

Natural History Note

Egg-Laying Butterflies Distinguish Predaceous Ants by Sight

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ABSTRACT: Information about predation risks is critical for herbivorous insects, and natural selection favors their ability to detect predators before oviposition and to select enemy-free foliage when offspring mortality risk is high. Food plants are selected by ovipositing butterflies, and offspring survival frequently varies among plants because of variation in the presence of predators. *Eunica bechina* butterflies oviposit on *Caryocar brasiliense*, an ant-defended plant. Experiments with dried *Camponotus* and *Cephalotes* ants pinned to leaves revealed that butterflies use ant size and form as visual cues to avoid ovipositing on plant parts occupied by ants more likely to kill larval offspring. Presence of sap-sucking bugs did not affect butterfly oviposition. This is the first demonstration that visual recognition of predators can mediate egg-laying decisions by an insect herbivore and that an insect will discriminate among different species of potential predators. This unusual behavioral capability permits specialization on a risky, ant-defended food plant.

Keywords: ant-butterfly interaction, ant-plant mutualism, enemy-free space, oviposition behavior, predator identification, trait-mediated indirect interaction.

Introduction

Foliage represents a major zone of biological interaction in terrestrial ecosystems, and herbivores have to cope with the regular threat of predation (Price et al. 1980). In systems involving multiple predators, different predator species pose different risks to their prey and thus should elicit qualitatively different responses to risk by the latter (Sih et al. 1998). While large herbivores such as gazelles and zebras can distinguish by sight among lions, cheetahs, and hyenas in the African savanna and react differently to each (Schaller 1972, pp. 387–388), it is uncertain whether an insect herbivore would visually discriminate among potential predators. Vision, however, can play an important role as insects search for food plants. For instance, ovipositing female butterflies are known to use visual cues

(leaf shape) to discover host plants conferring greater larval survival (Rausher 1978).

Insect herbivores live in a constant warfare: as they struggle to feed on profitable plant tissue for rapid growth, they have to avoid being consumed by members of the higher trophic level (Price et al. 1980). Ants are probably the major predators of insect herbivores in tropical habitats (Jeanne 1979; Floren et al. 2002), where they are extraordinarily abundant on foliage (Tobin 1995). Ant foraging on plants is promoted by the high occurrence of predictable liquid food sources such as extrafloral nectar and insect honeydew (Rico-Gray and Oliveira 2007). Stable isotope analyses of tropical arboreal ants have shown that dominant liquid-feeding species obtain their nitrogen low in the trophic chain by preying on herbivores (Davidson et al. 2003). Thus, if herbivores avoid foliage rich in predaceous ants, herbivore damage to ant-visited plants may be reduced (Abrams 1995). Because such an indirect effect of predators on plants results from a behavioral trait of herbivores, the relationship is known as a trait-mediated indirect interaction (Werner and Peacor 2003; Schmitz et al. 2004).

Information about predation risks is critical for ovipositing females of insect herbivores, and natural selection may favor the ability to detect predators and to select enemy-free foliage when offspring mortality risk is high (Schmitz et al. 2004). Although predator avoidance and selection of enemy-free space by insect herbivores are key aspects underlying theory on insect-plant interactions (Price et al. 1980), the behavioral mechanisms accounting for risk detection and risk response in egg laying remain unclear. Risk effects on prey behavior can be experimentally evaluated using cues that signal predation risk, such as presenting artificial models of the predator to visually oriented prey (Freitas and Oliveira 1996; Gonçalves-Souza et al. 2008).

