data support the deflection hypothesis; that these butterflies benefit from the "mimetic false head" through disoriented attack. Additional damage was observed suggesting attack by a larger predator. The behaviour of the predator towards the "mimic" is discussed. We propose that the eye-spots on these butterflies benefit the bearers through intrusion into the behavioural interactions between arboreal lizards. The possible mimicry of other saurian models by the genus *Caligo* is discussed.

Key words: mimicry, deflection hypothesis, geckonids, *Thecadactylus.*

INTRODUCTION

The conspicuous eye-spots on the hindwing undersides of the butterfly genera *Caligo* and *Eryphanis* have led to the common name of 'owl butterflies'. Such eye-spots are found on butterflies, reptiles, birds and fish where they function as a mode of interspecies communication and represent a form of auto-mimicry in many species (Stevens 2005), although the precise evolutionary function of eye-spots in many species is not understood or has been mis-interpreted in the past. The adaptive value of the very conspicuous eye-spots on the hindwing undersides of *Caligo* and *Eryphanis* has been the subject of much speculation over the past century (Thayer 1909; Cott 1940; Blest 1957; Kirkpatrick 1957; Barcant 1970; Linsenmaeir 1972; Stradling 1976; de Vries 1987; Stevens 2005).

Both Thayer (1909) and Stradling (1976) considered that 'owl butterfly' was a misnomer, the latter pointing out that both eye-spots would only be simultaneously visible (representing the owl face) in cabinet mounted specimens. Also, that the eye-spots and the surrounding underside markings on each side, resemble the profile of an amphibian or reptilian head. Stradling (1976) pointed to the tree frogs *Hyla* as the models for *Caligo* and the arboreal lizards *Anolis* as the models for *Eryphanis* and suggested that these patterns might benefit their bearers in some way by intruding in the behavioural interactions of diurnal lizards that inhabit tree trunks where the butterflies rest in the daytime. The pattern might therefore appear as either a territorial rival or potential mate. Whichever, it would confuse the potential assailant and result in a non-predatory response. In addition, the eye-spots could confuse assailants as to the orientation of their prey, rival or mate. This "deflection hypothesis" as it is now known has been suggested by several authors (Poulton 1890, 1908; Cott 1940; Blest 1957; Wickler 1968; and Robbins 1980).

Hill and Vaca (2004) studied marginal wing damage in the genus *Pierella* of the Nymphalid subfamily Satyrinae. They found that the marginal parts of the wings bearing deflection marks (eye-spots) are relatively weak and, having an increased tendency to tear when grasped by a predator, are consistent with the deflection hypothesis. *Pierella hyalinus* is the only member of this genus found in Trinidad.

METHODS

Study species

The four species, *Caligo brasiliensis minor* Kaye, *C. illioneus saltus* Kaye (Fig.1a), *C. teucer insulanus* Stichel and *Eryphanis automedon* Cramer (Fig. 2) (Casagrande 2004), have wide distributions in tropical South and Central America. All occur in Trinidad and are common at Haven Hill Farm, Leotaud Trace near Talparo (10° 31' 30.06" N; 61° 16' 36.92" W) where most of the observations reported here were made.

The gecko *Thecadactylus rapicauda* (Houttuyn) (Fig. 1b), ranges from Mexico through Central and South America to southern Amazonas, and northward through the Lesser Antilles as far as Necker in the Virgin Islands (Peters and Donoso-Barros 1970; MacLean 1982; Bergmann and Russell 2007). *Th. rapicauda* is a nocturnal gecko with a maximum snout to vent length (SVL) of 121 mm and a tail length shorter than the SVL for both sexes (Murphy 1997). In the field the sexes are indistinguishable unless the female is visibly gravid. The colour is a mixture of grey and various shades of brown in a variable complex of blotches that can be altered to match the background, so that the lizard is normally well camouflaged. It is an ambush predator whose normal locomotion is slow and steady (Quesnel 2004) and feeds on a wide range of arthropods besides *Caligo*, including

