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# Escape Behavior of Neotropical Homopterans in Response to a Flush–Pursuit Predator[1]

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## ABSTRACT

Insect defenses against avian predators often include both a primary defense that reduces the probability of being attacked and a secondary defense, typically escape behavior, employed if the primary defense fails. Escape behavior, however, can make insects potentially vulnerable to specialized flush–pursuit predators. Neotropical Redstarts of the genus *Myioborus* (Parulidae) exploit insect escape behavior by using their contrasting black-and-white plumage and animated foraging behavior to startle insect prey that are then pursued and captured in flight. We examined how insect primary defense strategy and natural variation in *Myioborus* plumage pattern influence escape behavior in six species of homopterans from Monteverde, Costa Rica. The six homopterans included two aposematic species of the family Cercopidae (*Ocoaxo* sp. and *Sphenorhina* sp.), two cryptic species of the family Cixiidae (both *Bothriocera* spp.), and two structurally defended species of the family Membracidae (*Campylocentrus* sp. and *Vestistilus variabilis*). We measured the distance at which models of *Myioborus* Redstarts elicited escape behavior in insects under field conditions. Response distances varied significantly with both homopteran primary defense and *Myioborus* plumage pattern. Structurally defended homopterans were the most sensitive to the models and cryptic homopterans were the least sensitive. The model simulating the plumage of endemic *M. miniatus comptus* of Costa Rica elicited greater responses than did models of other *Myioborus* taxa with either less or more white in the plumage. Our results suggest that (1) primary defense strategies can have a significant effect on insect vulnerability to flush–pursuit predators, and (2) geographic variation in the plumage pattern of *Myioborus* Redstarts may reflect adaptation to regional prey and habitat characteristics that maximizes flush–pursuit foraging performance.

## RESUMEN

Las defensas de los insectos contra aves depredadoras, frecuentemente incluye dos tipos de defensa: una primaria, que disminuye la probabilidad de ser atacado, y una defensa secundaria típica de comportamiento de escape, la cual es empleada si falla la defensa primaria. Sin embargo, el comportamiento de escape puede ocasionar que los insectos sean potencialmente vulnerables a depredadores especializados en vuelo y persecusión. Los colirrojos neotropicales del género *Myioborus* (Parulidae) explotan el comportamiento de escape de los insectos usando su plumaje contrastante blanco-negro, y su comportamiento de forrajeo animado para sobresaltar a los insectos a cazar, que luego son perseguidos y capturados en vuelo. Nosotros examinamos cómo la defensa primaria de insectos y la variación natural del plumaje en *Myioborus* influye en el comportamiento de escape en seis especies de homópteros de Monteverde, Costa Rica. Los seis homópteros estudiados incluyeron dos especies conspicuas de la familia Cercopidae (*Ocoaxo* esp. y *Sphenorhina* esp.), dos especies enigmáticas de la familia Cixiidae (ambos *Bothriocera* esp.), y dos especies de la familia Membracidae (*Campylocentrus* esp. y *Vestistilus variabilis*) que se defienden estructuralmente. Nosotros medimos la distancia en la cual los modelos colirrojos de *Myioborus* provocan el comportamiento de escape en insectos bajo de condiciones de campo. Las respuestas a las distancias variaron significativamente en ambas, en defensa primaria de los homópteros y el patrón del plumaje de los *Myioborus*. Los homópteros que se defienden estructuralmente fueron los más vulnerables a los modelos, y los homópteros enigmáticos los menos vulnerables. El modelo simulando el plumaje del colirrojo *M. miniatus comptus* endémico de Costa Rica, produjo mayor respuesta que los otros modelos *Myioborus* de otras taxas con menos o más color blanco en su plumaje. Los resultados de este estudio sugieren que: (1) las defensas de estrategia primaria pueden tener un efecto significativo en la vulnerabilidad de los insectos a los depredadores que vuelan y persiguen; y (2) la variación geográfica en el patrón del plumaje de los *Myioborus* colirrojos puede indicar adaptaciones a presas por regiones y a características del hábitat que maximizan su habilidad de volar y perseguir.

*Key words:* *Costa Rica; flush–pursuit foraging; Homoptera; insect defenses;* Myioborus *spp.; Redstarts.*

As PREDATORS AND PREY COEVOLVE, predators select for effective anti-predator defenses in their prey, which in turn favor predators that can best surmount prey defenses. In the resulting evolutionary "arms race" (Edmunds 1974, Dawkins & Krebs 1979), prey typically cannot develop a perfect defense that ensures their survival because they often face multiple predators, each with its own hunting technique (Matsuda *et al.* 1993). Therefore, prey often have two lines of defense: a primary defense to reduce the probability of being attacked and a

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secondary defense employed in case the primary defense fails (Robinson 1969, Edmunds 1974).