Intense ant visitation to plants with extrafloral nectaries reduces enemy-free space for butterflies because of heavy predation on caterpillars by foraging ants (Price et al. 1980; Thompson and Pellmyr 1991). Plants with extrafloral nectaries are abundant in the Brazilian “cerrado” savanna,

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where ant-plant-herbivore interactions are especially pervasive as a result of continuous ant attendance to these liquid food sources (Oliveira and Freitas 2004). Ant-exclusion experiments with *Caryocar brasiliense* (Caryocaraceae), a cerrado plant well endowed with extrafloral nectaries, demonstrated that visiting ants significantly reduce infestation by four species of insect herbivores, which translates into higher numbers of flowers and initial fruits by ant-visited compared with ant-excluded plants (Oliveira 1997). The butterfly *Eunica bechina* (Nymphalidae) oviposits exclusively on *C. brasiliense*, and ant-visited plants are less infested by eggs and larvae than ant-excluded ones; visiting ants ignore the butterfly's eggs but often kill the caterpillars (Freitas and Oliveira 1996; Oliveira 1997). In prior work we demonstrated that the presence of rubber ant models on *C. brasiliense* foliage significantly decreased oviposition by *E. bechina* compared with control leaves with rubber circles (Freitas and Oliveira 1996). However, because we did not vary the morphology of the artificial insect models exposed on foliage (see Oliveira et al. 2002), it remained unclear whether an avoidance response by *E. bechina* could also be produced by the presence of variable types of ants, or even by insects other than ants (e.g., herbivores) commonly found on the host plant.

Here, we used paired experiments with dried ant specimens pinned to leaves to show that *E. bechina* females use ant size and form as visual recognition cues to avoid laying eggs on plant locations occupied by aggressive ants more likely to kill larval offspring. Presence of sap-sucking bugs had no effect on oviposition decisions by the butterflies. This shows that visual identification of a predator can mediate egg-laying decisions by an insect herbivore, which will also discriminate among different species of potential predators.

Methods

Fieldwork was undertaken in a reserve of cerrado savanna near Itirapina, southeast Brazil (22°15'S, 47°49'W). The vegetation corresponds to the cerrado sensu stricto physiognomy, formed by a dense scrub of shrubs and trees inside a herbaceous matrix (Oliveira-Filho and Rater 2002). The study was carried out during the rainy season (September–December 2005 and 2006), when adult butterflies are abundant (~500/ha) and infestation by *Eunica bechina* on *Caryocar brasiliense* plants is highest (Freitas and Oliveira 1992).

Ant Censuses and Ant-Caterpillar Interactions

To estimate the relative probability of natural encounters between egg-laying butterflies and different ant species on host plants, we carried out a census of the ants visiting

extrafloral nectaries on young leaves and buds of *C. brasiliense* at the beginning of the rainy season. Ant species were sampled on 1.0-m-tall plants ($n = 100$) during peak hours of *E. bechina* egg-laying activity (1000–1400 hours; Freitas and Oliveira 1992). Ant aggressiveness toward *E. bechina* caterpillars in nature was assessed during trials involving the three most frequent ant species found on food plants in the daytime: *Camponotus crassus*, *Camponotus rufipes* (Formicinae), and *Cephalotes pusillus* (Myrmicinae; fig. 1A). Trials consisted of placing one live caterpillar (third instar) on a young leaf of an ant-visited plant. Ant attacks to caterpillars were recorded for 5 min after they encountered each other. Ant-caterpillar trials were performed during sunny days (1000–1400 hours) on different plant individuals visited by each ant species. Thirty trials were performed per ant species; tested insects were removed from plants after trials.

Oviposition Experiments

We used differences in shape and/or size between workers of *C. crassus*, *C. rufipes*, and *C. pusillus* to test visual discrimination by egg-laying *E. bechina* butterflies (fig. 2). Sap-sucking *Edessa rufomarginata* stinkbugs (Hemiptera: Pentatomidae) frequently seen on host plants (Oliveira 1997) were used as controls (fig. 2). Discrimination between insects was assessed in the field using paired branches of *C. brasiliense* (see below), between which free-flying *E. bechina* butterflies could choose to lay eggs in a 24-h period. Selected branches within plants had similar heights (~0.3–0.5 m) and numbers of young leaves (~4–6) and no signs of herbivory. All other branches were clipped off so as to induce prospective ovipositing butterflies to choose between selected branches during oviposition experiments. Only young leaves were left on experimental branches because these were preferred by *E. bechina* females as oviposition sites (fig. 3A) and by caterpillars as food (Freitas and Oliveira 1992, 1996). Eggs and larvae already present were removed from plants before trials to avoid potential effects on future ovipositions (Thompson and Pellmyr 1991; Renwick and Chew 1994). Ant access to plants was prevented by applying a sticky resin (Tanglefoot) at the trunk base and by pruning aerial plant bridges.