Fig. 1. Computer superimposition c) of the mimetic pattern of *Caligo illioneus* a) on photographic profile of *Th. rapicauda* b). The level of mimicry is greatly enhanced by the secondary smaller 'eye-spot', representing the lizard's tympanum, in addition to the highlighted profile of the head and shoulder region. The representation in (Fig. 1b) is diminished because the gecko was photographed in bright light with direct flash rather than natural overhead lighting. For this reason the pupil of the eye is reduced to a slit and the 'concavity' of the tympanum lost.

other Lepidoptera (Vitt and Zani 1977; Quesnel 2008). It is common in Trinidad where it lives on the trunks of forest trees. Bergmann and Russell (2007) point out that it is the only nocturnal arboreal lizard over much of its range and that also it is far larger than any other continental geckonid.

Although principally nocturnal, it is sometimes active well into daylight hours, and its calls have been heard at all hours of the day and night (Quesnel 2008). After dark it is attracted to the vicinity of artificial lights, where it preys upon the attracted insects. It eats a wide range of arthropods as well as some small saurian vertebrates (Murphy 1997; Quesnel 2008).

Caligo and *Eryphanis* species are crepuscular in activity (Quesnel 2003) and, attracted by domestic lights, frequently enter buildings. Over a period of eight years, observations were made of 142 butterflies that entered Haven Hill Farm where a fluorescent kitchen light was left on. The butterflies settled on the oiled wood walls or ceiling where they could easily be caught or observed. A total of 105 individuals was caught and the amount of wing damage recorded (see below), before being released outside. Forty-four additional individuals were caught resting on other buildings or in the surrounding forest. The house at Haven Hill Farm is occupied by about twenty *Th. rapicauda* which have become habituated to human presence and tolerate close observation (0.5 m).

Classification of wing damage

Wing damage was classified as being due to a) *Th. rapicauda* attack; b) possibly *Th. rapicauda* attack; c) attack by some other predator; and d) non-predator hazards. The key evidence was the bite shape of *Th. rapicauda* as illustrated in Fig. 3a which corresponds closely to much of the observed range of damage to *Caligo* wings (Fig. 3b-l). The failure of the attack to produce a complete bite mark (Fig. 3d,e,h) could be due to either the rapid escape reaction of the butterfly or the fact that the front teeth of the *Th. rapicauda* are about half the size of the back teeth. In a small number of butterflies the curved outline of a mouth twice the size of that of *Th. rapicauda* implies the lizard *Tupinambis teguixin* (Linnaeus) whose adult size is SVL 333 mm.

Direct observations

During this study a total of seven direct attacks of *Th. rapicauda* on resting *Caligo* and *Eryphanis* butterflies was recorded. Detailed observations were made on two of these.

RESULTS

The hindwing underside pattern, including the eyespots, of the three species of *Caligo* occurring in Trinidad bears a striking resemblance to the head profile of the gecko *Th. rapicauda* (Fig. 1a-c). Although a saurian head profile is also apparent on *E. automedon* (Fig. 2), it is significantly different from that on these three *Caligo* species and does not share a close resemblance to *Th. rapicauda*.

Fig. 2. Underside patterns of *Eryphanis automedon.*

Accumulated records representing 209 specimens (Table 1) include six direct observations of attack on *Caligo* and *Eryphanis* by the gecko *Th. rapicauda* in which the butterfly was eaten and one in which it escaped. The rest include undamaged ones and specimens for which wing damage has been subjectively classified as to its cause according to the scheme given in Fig. 3 and Table 1.

Direct observations

Detailed notes of two observed attacks by *Th. rapicauda* were made in the lighted room described and five other attacks were witnessed in part. Six attacks resulted in the prey being eaten and in the other it escaped. In four of the six cases that resulted in ingestion, the butterfly was attacked from the front, three being seized by the base of the forewing and one by the head and thorax. The three remaining cases involved the butterflies being attacked from the rear and one of these escaped.