Insects have evolved a wide array of primary and secondary defenses to counter avian predators. Primary defenses include cryptic coloration, morphological structures such as spines or horns, and chemical defenses that are often paired with aposematic coloration (Robinson 1969, Edmunds 1974, Sherry & McDade 1982, Brakefield 2003, Dietrich 2003, Joron 2003, Schmidt 2003). The most common secondary defense employed by insects is escape behavior. Insects with strong wing musculature and reflexes (*e.g.,* Diptera) use early detection and flight as a secondary defense, while slower insects (*e.g.,* Coleoptera) may drop from elevated positions. Orthoptera and some species of Homoptera launch themselves with their large muscular legs to evade capture (Robinson 1969, Edmunds 1974, Schmidt 2003).

Most avian predators rely on cryptic coloration or stealth to approach insect prey and capture them before they can initiate an escape response (Edmunds 1974). But a few species of birds, the flush–pursuit insectivores, exploit insect escape behavior by using conspicuous visual displays and animated foraging behavior to flush potential prey that can then be pursued and captured in flight (Remsen & Robinson 1990). These specialized predators typically have patches of contrasting plumage that are displayed prominently during foraging maneuvers and are thought to assist in startling potential prey (Jablonski 1999, Mumme 2002).

Recent investigations of avian flush–pursuit foraging have focused on the parulid warbler genus *Myioborus* (Jablonski 1999, 2001; Jablonski & Strausfeld 2000, 2001; Mumme 2002). The *Myioborus* Redstarts comprise 12 species of flush–pursuit insectivores found in montane forests throughout the American tropics and subtropics (Curson *et al.* 1994). In all members of the genus, both sexes have contrasting black-and-white plumage patches that are exposed by spreading the wings and tail during animated foraging displays. By experimentally darkening the white feathers of birds in the field, Jablonski (1999) and Mumme (2002) have independently demonstrated that these contrasting black-and-white plumage patches are important foraging adaptations that trigger prey escape behavior and enhance flush–pursuit foraging performance in both the Painted Redstart (*Myioborus pictus*) in southern Arizona (Jablonski 1999) and the Slate-throated Redstart (*Myioborus miniatus*) in Costa Rica (Mumme 2002).

What is not clear from this previous work is why the pattern and extent of white in the plumage of *Myioborus* Redstarts show considerable interspecific and intraspecific geographic variation (Curson *et al.* 1994). For example, although all *Myioborus* Redstarts have white-tipped outer tail feathers, the Painted Redstart also has conspicuous white wing patches that are lacking in all other members of the genus (Fig. 1). In the most widely distributed species in the genus, the Slate-throated Redstart, considerable variation in the extent of white in the tail exists among the 12 recognized subspecies, with the least amount of white evident in the subspecies *M. miniatus hellmayri* from northern Central America, an intermediate amount of white in *M. m. comptus* of Costa Rica, and the most extensive white found in *M. m. verticalis* from Bolivia (Curson *et al.* 1994; Fig. 1). This geographic variation in plumage pattern may be related to possible differences in habitat conditions in which birds use flush–pursuit foraging displays, geographic variation in constraints on plumage evolution, or geographical variation in either the type of prey exploited or the sensitivity of the visual system of prey (Mumme 2002).

Insect responses to the unusual foraging behavior of *Myioborus* Redstarts have been explored only recently. In an extensive series of field and laboratory experiments using model Redstarts, Jablonski and Strausfeld (2000, 2001) have shown that the three primary components of *Myioborus* flush–pursuit foraging displays—contrasting black-and-white plumage, spreading of the tail and wings, and exaggerated pivoting movements—all contribute to triggering early escape behavior in several taxa of flies (Diptera) that are important prey items of the Painted Redstart. By startling flies at greater distances, *Myioborus* flush–pursuit displays therefore increase the number of potential prey available for pursuit (Jablonski & Strausfeld 2000, 2001). In addition, the exaggerated pivoting movements of *Myioborus* Redstarts frequently stimulate flies to flush directionally across the birds' field of stereoscopic vision (Jablonski 2001), potentially increasing the probability of detection, pursuit, and capture.

Although the response of Diptera to *Myioborus* flush–pursuit foraging displays has been investigated extensively, little attention has been given to other important Redstart prey, such as Homoptera. Homoptera comprise approximately half of the food items delivered to nestlings of the Slate-throated Redstart in Costa Rica (Mumme, pers. obs.), and *ca* 19 percent of the diet of the Painted Redstart in Arizona (Jablonski & Straus-