Insect occupation on plants was simulated by pinning dried insects (ants or sap-sucking bugs) to young leaves (fig. 2). Branches in a pair were randomly assigned as treatment (insects present) or control (no insects), or as treatment 1 and 2 (each with a different ant species). Two insects were pinned to treated branches, matching the density per plant of the three most frequent ant species, *C. crassus*, *C. rufipes*, and *C. pusillus* (fig. 1A). Pins had no effect on oviposition: females oviposited randomly on

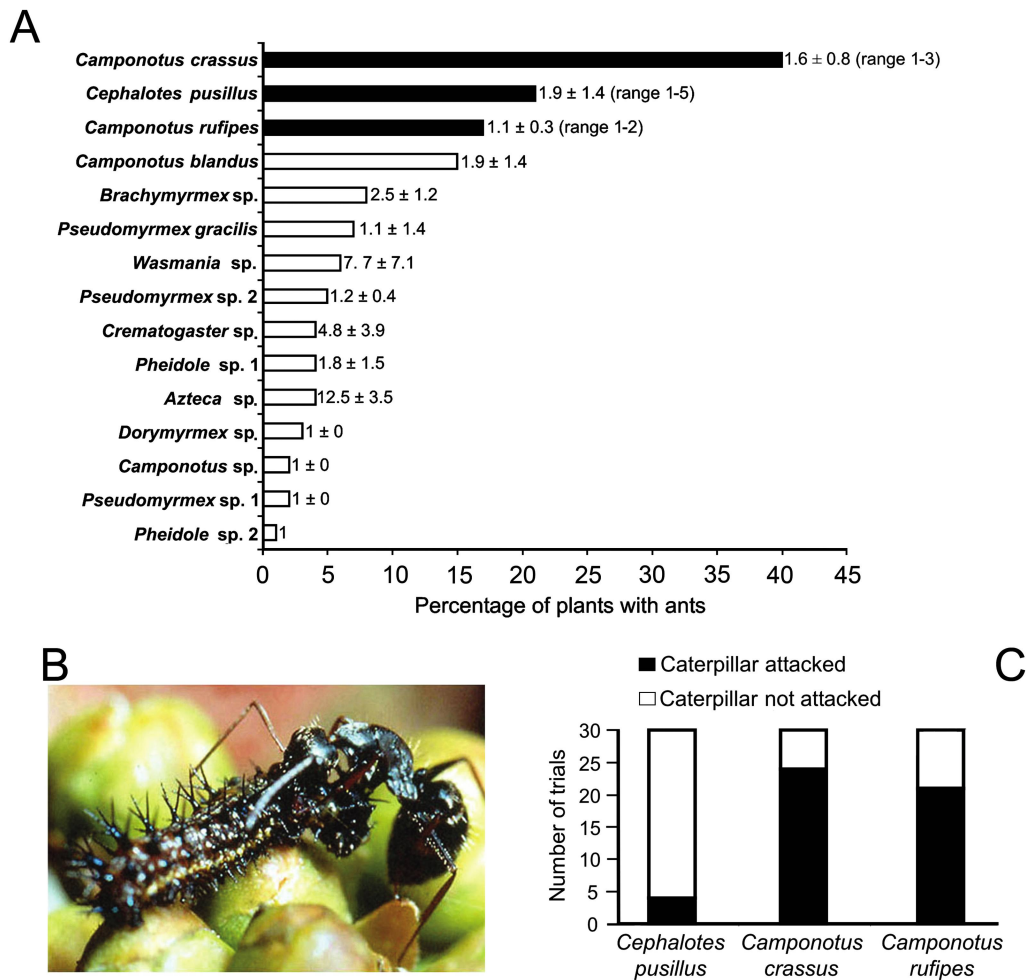


Figure 1: A, Frequency of ant species visiting the extrafloral nectaries of *Caryocar brasiliense* in a Brazilian cerrado savanna ($n = 100$ plants). Values next to bars indicate mean number of ants per occupied plant (\pm SD); range is given for the three most frequent species (black bars). B, *Camponotus* worker attacking *Eumica bechina* caterpillar on the host plant, *C. brasiliense*. C, Ant-caterpillar interaction trials on ant-visited plants ($n = 30$ trials per ant species); aggressiveness toward *E. bechina* caterpillars differed significantly among the ant species tested (G -test: $G = 33.82$, $df = 2$, $P < .001$).

