Postural Changes Accompany Perch Location Changes in Male Butterflies (*Asterocampa leilia*) Engaged in Visual Mate Searching

Ronald L. Rutowski


**Abstract**

Males of the nymphalid butterfly *Asterocampa leilia* perch and wait during the morning at places where females are likely to appear. Males leave their perches to court passing females and chase away intruding males. As air and ground temperatures rise during the morning, males switch from perching on the ground to perching off the ground (average height = 0.87 m) for thermoregulatory reasons. To evaluate how this switch in perch location might affect mate detection, I have investigated how the three-dimensional posture of the male’s body and head varies with perch location and how conspecifics fly through male perching areas. The body posture of males varies with perch location, as measured by pitch and roll relative to gravity, and yaw relative to the sun. Moreover, the pitch and roll of the head relative to the body is adjusted in a way that compensates for variation in body pitch and roll. These results, along with information on conspecific flight altitudes, suggest that when a male is perched on the ground his visual system is positioned in such a way that he is less likely to detect conspecifics flying nearby than when he is perched off the ground. Hence, it appears that early in the morning visual detection of mates and intruding males may be compromised by thermoregulatory concerns.

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**Introduction**

Stationary perching in exposed places is a strategy, often called a sit-and-wait strategy, used by many insects and other organisms to enhance the probability of visually detecting prey or potential mates (Thornhill & Alcock 1983; Alcock 1998). A variety of studies indicate that animals engaged in this tactic have strong and specific perch and body orientation preferences (e.g. O’Neill & O’Neill 1988; Rutowski et al. 1991; Hastings et al. 1994). However, understanding the adaptive
significance of these behavioral preferences will involve understanding interactions between several, and potentially conflicting, selection pressures that may shape them.

First, there will be selection to position the visual system in the ideal position for detecting targets of interest (prey, mates and potential competitors) as they pass by. Insect eyes typically have regions of heightened acuity owing to morphological or neural modifications (Land 1989, 1990, 1997); these regions should be directed toward places where targets are likely to appear to the extent these places can be predicted. Secondly, there will be selection to perch in ways that maintain thoracic temperature optimal for rapid and effective response to passing prey or mates. Over a broad range of environmental temperatures, perched insects regulate body temperature within a narrow range, most often by adjusting heat load through changes in body position and perch preferences (Casey 1981; May 1985; Heinrich 1993). Thirdly, risk of predation or the likelihood of detecting predators may vary with perch location in a way that will favor preferences for some perch locations over others. Moreover, these various demands may be in conflict in that perching in exposed places, while being optimal for detecting prey or mates, may expose an insect to intense solar radiation leading to high heat loads and potentially lethal thoracic temperatures or to high risk of predation.

To learn about the proximate and ultimate interactions among such demands, I have studied the perching behavior of territorial males of a nymphalid butterfly, Asterocampa leilia. Males of this desert butterfly occupy perch sites on or adjacent to the larval foodplant, the desert hackberry Celtis pallida, where they sit and wait for females to appear (Austin 1977; Rutowski & Gilchrist 1988). The body posture and perch preferences of a male change over the course of the morning activity period (Rutowski et al. 1991, 1994). Early in the day males perch on the ground and later, when the air is warmer, they perch at an average height (not correlated with temperature) of 0.87 m above the ground. This change in perch preference is driven by thermoregulatory concerns (Rutowski et al. 1994). At all times, males engaged in mate-locating maintain their body temperature within a narrow range of 38–40°C by perching each day initially on the ground to maximize heat gain when air temperatures are low, and then later off the ground, typically on the larval foodplant, to reduce heat load.

How does this change in perch location affect a male’s ability to detect conspecifics passing by his perch? Thermally driven changes in the perch preferences of males engaged in sit-and-wait mate location are known for other insects (e.g. O’Neill & O’Neill 1988; Hastings et al. 1994), but their consequences for success in mate detection have yet to be determined. To answer this question, I investigated the orientation of the visual field of perched males in space and the flight behavior of the targets (females and intruding males) that elicit visually guided approach. Although the structure of the visual field of butterflies is not well known, Horridge (1977) and Land (1997) report that the compound eyes of butterflies, like those of most insects, have at least frontal and equatorial regions, so-called acute zones, of heightened visual acuity. Moreover, these reports are supported by the observation that A. leilia males have enlarged facets in the frontal and equatorial regions of the
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eye (Wallace & Rutowski, in press). I expect that this band will view a region of the visual field in which detection of small moving objects is good. Hence, males should perch in ways that direct these acute zones toward the probable flight paths of conspecifics.