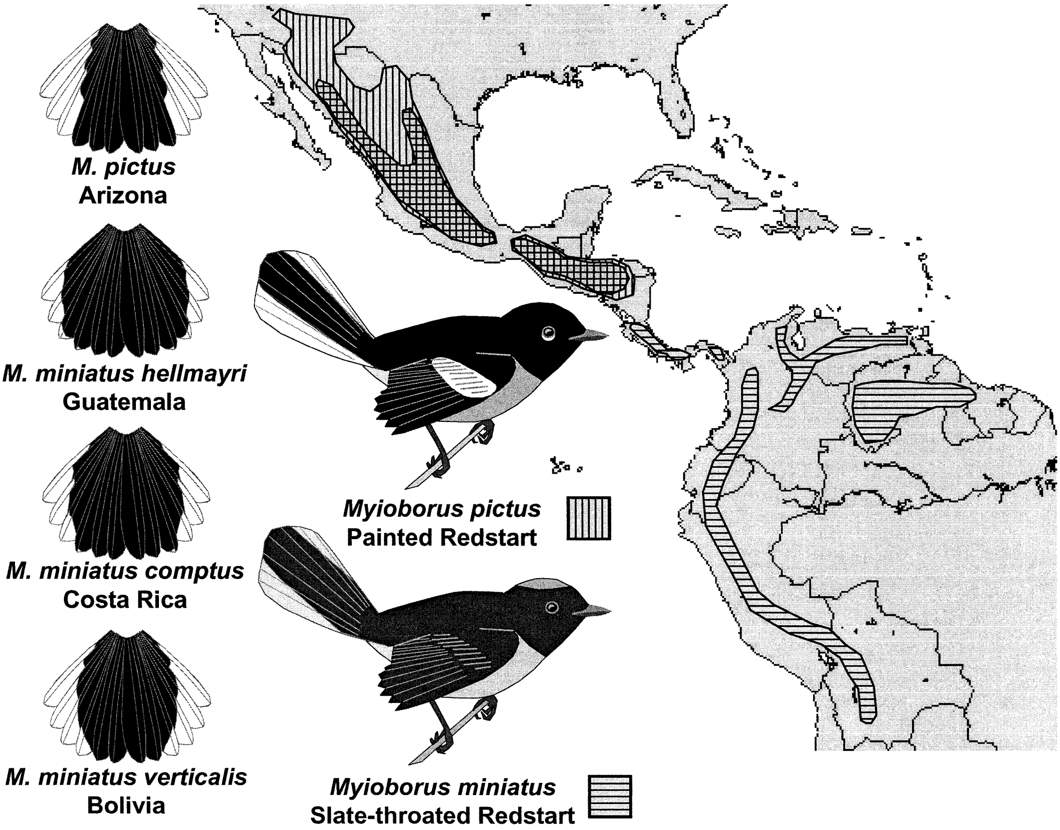


FIGURE 1. Geographic range of *Myioborus pictus* and *Myioborus miniatus* and representative geographic variation in tail pattern and overall plumage in the two species.

feld 2001). The vulnerability of homopterans to flush–pursuit predators is of particular interest because of their escape behavior (Heady & Nault 1985) and the wide variety of primary and secondary defense strategies they employ. Some planthoppers (superfamily Fulgoroidea) are cryptic while others are aposematic and possibly distasteful. Still others have inflated head capsules or, as a secondary defense, produce long plumes of wax from their abdomens (Hogue 1993). Treehoppers (Membracidae) have a hardened pronotum that can make them difficult for certain predators to swallow, and the size and hardness of the pronotum can change during the course of development, in some species changing in concert with changes in cryptic and aposematic coloration (Wood 1977, Hogue 1993). Froghoppers (superfamily Cercopoidea) have either aposematic or cryptic coloration and jump and fly readily (Hogue 1993). Other homopteran taxa are Batesian mimics that resemble venomous wasps (Dietrich 2003). Whether differences in primary defenses among homopterans result in differences in escape behavior and sensitivity to flush–pursuit predators has not been explored.

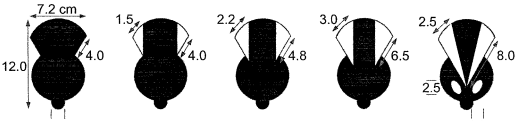
Here, we examine how primary defense strategy and natural variation in *Myioborus* plumage pattern affect escape behavior and potential vulnerability to flush–pursuit foraging of six species of Neotropical homopterans from a montane cloud forest in Costa Rica. By performing field experiments with models of *Myioborus* Redstarts, we sought to answer two questions: (1) Does the primary defense strategy employed by a particular Homoptera species affect its escape behavior and sensitivity to *Myioborus* flush–pursuit foraging displays?; and (2) Does natural geographic variation in the plumage pattern of *Myioborus* Redstarts influence the escape response of homopteran potential prey? Our results indicate that both primary defense strategy and *Myioborus* plumage pattern significantly influence the escape behavior of homopterans in the field.

# METHODS

STUDY SITE.—The study was conducted during May and June 2003 at the Estación Biológica Monteverde (EBM) and surrounding properties in Monteverde, Costa Rica (10°18′N, 84°48′W; Nadkarni & Wheelwright 2000, Mumme 2002). Two species of *Myioborus* Redstarts occur in Monteverde, the Slate-throated Redstart (*M. m. comptus*) at lower elevations (1300–1600 m) and the Collared Redstart (*Myioborus torquatus*) at higher elevations (1600–1900 m).