paired branches with or without pins (G -test, $df = 1$, $P = .87$, $n = 36$ pairs). Paired branches were established at 1500 hours, and *E. bechina* ovipositions were checked after 24 h. Only plants receiving at least one egg on either branch were considered for the analyses. Experiments were replicated on different days until we reached at least 32 valid pairs for any given discrimination assessment. Results for all oviposition experiments are expressed as the number of experimental branches with and without eggs in 24-h trials, irrespective of the number of eggs laid on a given branch. Indeed, mean number of eggs per infested branch (mean \pm SD = 1.38 ± 0.64 , $n = 291$) did not differ between paired branches in any of the oviposition experiments performed (Mann-Whitney U -tests, $df = 1$, $P > .42$).

Large numbers of plants (52–283) were used in each of the 24-h oviposition trials to reach sufficiency of valid branch pairs (see above), and oviposition decisions by *E. bechina* were assumed to be independent (i.e., made by different females). Indeed, adult longevity in *E. bechina* is about 1 week, and the series of oviposition experiments were performed over 4 months in the rainy season. About 500 free-flying butterflies occur in the 1-ha study plot, and over 20,000 butterflies are estimated to occur in the 50-ha cerrado reserve.

Results

Fifteen ant species in nine genera were recorded visiting the extrafloral nectaries of *Caryocar brasiliense*, with at least