Ingestion may include the wings as well as the body of the prey, although discarded wings were noted for two of the specimens that had been eaten. Stalking is a protracted affair, with the geckos spending 40-75 minutes in close proximity (10-35 cm) to the prey. In the case where the butterfly escaped, the gecko orientated to the butterfly's eye-spot, wiping its own eyes and moving its head to assist in aligning itself prior to attack. The final strike was clearly at the mimetic eye-spot on the butterfly and resulted in a typical loss of wing fragment (Fig. 3b).

Table 1. Classification and frequency of wing damage in *Caligo* and *Eryphanis* spp. observed in this study.

Damage Category	Data for both *Caligo* spp. and *Eryphanis automedon.*	Data for *Caligo* spp. only.	Data for *Eryphanis automedon* only.	Categories 2 and 4 ascribed to category 3.	Category 4 ascribed to category 5.	Category 2 ascribed to category 1 and category 4 ascribed to category 5.	Categories 2 and 3 ascribed to category 1 and category 4 ascribed to category 5.	All damage ascribed to category 1.
Consistent with attack by *Th. rapicauda* (Figs. 1b, 1c, 1d, 1e).	71	66	5	71	71	86	98	119
Possibly due to *Th. rapicauda* attack (Fig 1f).	15	12	3	0	15	0	0	0
Possibly due to a predator other than *Th. rapicauda* (Figs. 1g, 1j, 1k).	12	11	1	48	12	12	0	0
Due to non-predator hazards (Fig. 1l).	21	21	0	0	0	0	0	0
Undamaged individuals.	90	83	7	90	111	111	111	90
Total	**209**	**193**	**16**	**209**	**209**	**209**	**209**	**209**
Proportion (%) attacked by *Th. rapicauda* and escaped.	34.0	34.2	31.3	34.0	34.0	41.1	46.9	56.9

Wing Damage

Wing damage for 193 *Caligo* and 16 *Eryphanis* individuals was recorded (Table 1). This identifies the gecko *Th. rapicauda* as an important predator of these butterflies in Trinidad, with 34% of wing damage attributed to this species. The data are summarised in Table 2 and show 60% of damage commensurate with attack by *Th. rapicauda*. Fourteen butterflies bore evidence of more than one attack (Fig. 3i, Fig. 3j) and in 12 butterflies, bite marks were consistent with attacks by juvenile *Tu. teguixin* (see discussion).

Table 2. Summary of wing damage recorded from 193 *Caligo* and 16 *Eryphanis* individuals.

	Caligo spp.	*Eryphanis automedon*
Undamaged individuals (%).	43	44
Damaged individuals (%).	57	56
Damage attributed to *Th. rapicauda* (%).	35	31
% of damaged individuals attributed to *Th. rapicauda.*	60	56
Damage attributed to *Tu. teguixin* (%).	6	6
Damage attributed to other causes, wear & tear (%).	11	0

DISCUSSION

What is the model for the pattern on the wing undersurface of *Caligo* species? Stradling's (1976) initial interpretation was that it represented a frog of the genus *Hyla*. In this study we present new evidence that in Trinidad, the eye-spots of *Caligo illioneus* closely resemble the head profile of one of its own predators, the gecko *Th. rapicauda* and propose that *C. illioneus* mimics *Th. rapicauda*. The relative sizes of eye-spot and ear-spot (tympanum) and their positioning strongly suggest this. We also present data showing that in the field, a great many butterflies of this genus bear marks indicating attacks to the rear margin of the wings by this gecko, thus supporting the deflection hypothesis.

In his review of eye-spot mimicry, Stevens (2005) rightly points out that it is unsatisfactory to consider the perception of these patterns from a human perspective but then proceeds to consider them from an essentially avian point of view. Here we have evidence that for *Caligo* at least, the principal target is a gecko.