INSECT SPECIES.—We focused on six species of Homoptera with three different forms of primary defenses: two aposematically colored members of the family Cercopidae (*Ocoaxo* sp. and *Sphenorhina* sp.), two cryptic members of the family Cixiidae (*Bothriocera* sp. A and B), and two structurally defended members of the family Membracidae (*Campylocentrus* sp. and *Vestistilus variabilis*). *Ocoaxo* sp., *Bothriocera* sp. A, and *Campylocentrus* sp. were found primarily at lower elevations (1400–1600 m) in Monteverde while the other species were more common at higher elevations (1700–1800 m). The aposematically colored *Ocoaxo* sp. is predominantly orange with longitudinal black stripes and a terminal black band on the posterior end of the wings, while *Sphenorhina* sp. is red–orange with small black spots on the posterior end of the wings. Both species of *Bothriocera* have semi-transparent wings with either a mix of brown, black, and gray splotches (species A) or small black spots (species B). The structurally defended *Campylocentrus* sp. is predominantly black with a few white spots and two sharp sclerotized spikes protruding outward above the head and a long spike running posteriorly the length of the spine. *Vestistilus variabilis* is tan–brown in coloration with the same spike configuration as *Campylocentrus* sp.

BIRD MODEL.—Models simulating four different plumage patterns found in *M. miniatus* and *M. pictus*, plus an all-black control model, were constructed based on Jablonski and Strausfeld (2000). The different *Myioborus* plumage patterns represented *M. m. hellmayri*, *M. m. comptus*, *M. m. verticalis*, and *M. pictus* (Figs. 1 and 2). Because the extent of white in the tail of *M. torquatus* is comparable to that of *M. m. comptus* of Costa Rica, we did not construct or test a separate model of the Collared Redstart. Models were made from stiff black cardboard and had the size and two-dimensional projection of an approaching *Myioborus* Redstart in its characteristic foraging display: crouched with an erect spread tail and drooped spread wings (Fig. 2; Jablonski & Strausfeld 2000). The white portions of models were painted with white flat enamel paint and sprayed with a UV-resistant matte finish. Models were attached at an angle 45–60° from the horizontal to a 2 m pole that was painted black and marked with 1 cm increments for measuring distances to test insects.



All Black (control)

*Myioborus miniatus hellmayri*

*Myioborus miniatus comptus*

*Myioborus miniatus verticalis*

*Myioborus pictus*

FIGURE 2. Dimensions of the bird models used in the experiment.

HOMOPTERAN RESPONSE TO BIRD MODELS.—Because a separate experiment showed that caged homopterans were generally unresponsive to models of approaching *Myioborus* Redstarts (Galatowitsch 2004), we tested homopterans under natural field conditions using methods similar to those of Jablonski & Strausfeld (2000, 2001). Homoptera were found by searching for populations on plants in secondary forest and along forest edges within or near territories of *Myioborus* Redstarts. When an individual of one of the six focal species was encountered, a camouflaged investigator attached one of the five bird models to the pole and moved the model toward the insect, starting from a distance of *ca* 1.5 m. The foraging behavior of *Myioborus* Redstarts was simulated by moving the model toward the perched homopteran in 16 cm segments, followed by two seconds of pivoting the model side to side and then by a two-second pause. These movements imitate the flush–pursuit foraging behavior of *Myioborus* Redstarts (Jablonski & Strausfeld 2000). If a homopteran showed escape behavior (*i.e.,* it jumped and/or flew), the distance between the model and the insect when it first moved was recorded. If the model did not elicit a response, the response distance was recorded as zero. The order of Homoptera taxa used was based on the order in which insects were encountered in the field, while the order of model presentation was randomized. For each trial, we also recorded time, temperature, and ambient light intensity; however, because variation in these physical parameters had little or no effect on homopteran response distances

TABLE 1. *Analysis of variance of the effects of Homoptera primary defense (aposematic, cryptic, or structural), Homoptera species (nested within primary defense), and bird model type on homopteran response distance. To normalize and equalize variances in response distance, log (distance + 1 cm) was used as the dependent variable.*

| | df | Sum of squares | Mean square | *F* | *P* |
|---|---|---|---|---|---|
| Primary defense | 2 | 55.701 | 27.850 | 317.219 | <0.0001 |
| Homoptera species (primary defense) | 3 | 5.519 | 1.840 | 20.953 | <0.0001 |
| Bird model | 4 | 5.655 | 1.414 | 16.104 | <0.0001 |
| Primary defense*bird model | 8 | 1.347 | 0.168 | 1.917 | 0.0567 |
| Bird model*species (primary defense) | 12 | 1.055 | 0.088 | 1.002 | 0.4470 |
| Residual | 330 | 28.972 | 0.088 | | |

(Galatowitsch 2004), the data are not presented here.