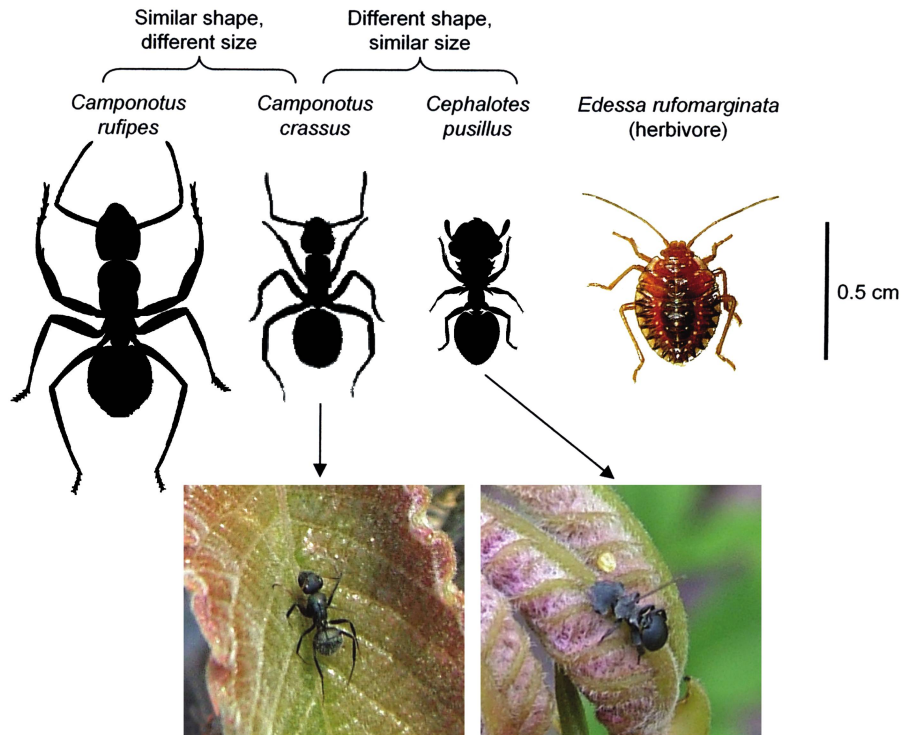


Figure 2: Ant and stinkbug species pinned to leaves to simulate occupation of host plants (*Caryocar brasiliense*) in experiments evaluating visual discrimination by egg-laying *Eunica bechina* butterflies. *Camponotus rufipes* and *Camponotus crassus* workers have long legs and antennae and a slender and evenly convex body, whereas *Cephalotes pusillus* ants are characterized by short legs and antennae and a strongly flattened and broad body and head. Note yellow egg of *E. bechina* near pinned *C. pusillus* worker.

one ant seen on 84% of the plants monitored (fig. 1A). *Camponotus crassus*, *Camponotus rufipes*, and *Cephalotes pusillus* were the most frequently recorded ants, with 67% of the plants having at least one of these species on their leaves. Average ant density on plants did not differ significantly among these three species and ranged from one to two individuals per plant (fig. 1A; Kruskal-Wallis test: $H = 4.762$, $df = 2$, $P = .093$, $n = 45$ plants).

Camponotus crassus, *C. rufipes*, and *C. pusillus* differed significantly in their aggressiveness toward larvae of *Eunica bechina* during trials performed on the host plant. The two common *Camponotus* species rapidly and fiercely attacked the larvae, occasionally killing them and carrying them to their nearby nests in over 70% of the tests (fig. 1B, 1C). On the other hand, the mostly timid workers of *C. pusillus* generally ignored the larvae after encountering them on leaves; attacks occurred on only 13% of the trials, and no caterpillar was killed (fig. 1C).

Eunica bechina females normally flutter around plants for 5–10 s before oviposition, which lasts 1–3 s. Presence of sap-sucking bugs or innocuous *C. pusillus* ants had no effect on egg laying by *E. bechina* compared with insect-free branches (fig. 3B, 3C). However, presence of either

predaceous *Camponotus* species significantly reduced oviposition compared with controls (fig. 3D, 3E). In paired trials using two ant species, egg laying was random between branches occupied by ants differing only in size (*C. rufipes* vs. *C. crassus*) or only in shape (*C. crassus* vs. *C. pusillus*; fig. 3F, 3G). However, given a choice between branches occupied by ants differing in both shape and size, *E. bechina* females significantly avoided ovipositing near aggressive *C. rufipes* compared with innocuous *C. pusillus* ants (fig. 3H).

Discussion

By concentrating on only one species of host plant, phytophagous insects may find the host more efficiently and thus process more information about it, including variation in the quality of individual plants or in the occurrence of natural enemies (Bernays 2001). Indeed, information about predation risks on food plants can be critical for specialist herbivores (Thompson and Pellmyr 1991; Renwick and Chew 1994). Here we show that brief inspection flights around host plants enable monophagous *Eunica bechina* butterflies to visually detect predatory ants and

