

Malagasy birds as hosts for eye-frequenting moths

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While tear-feeding in moths on mammals is widespread, there have been no reports of this behaviour in Madagascar and none on birds. We report that a moth, *Hemiceratoides hieroglyphica* belonging to the Calpini, a generally fruit-feeding or blood-feeding lineage of noctuids, attacks sleeping birds in Madagascar. This moth is able to intrude its sharply tipped proboscis into a closed bird's eye. The proboscis is characterized by a specific armoury of hooks, barbs and spines similar to that in piercing calpines but dissimilar to that in other tear-feeding moths. This is the first report of exploitation of tears by Lepidoptera from the closed eyes of sleeping birds.

Keywords: ophthalmotropism; Madagascar; mouthparts

1. INTRODUCTION

The unique nature of biotic interactions in Madagascar has long attracted the focus of researchers. Specific interactions between vertebrates and invertebrates exhibit peculiarities absent from neighbouring mainlands, and vice versa. As an example, one of us (W.B.) has long been intrigued as to whether attraction to vertebrate eyes (ophthalmotropism) might occur among the lepidopteran fauna of Madagascar, given the prevalence of this phenomenon in Africa, Asia and South America. Indeed, Lepidoptera in several families are now known to be attracted to tears of a range of mammals and reptiles (Büttiker 1964, 1997b; Bänziger 1987, 1992), but there have never been any observations of this behaviour in Madagascar.

The evolution of an attraction to vertebrate tears is perhaps not so unusual, considering that many species of adult Lepidoptera feed on moist ground, perspiration, excrement or animal carcasses to suck water and dissolved nutrients (Arms *et al.* 1974; Adler & Pearson 1982). In general, this 'puddling' behaviour is thought to be a strategy to replenish mineral stocks in terms of maximizing reproductive success (Boggs & Gilbert 1979; Adler 1982; Beck *et al.* 1999).

However, during 48 years of research on this topic, not one case of tear-feeding on birds as hosts has ever been reported (although lachrymophagy on crocodiles is known; Turner *et al.* 1986). Here, we report this specialized interaction for the first time and interpret its significance in the context of proboscis morphology and knowledge of this behaviour pattern worldwide.

2. MATERIAL AND METHODS

R.H. and M.R. made the observations in the Kirindy forest in western Madagascar. This is a dry deciduous forest, 60 km north-east of Morondava (44°39' E, 20°03' S; figure 1a). The observations were made in two forest blocks known as N5 and CN5 in the 12 500 ha concession of the Centre de Formation Professionnelle Forestière de Morondava. Observations reported here coincide with mid-rainy season (Sorg & Rohner 1996).

For SEM preparation (done by H.W.K.), a cut-off and dried proboscis of *Hemiceratoides hieroglyphica* (Saalmüller 1891) (Noctuidae) was soaked in 30% ethanol for 24 h before ultrasound cleaning. The specimen was dehydrated in ethanol and submerged in hexamethyldisilazane before air-drying. The proboscis was mounted, sputter-coated with gold and viewed with a Phillips XL 20 SEM.

3. RESULTS

On 15th February 2004 at 23.00, a single Common Newtonia bird (*Newtonia brunneicauda*) (Newton 1863), Vangidae, was located with the calpine noctuid moth *H. hieroglyphica* (Saalmüller 1891) on its neck. The bird was sleeping in a bush while the moth, sex unknown, had its proboscis tip in the eye of the bird (figure 1b). The later captured (male) moth measured 26 mm long and 47 mm in wingspan, with a proboscis 10.5 mm long. The distal half of the proboscis was intruded beneath the lid of the closed eye (figure 1d). Flashlights briefly disturbed the Common Newtonia, which rotated its head so that the moth's proboscis lost contact with the bird's eye. However, the moth stayed on the neck of the bird. After some seconds, the moth searched actively with its proboscis, inserting it beneath the closed eyelid. The moth stayed for at least 35 min in this position, apparently drinking tears.

On 21st February 2004 at 00.30, we located another *H. hieroglyphica* on a sleeping male Madagascar Magpie Robin (*Copsychus albospectularis*) (Eydox & Gervais 1836), Muscicapidae. This moth stayed for over 30 min on the neck, its proboscis in continuous contact with the eye from which it was apparently also drinking fluid (figure 1c). Although the moth raised its wings in response to the flash, the bird remained surprisingly quite still.