Field trials were conducted 1–15 June 2003 between 1000 and 1600 h. Sixty individuals of each homopteran species were used, and we conducted tests in several different locations to reduce the probability that any individual homopteran was tested more than once. Sample size was 12 for each combination of the 6 Homoptera species and 5 bird models, for a total sample of 360 field trials.

Homopteran movement rate.—To determine if the natural movement rate of homopterans may have contributed to between-species differences in escape behavior, we measured location–residence time of the six species of Homoptera in the absence of exposure to a bird model. Once encountered, a homopteran was timed until either the insect left that location (by jumping or walking) or 180 seconds had passed. A camouflaged observer stood *ca* 1.5 m away and minimized any movement during the trials. Twenty individuals of each species were timed 18–25 June 2003 between 1000 and 1600 h.

Data analysis.—For the field experiment examining homopteran response to bird models, two null hypotheses were tested: (1) response distance was unrelated to homopteran primary defense strategy, and (2) response distance was not sensitive to variation in *Myioborus* plumage pattern. Data were analyzed using a three-factor nested ANOVA that tested the relationship between one dependent variable (homopteran response distance) and three independent variables (homopteran primary defense, bird model, and homopteran species nested within primary defense). To equalize variances and avoid problems with response distances of 0 cm, we transformed the data by calculating log(response distance + 1 cm). *Post hoc* pairwise comparisons were performed using Student–Newman–Keuls procedure (Ott 1993).

A two-factor nested ANOVA was used to analyze the length of time homopterans remained in the same location. Homopteran primary defense and homopteran species nested within primary defense were used as independent variables, while log(sec remaining at the original location) was the dependent variable.

## RESULTS

Homopteran response to bird models.—Homopterans responded to an approaching model in 89 percent of the field trials. Structurally defended homopterans showed the highest frequency of response (95%), followed by the aposematically (90%) and cryptically (81%) colored homopterans. Variation in model plumage pattern had relatively little effect on overall response rate. The *M. m. comptus* and *M. m. verticalis* models triggered the highest percentage of responses (91%) and the all-black control model the fewest (84%).

Analysis of variance of response distance data revealed no significant two-way interactions between bird model type and either primary defense or homopteran species (Table 1); however, primary defense had a strong and highly significant effect on response distance ($F_{2,\ 330} = 317.22$, $P < 0.0001$; Table 1 and Fig. 3). Structurally defended Homoptera were the most sensitive to *Myioborus* models (mean response distance = 19.6 cm), followed by aposematic (11.9 cm) and cryptic (1.1 cm) homopterans. All three groups differed significantly from each other (Student–Newman–Keuls, $P < 0.05$ for all pair–wise comparisons).

Homopteran response distance was also significantly influenced by the type of bird model used ($F_{4,\ 330} = 16.10$, $P < 0.0001$; Table 1 and Fig. 3). The *M. m. comptus* model elicited the greatest mean response distances (15.6 cm), followed by *M. m. verticalis* (14.0 cm), *M. pictus* (10.3 cm), *M. m. hellmayri* (9.1 cm), and the all-black model (5.2