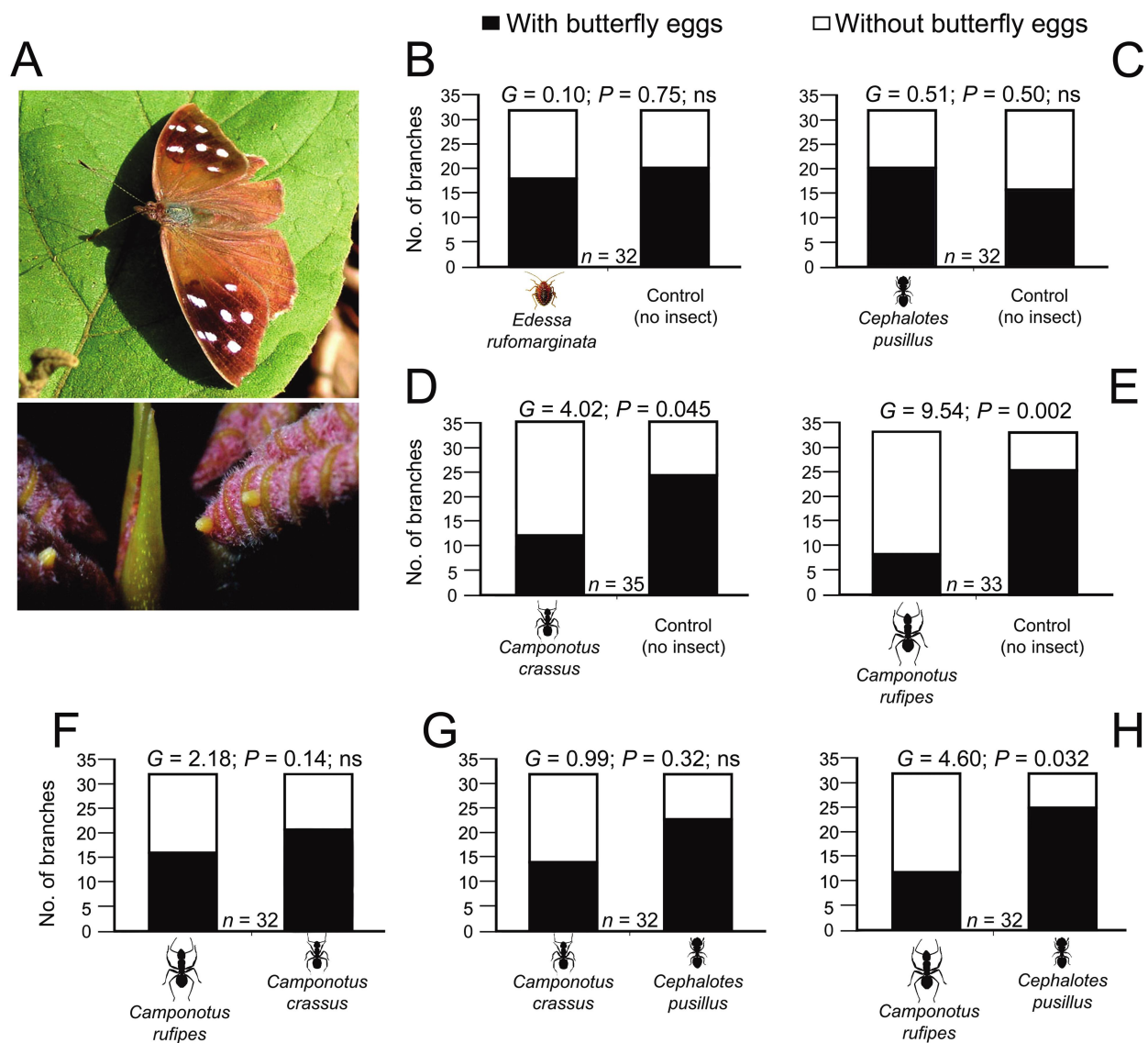


Figure 3: A, Adult female of *Eunica bechina* (top) and recently laid eggs on young leaves of *Caryocar brasiliense* (bottom). B–H, Oviposition patterns in *E. bechina* butterflies during choice experiments (24-h trials) using paired branches of the host plant. B–E, Bars show egg-laying response toward insect-occupied versus insect-free control branches. B, *Edessa rufomarginata* stinkbug × control. C, *Cephalotes pusillus* × control. D, *Camponotus crassus* × control. E, *Camponotus rufipes* × control. F–H, Bars show egg-laying response toward branches occupied by different ant species. F, Ant species of different size: *C. rufipes* × *C. crassus*. G, Ant species of different shape: *C. crassus* × *C. pusillus*. H, Ant species of different size and shape: *C. rufipes* × *C. pusillus*. Photograph of butterfly courtesy of A. Christianini.

select less vulnerable foliage for oviposition, corroborating our previous experiments with artificial ant models (Freitas and Oliveira 1996). Interaction trials between caterpillars and common foliage-dwelling ants confirm that such an avoidance response by ovipositing *E. bechina* may markedly reduce offspring mortality risks on the host plant. Remarkably, paired experiments using different ant species indicate that ovipositing females can also distinguish predatory from innocuous ants. Predaceous *Cam-*

ponotus species are avid consumers of plant and insect exudates (Davidson et al. 2003) and act as herbivore deterrents in numerous associations with plants bearing extrafloral nectaries in cerrado savanna (Oliveira et al. 1987) and worldwide (Rico-Gray and Oliveira 2007). On the other hand, pollen- and detritus-gathering *Cephalotes* are normally timid ants and only occasionally will feed on weak or dead prey (Davidson et al. 2003). *Cephalotes* ants may, however, react aggressively to other ant species (Corn

1980) or when under attack by a predator (Oliveira and Sazima 1984). Our results show that size and shape discrimination among co-occurring ant species allows *E. bechina* females to shift egg laying to less risky foliage. The difference between response based on only shape or size versus both features suggests that visual cues were used rather than odor, although it is true that different species of ants will be accompanied by different odor cues (Hölldobler