On 13th December 2005 at 19.00, Mario Ramohavelo Heriniaina observed another *H. hieroglyphica* on the head of a sleeping Common Newtonia, with its proboscis also inserted beneath the bird's closed eye. The moth stayed for 5 min in this position until the bird was disturbed and the moth was caught as it flew away.

Morphological investigation of this captured male (we examined no females) reveals that the distal third of the proboscis of *H. hieroglyphica* is armoured with various cuticular spines and bristles. The apical region is sharply tipped and has large, darkly sclerotized, broad-based hooks that give the proboscis tip the appearance of an ancient harpoon (figure 2a). The long projecting structures are homologous to two

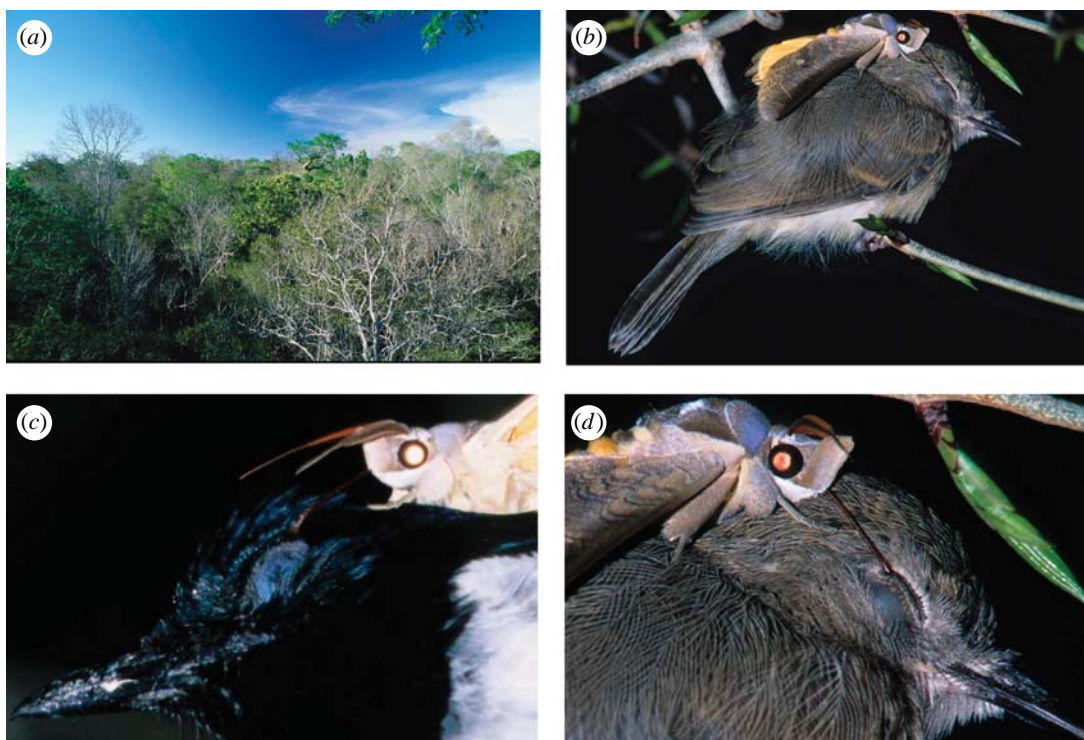


Figure 1. (a) Canopy view of the western deciduous forest to which the noctuid moth *Hemiceratooides hieroglyphica* is endemic (Kirindy). (b) Common Newtonia (*Newtonia brunneicauda*) with *H. hieroglyphica* on its neck. (c) Head of Magpie Robin (*Copsychus albospectularis*) facing to the left with *H. hieroglyphica* on its neck. The proboscis of this moth is visible directly below its left antenna and oblong left labial palp, intruded beneath the closed lid of the eye. (d) Detail of (b): the proboscis of the moth is intruded beneath the closed lid of the eye of *N. brunneicauda*.

types of proboscis sensilla and to the cuticular structures linking the halves of the proboscis (i.e. galeae). The apex of the proboscis is unlinked, giving the proboscis a bifid appearance. The modified sensilla styloconica are arranged in one row on the dorsal side of each galea. They are 100–300 μm long, composed of a flat stylus and a blade-shaped projection lateral to the short sensory cone (figure 2b). The sensilla trichodea are thick bristles, slightly curved and about 300 μm long. They project to each side of the proboscis, but are restricted to an area close to the harpoon-shaped tip (figure 2b). The linking structures consist of multi-pointed spines projecting in a proximal direction. These are rather short near the apex and develop into a row consisting of approximately 200 μm long spines on the distal third of the proboscis.