Since *Th. rapicauda* in its feeding will strike at a simple eye-spot, one may ask what is the advantage to the butterfly of such a detailed imitation of a *Th. rapicauda* head. One possible explanation is that on the curved surface of a tree trunk, the gecko predator may first see a

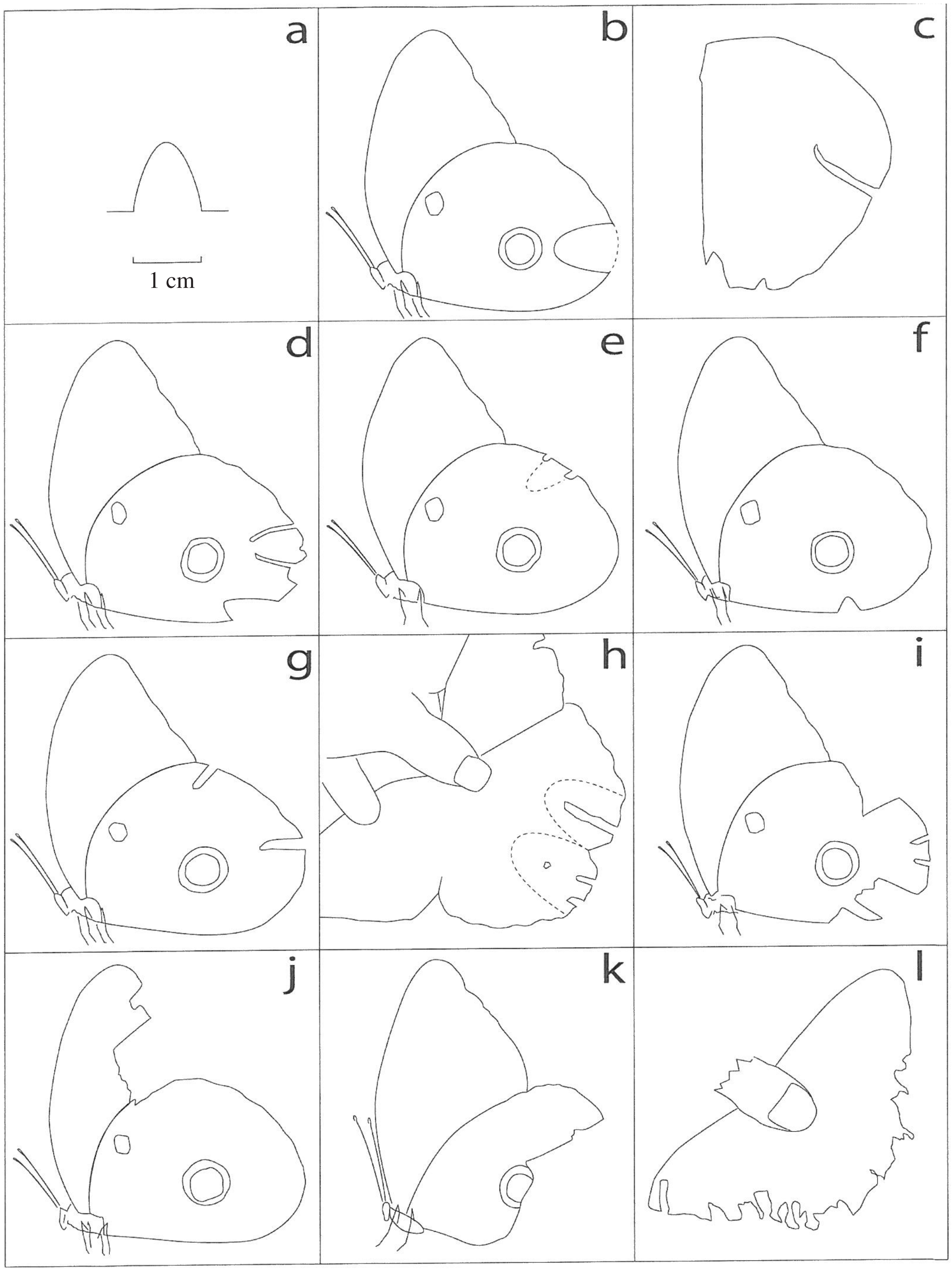

Fig. 3. Types of damage recorded from wings of *Caligo* spp. and *Eryphanis automedon* (mostly the former) with probable interpretations. **a)** Outline of 'bite' of *Th. rapicauda* produced by drawing around skull. **b)** Typical damage inflicted by *Th. rapicauda* - Category 1 (dotted line represents edge of wing if it were present). **c)** Cut in wing made by mandible and maxilla of one side of *Th. rapicauda* mouth - Category 1 (butterfly flew before complete closure of predator's mouth). **d)** Typical damage inflicted by *Th. rapicauda* - Category 1. Lower bite - wing fragment removed; Upper bite - butterfly flew before jaws fully closed. **e)** Two nicks in wing from back teeth of *Th. rapicauda* - Category 1. Butterfly flew before jaws fully closed. **f)** Small area of wing removed - Category 2. Damage caused by tip of predator's mouth closing on wings as prey flew away. Probably inflicted by *Th. rapicauda,* but possibly a bird. **g)** Damage inflicted by a predator other than *Th. rapicauda* - Category 3. **h)** Typical damage inflicted by both *Th. rapicauda* and a larger predator (probably *Tu. teguixin*) - Category 1. **i)** Evidence of 3 attacks - Category 1. 1) *Tu. teguixin* with wing-tearing before complete closure of mouth; 2) *Th. rapicauda* damage as in e); 3) Possible attack by *Th. rapicauda* with wing-tearing. **j)** Damage inflicted by *Tu. teguixin* - Category 3. **k)** Damage inflicted by *Tu. teguixin* - Category 3. **l)** General wear and tear from non-predator hazards - Category 4. This type of damage could obscure that caused by *Th. rapicauda* as in e) and f).