and Wilson 1990). Additional experiments using artificial ant models impregnated with chemical extracts from different ant species (and proper controls with solvent) would help clarify a possible effect of odor cues on oviposition decisions by *E. bechina*. Similar studies evaluating risk effects on prey behavior have shown that the presence of crab spiders can reduce flower visitation by bees, but the exact identity of the clues (visual or olfactory) used by the visitors remains unclear (Morse 2007). However, recent experiments using artificial spider models have provided strong evidence that flower-visiting bees can detect predatory risk through visual cues (Gonçalves-Souza et al. 2008). Additionally, Ings and Chittka (2008) demonstrated that bee foragers slow their inspection flights after learning that there is a risk from cryptic crab spiders (robotic models). The adjustment of visual inspection effort results in accurate predator detection, leveling out predation risk at the expense of foraging time.

Butterflies and other Lepidoptera are known to use visual cues to evaluate plant quality before oviposition (Rauscher 1978; Thompson and Pellmyr 1991; Renwick and Chew 1994; Allard and Papaj 1996; Weiss and Papaj 2003). Although there is evidence that ant presence can mediate oviposition decisions in myrmecophilous butterflies (Pierce et al. 2002), the cues eliciting the oviposition response remain unknown. To our knowledge, the experiments with *E. bechina* provide the first demonstration that visual recognition of different types of natural enemies (i.e., different ant species) can mediate selection of oviposition site in a monophagous nonmyrmecophilous butterfly. Our finding is relevant in view of the fact that egg-laying decisions by *E. bechina* females are under the influence of the third trophic level (Price et al. 1980; Schmitz et al. 2004) rather than a trait of the host plant or of the herbivore itself (Shapiro 1981; Williams and Gilbert 1981). Reduction of offspring mortality through predator identification by sight in *E. bechina* butterflies represents an unusual case of a behavioral adaptation permitting herbivore specialization on a risky, ant-defended host plant.

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A view of the Brazilian savanna and the butterfly *Eunica bechina*. Photographs by Alexander Christianini.