4. DISCUSSION

Moths feeding on tears from bird eyes have not previously been reported. Thus, these observations from Madagascar appear highly significant. For most ophthalmotropic moth species, tears form the largest part of their diet and they are not specialized to a single host species (Büttiker 1964, 1967; Bänziger 1972, 1987, 1992). The Malagasy noctuid species fed on the secretions of the eyes of two widespread bird species, *N. brunneicauda* and *C. albospectularis*, indicating a lack of restriction to a single bird species or family as an ectoparasite. However, the bird's size might have an influence on the host selection, since tear-drinking would be difficult with larger birds where the proboscis might be too short to reach the

eye while still sitting on the neck. The extended proboscis is about half the moth's body length, extended (figure 1d) with a similar morphology to that of the related blood-sucking noctuids in the genus *Calyptra*. Their proboscis, including that of the Malagasy *Calyptra triobliqua* (Saalmüller 1980), is characterized by apical tearing hooks, erectile barbs and rasping spines (Bänziger 1970; Büttiker *et al.* 1996; data for *C. triobliqua*, unpublished). All these structures play a potentially crucial role in the piercing mechanism in *Calyptra* (Bänziger 1970). Exactly the same features occur on the proboscis of *H. hieroglyphica*. The proboscis apex is armoured with hooks and the proboscis sensilla correspond with the erectile barbs in composition and arrangement. Similar multi-pointed spines exist on the dorsal side of the proboscis (figure 2a,b). Such structures can be homologized with common features of the ground plan of the proboscis of higher Lepidoptera (Krenn & Kristensen 2000). They represent derived character states shared by *Calyptra* and *H. hieroglyphica* and are potentially synapomorphic, hence a molecular systematic analysis is desirable. This morphology is also distinct from the proboscis of other eye-frequenting Noctuidae. These have a soft and flexible tip region that is characterized by few sensilla forming the apical end and strongly elongated, dentate plates of the dorsal proboscis linkage, curved in a distal direction.

While the bird's eye was closed and the moth continued feeding, the host never showed signs of being disturbed. This is rare in eye-frequenting moths since only the noctuid *Lobocraspis griseifusa*