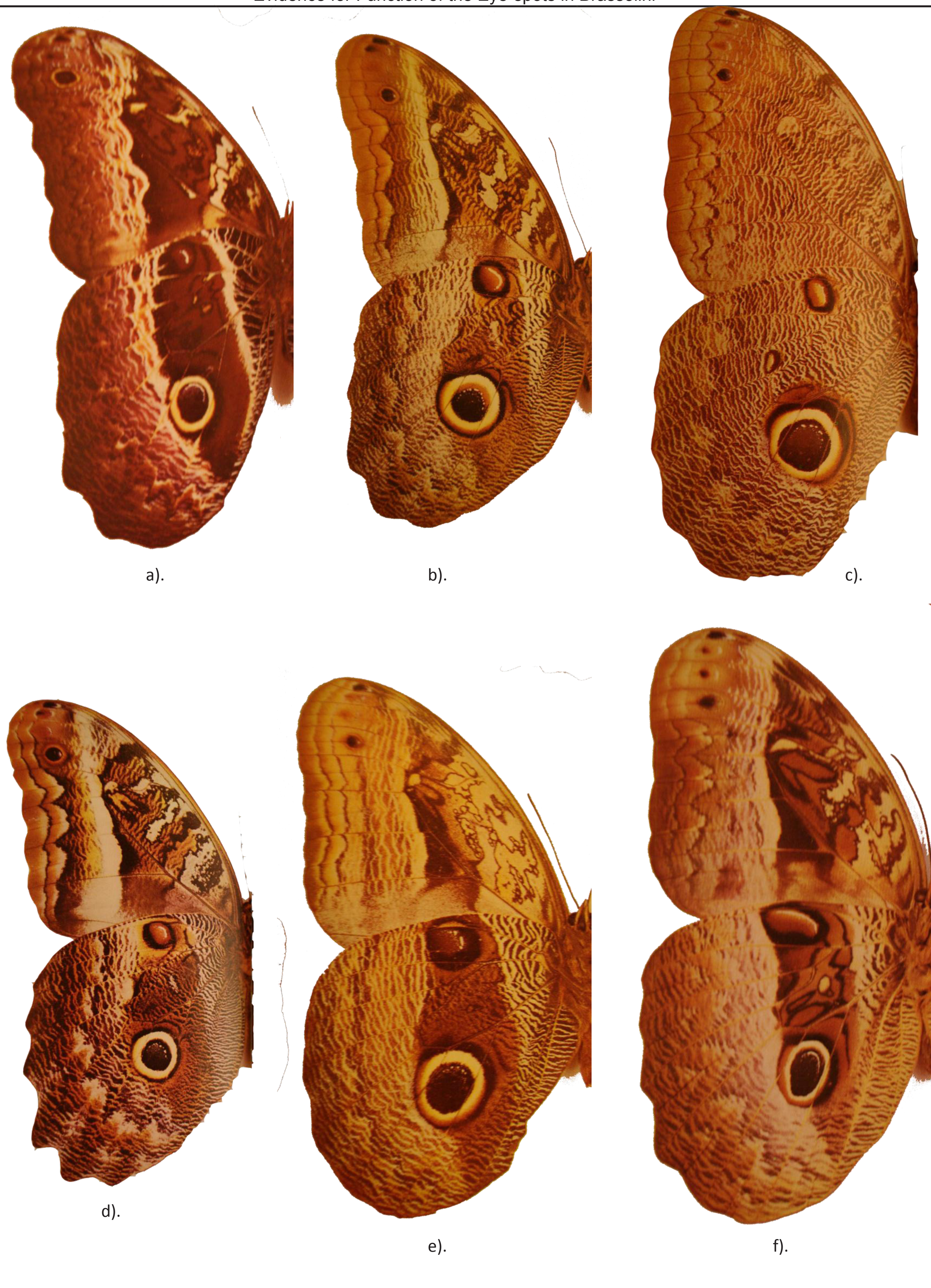

Fig. 4. Underside patterns of various *Caligo* species. **a)** *Caligo oberthurii* Deyrolle ssp. *phokilides* Fruhstorfer (Peru). **b)** *Caligo idomeneus* (Linnaeus) ssp. *idomenides* Fruhstorfer (Peru). **c)** *Caligo eurilochus* (Cramer) ssp. *livius* Staudinger (Peru). **d)** *Caligo superbus* Staudinger ssp. *agamemnon* Weymar (Ecuador). **e)** *Caligo placidianus* Staudinger (Peru). **f)** *Caligo beltrao* Illiger (Brazil).

resting butterfly from close quarters and react to the mimetic pattern as it would to a rival or mate with a prefatory display rather than be intimidated as it might to a predator of itself (Stevens 2005). In this case the butterfly may have time to escape. The Fig. 1a in Stevens (2005) is that of a cabinet mounted specimen in which the pattern surrounding the eye-spot is omitted and therefore fails to present the full extent of the pattern.