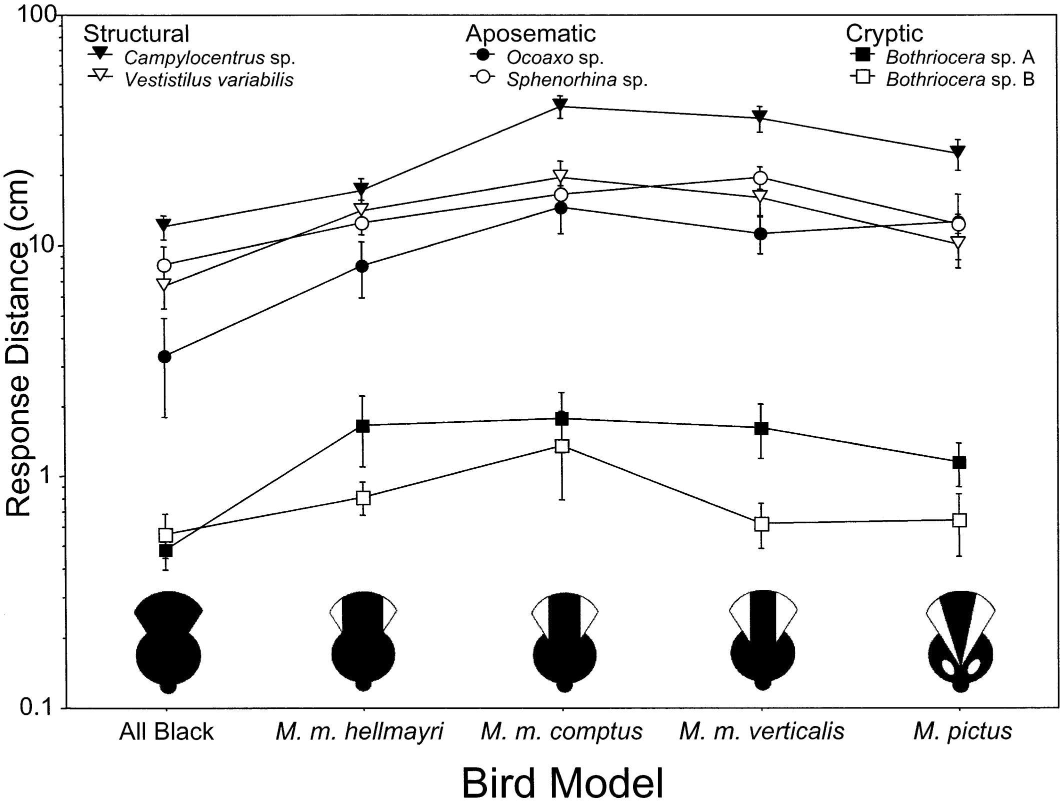


FIGURE 3. Mean response distance of the six focal species of homopterans in reaction to an approaching bird model. Filled symbols represent low elevation homopterans and open symbols are high elevation species. Error bars represent ± 1 SEM.

cm). In *post hoc* comparisons, all four *Myioborus* models differed significantly from the all-black control model (Student–Newman–Keuls procedure, all $P < 0.05$; Fig. 3). In addition, response distances for *M. m. comptus* differed significantly from those for *M. m. hellmayri* and *M. pictus* (Student–Newman–Keuls procedure, both $P < 0.05$), but not *M. m. verticalis* (Fig. 3).

The nested ANOVA also revealed significant differences among the six homopteran species ($F_{3, 330} = 20.95$, $P < 0.0001$; Table 1). The structurally defended *Campylocentrus* sp. was the most sensitive homopteran tested (mean response distance = 21.4 cm), followed by aposematically colored *Sphenorhina* sp. (11.5 cm), structurally defended *V. variabilis* (10.0 cm), aposematically colored *Ocoaxo* sp. (5.5 cm), cryptically colored *Bothriocera* sp. A (1.05 cm), and cryptically colored *Bothriocera* sp. B (0.67 cm; Fig. 3).

HOMOPTERAN MOVEMENT RATE.—The amount of time that homopterans remained at a particular location in the absence of a bird model differed significantly with both primary defense ($F_{2, 174} = 37.75$, $P < 0.0001$) and species nested within primary defense ($F_{3, 174} = 19.26$, $P < 0.0001$; Fig. 4). The two cryptically colored species (*Bothriocera* spp. A and B) were the least active, remaining motionless an average of 157 seconds during the 180-second trials, compared to 129 seconds for the aposematic species and 82 seconds for the structurally defended membracids (Fig. 4); however, the short mean residence time for the structurally defended membracids was largely attributable to the highly active *Campylocentrus* sp., which remained at the same location an average of only 40 seconds during the trials (Fig. 4).

## DISCUSSION

HOMOPTERA PRIMARY DEFENSE AND ESCAPE BEHAVIOR.—Our results indicate that the escape behavior of Neotropical homopterans is significantly influenced by their primary defense strategy. We found

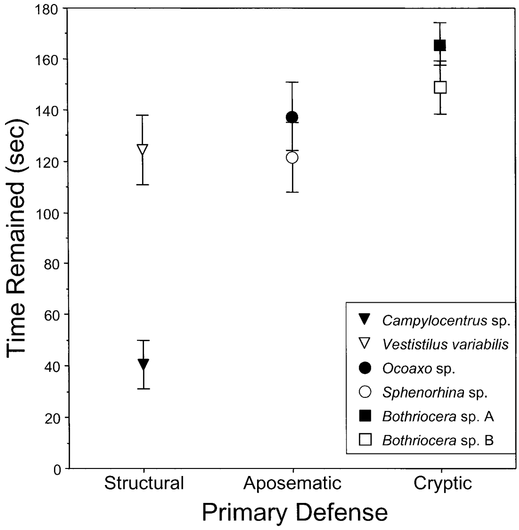


FIGURE 4. Spontaneous movement rate of the six focal species of homopterans, as measured by the mean time insects remained at a particular location during three-minute field trials. Filled symbols represent low elevation homopterans and open symbols are high elevation species. Error bars represent ±1 SE.

that structurally defended membracids were the most sensitive to models of *Myioborus* Redstarts and showed the greatest response distance, followed by aposematically colored cercopids and cryptically colored cixiids. It is not surprising that cryptically colored homopterans showed escape behavior at only very close range (Fig. 3); because crypic species have no other predator deterrent besides remaining motionless and avoiding detection, escape behavior should be employed only when detection and/or capture appear to be imminent (Edmunds 1974, Brakefield 2003, Schmidt 2003). In contrast, selection to remain motionless and avoid detection is likely to be weaker in aposematically and structurally defended homopterans as their primary defense can discourage attack even after they have been detected (Edmunds 1974, Joron 2003).