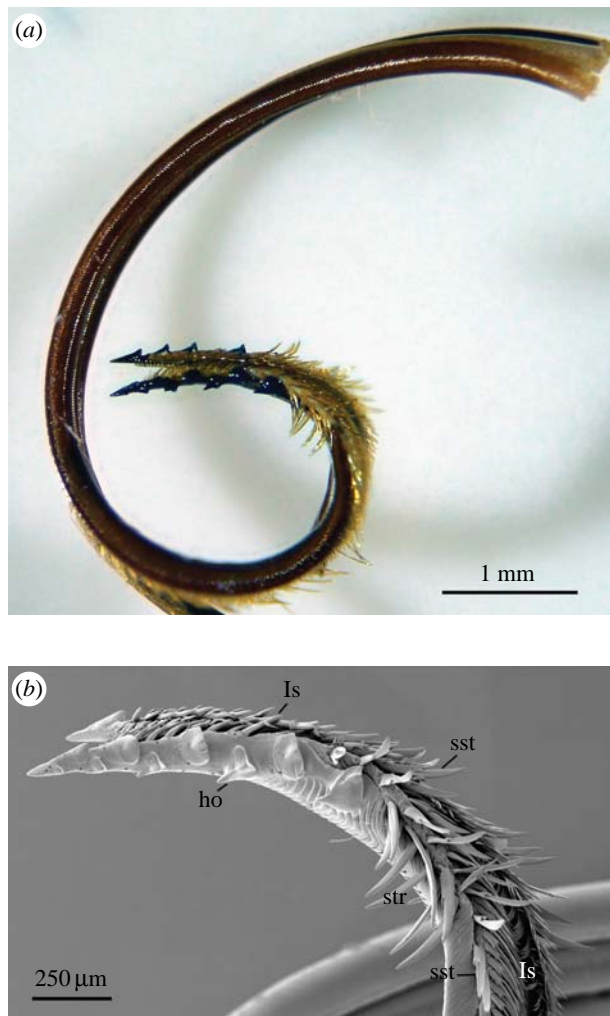


Figure 2. (a) Proboscis of the eye-frequenting moth *Hemiceratooides hieroglyphica*. The distal third of the proboscis bears hooks, numerous barbs, bristles and spines. (b) The armoured tip of the proboscis of *H. hieroglyphica*. The apex bears big cuticular hooks (ho), modified sensilla (sst, str) and proboscis linking spines (ls), structures that may anchor the proboscis in the bird's eye.

Hampson 1895 in Southeast Asia is known to continue to feed when its host sleeps with its eyes closed (Bänziger 1990). However, in contrast to mammals, birds have an upper and lower lid and a nictitating membrane to protect their eyes. To insert the proboscis into the bird's eye it needs, therefore, a more sophisticated technique, probably relying on the pointed apex of *Hemiceratooides* as in the piercing mechanism of *Calyptra*.

After the pointed proboscis tip of *H. hieroglyphica* enters the bird's closed eye, the projecting sensilla and barbs presumably anchor the proboscis. The proboscis morphology of *H. hieroglyphica* is consistent with an evolution of ophthalmotropy from fruit-piercing in the Calpini lineage (Kitching & Rawlins 1998) and appears still suited to pierce fruits. Bänziger (1988) suggested that tear-drinking moths seek salt and/or moisture during hot dry weather. Additionally, tears also contain proteins like albumin and globulin that could represent a high-quality resource throughout the year. Local scarcity of environmental sodium (Na^+) in the soil may lead moths to use other resources (Beck *et al.* 1999).

We observed tear-drinking during the rainy season when vegetation is usually wet at night, so we would suggest that moisture deficit was not the primary reason for lachryphagy. Scarcity of salt and the need for salt and/or proteins would better explain our observed case, although observations on the male limitation typical of such behaviour are yet lacking.

Minimization of predation risk could be an additional explanation of why moths seek tear-feeding instead of simply visiting puddles or saltlicks as is common in other species. Predation could be high on mud puddles at night, where frogs are particularly abundant. Thus, sitting on a sleeping bird's neck could be a relatively safe place to replenish mineral stocks. An interesting question now emerges as to why moths evolved tear-drinking on Malagasy birds but not, to our knowledge, on mammals. While similar observations of sleeping mammals in Madagascar are also needed, the current mammalian fauna of Madagascar differs strikingly from the fauna of Asia, America and Africa. Typically, the primary hosts of ophthalmotropic moths are large mammals (Cetartiodactyla; Perissodactyla), mainly nocturnal, and considered relatively placid and tolerant to attacks by insects. Bänziger (1990) assumed such host placidity as essential for typical fluttering behaviour around the eyes to lead to successful tear-feeding. In Madagascar (ignoring anthropic introductions), such animals are absent and the largest extant mammals are strepsirrhine primates and herpestid carnivores. Such groups are not known elsewhere to offer lachrymal resources to moths, even though most local members of these groups are nocturnal (Goodman & Benstead 2003). By contrast, the cetartiodactyl lineage have generally large exposed eyes, often open at night, and these mammals lack behavioural methods to dislodge such unwanted visitors except by occasional shaking of the head. Lemurs would be able to fend off the approaching moths with their hands. However, chemical composition of tears may also be an important factor that leads to preferences for certain host species (Bänziger 1990). For example, analysis of moth gut contents has shown the midgut digestion of leucocytes (Büttiker 1997a). Furthermore, it would be interesting to know whether the moths are able to introduce compounds such as antihistamines or narcotics to reduce irritation while feeding or to keep a bird asleep over a relatively long period of time. In both cases, saliva that had been delivered from the proboscis tip prior to feeding could convey such substances. Another question is the possible transmission of eye diseases of birds similar to the conditions observed by Büttiker & Nicolet (1975) and in African cattle by Gous *et al.* (1995).

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