Alternatively, the gecko may by stealth, approach close enough to remain undetected. Escape for the butterfly then depends entirely on misorientation to the mimetic eye, (deflection hypothesis), the attack having been mounted at the mimetic, rather than the real head of the butterfly. Other genera of brassolini such as *Opisphanes* also bear eye-spots but without the associated pattern that suggests a reptilian head profile. This is also true of some *Caligo* species, e.g. *C. eurilochus livius* Staudinger (Fig. 4c). The evolutionary addition of patterns representing a tympanum and demarking the head profile of a gecko reinforce the misorientatory effect by indicating that the snout of the mimetic gecko head is at the anal angle of the butterfly's hindwing. Furthermore, the representation of the tympanum includes a white crescentic area implying a three dimensional concavity, although the details of its orientation in relation to ambient light in natural conditions is not clear and calls for further investigation. We suggest that such a stepwise elaboration would change the perception of the mimetic pattern by a stealthy predator from a potential prey item to another individual of its own species. This in turn might result in an intraspecific interaction rather than a predatory one. Such behaviour would be broadly divided into competitive/territorial between individuals of the same sex, and courtship/mating between individuals of the opposite sex. *Thecadactylus rapicauda* individuals have been observed head to head with jaws locked together rolling over and over on the floor (VQ, pers. obs.). Presumably the combatants were both male and this aggressive behaviour resulted in a bite targeted at the head. Preliminary courtship behaviour by male *Th. rapicauda* consists of a bite to the female's neck (Quesnel 2006). Whichever sex the mimic presents, the response is likely to be a bite to the perceived head region. Groups of two or three *Th. rapicauda* consisting of females, or females with one male, may often be found in a daytime retreat. This implies that intraspecific interactions between males are frequent. Thus the more elaborate mimic of the predator itself, reinforces the misdirected attack whether the butterfly is perceived as prey, rival or mate. This is in broad agreement with the suggestion by Stradling (1976) that these butterflies benefit through an intrusion into the behavioural interactions between arboreal lizards.

Direct observations confirm the identity of the geckonid lizard *Th. rapicauda* as a predator of adult *Caligo* and *Eryphanis* butterflies. During attack, the prey is stalked slowly, allowing plenty of time for the predator's attention to be diverted by the eye-spot. This is supported by the data presented here which show survival of 34% of butterflies with wing damage commensurate with attack by geckonid lizards (Table 1). With all undamaged individuals included, escape from capture through misdirected attack amounts to a minimum of 41%. Of the five butterflies exhibiting evidence of attack by the larger *Tu. teguixin* predator, three bore damage to the forewings. This implies that the predator was not diverted by the eye-spot.

If the patterns of these three Trinidad *Caligo* spp. are the result of natural selection to mimic their principal predator *Th. rapicauda,* why is the *Eryphanis automedon* eye-spot pattern so different and what is the model? Stradling (1976) suggested *Anolis chrysolepis* (Troschel) as the model but this is unlikely due to its small size and shape. For *E. automedon* then, a hypothetical lizard is the more important predator in some other part of its range. Trinidad, an island of 4828 km^2, represents a small proportion of the range of these Neotropical genera which contain 21 species of *Caligo* and five species of *Eryphanis* (D'Abrera 1987; Casagrande 2004) and a corresponding 116 Neotropical species of *Anolis* (Peters and Donoso-Barros 1970). By contrast, the three species of *Caligo* in Trinidad all seem to have the same model, *Th. rapicauda,* for the lizard pattern. Furthermore, Bergmann and Russell (2007) consider that there are only two species of *Thecadactylus* throughout its enormous Neotropical range albeit with extensive local variability of *Th. rapicauda*.

At least five other species have lizard-like patterns on their hindwings (Fig. 4) which may represent local variants of the model, while species such as *C. eurilochus livius* (Fig. 4c) cited above, lack a saurian head profile surrounding the eye-spot altogether and may represent an ancestral form.

If the mimicking of lizard predators has driven speciation in these butterflies, how important is the precision with which the model is mimicked? The five species figured (Fig. 4a-e) show considerable variation in the detail of the patterns surrounding the eye-spot. Do they represent different models? The experimental exposure to gecko attack of butterflies from which the mimetic pattern has been wholly or partly erased could well throw light on this. None the less, the striking implication of the present data to the power of natural selection calls for experimental corroboration. Does attack by *Th. rapicauda* demand a more elaborate mimetic pattern than that found on *C. eurilochus livius*? If these butterflies are mimicking several different saurian models, the implication is that the natural selection is finely tuned. The complex network of interactions between these butterflies and their predator models undoubtedly merits more investigation.

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