Data on homopteran movement rates (Fig. 4) suggest that the responses we observed in our field trials were generally reactions to the approaching models rather than spontaneous movements. Five of the six species tested tended to remain motionless for 2 minutes or more in the absence of a model, compared to 30 to 40 seconds when tested with an approaching model. The only exception was the structurally defended *Campylocentrus* sp., which was much more active than the other species tested and moved spontaneously after an average of just 40 seconds (Fig. 4). Thus, some of the "escapes" observed in this species may have been spontaneous movements rather than responses to an approaching model; however, because the response distance of *Campylocentrus* sp. was strongly influenced by variation in the *Myioborus* models (Fig. 3; one-way ANOVA, $F_{4,\,55} = 11.32$, $P < 0.0001$), spontaneous movements during the model tests were probably infrequent.

We found that mean model response distance varied interspecifically among the homopterans by more than an order of magnitude, from 0.67 cm for *Bothriocera* sp. B to 21.4 cm for *Campylocentrus* sp. In contrast, Jablonski and Strausfeld (2001) found a generally greater but more uniform range of mean response distances (*ca* 25–42 cm, estimated from Fig. 6 of Jablonski & Strausfeld 2001) for representatives of seven families of brachyceran Diptera; however, given that brachycerans are all strong fliers that typically rely on early detection and rapid escape to avoid predation, and generally lack other defenses, the greater and more uniform response distances of brachycerans are not surprising.

Jablonski and Strausfeld (2001) also found that taxonomic variation in response distance of brachyceran Diptera was largely attributable to variation in the neuroanatomy of the giant fiber system, the component of the fly nervous system that mediates escape behavior in response to visual stimuli. Greater response distances were found in flies with large-diameter giant fibers that extend short distances from the brain to motor neurons than in flies with smaller-diameter and longer fibers. Unfortunately, we do not know if the variation in homopteran response distance we observed in our study (Fig. 3) is potentially related to variation in neuroanatomy, because the neural basis of escape behavior in Homoptera has not been investigated. Such an investigation could provide a proximate explanation for the strong association we observed between primary defense strategy and response distance (Fig. 3).

VULNERABILITY OF HOMOPTERA TO FLUSH–PURSUIT PREDATORS.—By using their contrasting plumage and animated behavior to elicit prey escapes at greater distances, flush–pursuit predators increase the number of potential prey available for pursuit and capture (Jablonski 1999, 2001; Jablonski & Strausfeld 2000, 2001; Mumme 2002). We might therefore predict that structurally defended and aposematically colored homopterans, which flush at greater distances in response to approaching model Redstarts, are potentially more vulnerable to flush–pursuit predators than are cryptically colored homopterans, which respond at only very close range (Fig. 3). We tested this prediction by examining diet samples collected from Slate-throated Redstarts (*M. m. comptus*) at low elevations (1400–1600 m) at our study site. Surprisingly, of the three low elevation species of homopterans investigated in our study (*Campylocentrus* sp., *Ocoaxo* sp., and *Bothriocera* sp. A.), only the cryptically colored *Bothriocera* sp. A has been identified in diet samples of Slate-throated Redstarts (M. L. Galatowitsch, pers. obs.).

There are several possible reasons why less responsive cryptically colored homopterans may be well represented in diet samples while more responsive aposematic and structurally defended homopterans are not. First, aposematic coloration and structural defenses may discourage predation by *Myioborus* Redstarts. Both of the aposematic species we investigated (*Ocoaxo* sp. and *Sphenorhina* sp.) had a slight bitter flavor (Galatowitsch 2004), and it is possible that *Myioborus* Redstarts recognize and avoid aposematic prey. For example, when Great Tits (*Parus major*) were exposed to aposematic and cryptic forms of *Lygaeus equestris* (Heteroptera), the birds were more cautious with aposematic individuals and killed fewer of them, even though there was no indication that the aposematic forms were more distasteful than the cryptic individuals (Sillén-Tullberg 1985). Structurally defended membracids, with their sharp spines and thick sclerotized exoskeleton, may also be avoided by *Myioborus* Redstarts. Experiments with *Umbonia crassicornis* (Membracidae) and *Anolis* lizards have shown that lizards reject highly sclerotized homopterans (Wood 1975). In a study by Sherry and McDade (1982), White-fronted Nunbirds (*Monasa morphoeus*) and Bright-rumped Attilas (*Attila spadiceus*) of the Neotropics had greater difficulty handling insects with either aposematic coloration or hard exoskeletons.

A second possibility is that cryptically colored homopterans are much more abundant than are either aposematic or structurally defended homopterans. Under this hypothesis, cryptic prey are better represented in the diet simply because Slate-throated Redstarts encounter them more frequently, notwithstanding the reduced probability of flushing cryptic prey from a distance. Although quantitative sampling of homopterans in locations where Slate-throated Redstarts forage would be required for a definitive test, our subjective impressions argue against this hypothesis; we encountered the cryptic *Bothriocera* species in the field at approximately the same rate as we encountered the other homopterans. A third possibility is that Slate-throated Redstarts rely on foraging strategies other than flush–pursuit foraging (*e.g.,* flycatching or gleaning; Mumme 2002) to capture cryptic prey that are relatively unresponsive to flush–pursuit displays.

A final possibility is that Costa Rican Slate-throated Redstarts benefit more from insects having short predator response distances. Under this hypothesis, *M. m. comptus* may be unable to pursue and successfully capture insect prey that flush beyond a certain critical distance. If such a critical distance exists and is relatively short in Costa Rican Redstarts, cryptically colored homopterans should predominate in the diet, as we observed; however, we have no direct evidence that a short critical prey-flushing distance exists in Costa Rican Redstarts.

*MYIOBORUS* PLUMAGE PATTERN AND HOMOPTERA ESCAPE BEHAVIOR.—The absence of significant interactions involving bird model type in our experiment allows us to generalize about the significant main effect of variation in *Myioborus* plumage pattern (Table 1). Averaging across all homopteran species tested, the model of the endemic *M. m. comptus* elicited the greatest mean response distance (15.6 cm) but did not differ significantly from the model of *M. m. verticalis* (14.0 cm); however, models with either less white (*i.e., M. m. hellmayri* and the all-black control model) or more white (*i.e., M. pictus*) were significantly less effective at eliciting homopteran escape behavior (Fig. 3). These results are corroborated by the results of ongoing plumage-manipulation experiments conducted with Slate-throated Redstarts in the field (Mumme 2002). When the amount of white in the tail of Costa Rican *M. m. comptus* was reduced to simulate the plumage of *M. m. hellmayri* (Fig. 1), flush–pursuit foraging success declined significantly; however, increasing the amount of white in the tail to simulate the plumage of *M. miniatus verticalis* (Fig. 1) had no significant impact on flush–pursuit foraging performance (R. L. Mumme, pers. obs.).

Collectively, these results raise the question of why *Myioborus* Redstarts in some regions (*i.e.,* Arizona and northern Central America) have plumage patterns that in Costa Rica are demonstrably less effective at eliciting escape behavior in important prey. One potential answer is that geographic variation in either habitat conditions (*e.g.,* ambient light and/or density of vegetation) or the primary type of prey exploited (*e.g.,* Diptera vs. Homoptera) may select for different plumage patterns in different geographic regions. Presently, however, we do not have sufficient data to address this issue.

*Myioborus* Redstarts also show major clinal geographic variation in their belly coloration, from dark red in both *M. pictus* and *M. m. miniatus* of Mexico to orange in *M. m. comptus* of Costa Rica and yellow in *M. m. verticalis* of Bolivia (Curson *et al.* 1994); however, because foraging *Myioborus* Redstarts generally flush insects that are above or in front of them (Jablonski 1999), geographic variation in ventral coloration may be unrelated to flush–pursuit foraging performance.

Regardless of the evolutionary importance of geographic variation in *Myioborus* plumage pattern, the results of our study strongly suggest that the tail pattern of the Costa Rican Slate-throated Redstart *M. m. comptus* has evolved to match the neural sensitivity of its primary prey. Costa Rican Redstarts with slightly less or dramatically more white in the plumage would startle fewer homopteran prey (Fig. 3) and have reduced flush–pursuit foraging performance relative to birds in typical plumage; we have no evidence, however, that the escape behavior of Costa Rica homopterans has been evolutionarily modified through selection exerted by *Myioborus* Redstarts. For example, if homopterans have evolved in response to predation by *Myioborus* Redstarts, we would expect to find that species commonly consumed by Redstarts (*i.e., Bothriocera* sp. A) are weakly responsive to models of *M. m. comptus* and more responsive to other bird models. In fact, we did not find such a pattern; all six homopteran species investigated were maximally responsive to models of Costa Rican *M. m. comptus*, regardless of the homopteran's primary defense strategy and overall degree of sensitivity (Table 1 and Fig. 3).

Why has selection exerted by *Myioborus* Redstarts had no measurable evolutionary effect on the escape behavior of their homopteran prey? As argued by Jablonski (1999, 2001), two factors are likely to be involved. First, because specialized flush–pursuit predators like *Myioborus* Redstarts comprise a small and relatively rarely encountered group of insectivorous birds, homopteran escape behavior may be maintained through selection exerted by more common predators that lack flush–pursuit specializations. Second, the extreme simplicity of the insect neural circuits responsible for the detection of approaching predators and escape behavior may place severe evolutionary constraints on the ability of insects to discriminate among normal predators, when escape behavior is almost always advantageous, and flush–pursuit predators, when escape behavior could be fatal (Jablonski & Strausfeld 2000, 2001). Thus, in the coevolutionary arms race between *Myioborus* Redstarts and their insect prey, it is likely that Redstarts have an evolutionary advantage.

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