I have addressed three questions about *A. leilia* males and their body position when perched either on or off the ground. First, how does typical three-dimensional posture (pitch, roll, and yaw) of perched males change when they move from perches on the ground to those off the ground? A previous study (Rutowski et al. 1991) found that males perched on the ground consistently face away from the sun, while males perched off the ground have no typical orientation relative to the sun but consistently face out of or away from the center of the plant on which they are perched. Other aspects of body posture are not known. Secondly, does body posture accurately indicate orientation of the visual system or does the postural relationship between the head and the body change as pitch and roll change? During the study of body pitch and roll, I noted that the posture of the head relative to the body was not constant. This second part of the study examined the relationships between head and body posture. Thirdly, what are the typical flight altitudes of conspecific males and females as they pass by perched males? The overall aim then, was to evaluate the possible consequences of changes in perch location for the detection of potential mates and intruding competitors.

**Methods**

**Study Site**

The measurements and observations reported in this study were made on *A. leilia* at two field sites in the upper Sonoran Desert of Arizona. These sites, known as Blue Point and Round Valley, respectively, have been described in previous studies (Rutowski & Gilchrist 1988; Rutowski et al. 1991). In general, data were collected on sunny days, during the morning activity period, typically 08:00–11:00 h (Rutowski et al. 1996), in the 1991 through 1996 flight seasons (Apr. to Oct.).

**Body Posture**

To describe the three-dimensional orientation or body posture of a perched male, I developed techniques for measuring the pitch, roll, and yaw of the body. I measured body pitch and roll of perched males in the field with a protractor outfitted with a plumb line that hung from its center. To measure body pitch, a line running through the center of the protractor was aligned with the anteroposterior axis of the male’s body while holding the plane of the protractor vertical. The pitch of the male’s body in degrees relative to horizontal could then be determined from where the plumb line intersected the scale on the protractor. A negative pitch was recorded if the head end of the male’s body axis pointed below horizontal. Body roll was measured using the same device and was recorded as the angle of the plane bisecting the two wing planes in degrees relative to vertical.
Body roll deviations from vertical that were clockwise (viewed from the front) were recorded as positive and those counterclockwise as negative.

A male’s orientation around the dorso-ventral axis was measured relative to magnetic north using a hand-held compass. A male’s body yaw is described as the direction (in degrees) in which the anterior end of the body was pointing, clockwise (from above) relative to the solar azimuth.

When I measured these three descriptors of a male’s body posture, I also measured whether he was perched on or off the ground, whether his wings were open or closed, and the solar elevation (using the protractor with plumb line) and compass bearing to the solar azimuth to the nearest degree.

**Head Posture Relative to the Body**

After this initial study, and to document the orientation of the head relative to the body, I photographed perched males from directly in front, from the side at 90° relative to the antero-posterior axis of the male’s body, and from directly overhead. All photographs of males off the ground included a reference plumb line in the frame. However, for each male perched on the ground, I had to take two photographs, one of the male and then, without moving the camera, one of a plumb line. This was necessary because if a plumb line was moved close to a perched male on the ground he typically flew away before the photo could be taken. Overhead photographs included a marker indicating the direction to the sun.

These photographic transparencies were projected onto a flat surface parallel to the plane of the film. All angular measures were made from these projected images. For lateral views, I measured body pitch as the position of the antero-posterior axis of the body relative to horizontal, as inferred from the plumb line, and head pitch as the angle from a line perpendicular to the plane of the back of the head (head axis) to the body axis (Fig. 1a). For frontal views, I measured body roll as the angle of the plane bisecting the wings relative to the plumb line and head roll as the angle from a line bisecting the head dorsoventrally to the wing plane (Fig. 1b). For overhead views, I measured body yaw as the angle between the line showing the compass bearing the male was facing and the line from the male to the marker showing the direction to the sun, and head yaw as the angle between the plane of the back of the head and the long axis of the body. Because the analysis of these photographs generated a new data set, the sample sizes in Table 1 do not correspond to those reported for the analysis of head posture.

**Flight Paths**

To describe the flight of *A. leilii* in male perching areas, I measured flight altitude for two groups of *A. leilii*: intruding conspecifics as they flew into and through a male’s perching area, and resident males on flights around their perching area in which they were neither descending to perch nor chasing a conspecific. Flight altitude was measured to the nearest 0.1 m with reference to a vertical pole marked at 0.25 m intervals and placed within 1 m of a perched male. In addition,
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![Fig. 1: Diagrams showing how body pitch and roll measurements and the measurements of head posture relative to the body were made for perched *A. leilia* males. (a) Side view of a male, with body pitch (bp) being the angle between the antero-posterior body axis (BA) and horizontal (H), and head pitch relative to the body (hp) being the angle between the antero-posterior head axis (HA; perpendicular to the plane of the back of the head) and the body axis. (b) Front view of a perched male, with body roll (br) being the angle between the wing plane (WP) and vertical (V), and head roll relative to the body (hr) being the angle between the dorso-ventral head midline (HM) and the wing plane.]

*Table 1:* Three-dimensional body posture of perched *A. leilia* males as a function of perch location (on or off ground) and wing position (open or closed). Body pitch angles are relative to horizontal, body roll is relative to vertical, and body yaw is relative to the solar azimuth. The results for all body posture parameters deviate significantly from a random circular distribution (Rayleigh test, p < 0.001). Abbreviations: n, sample size; AD, angular deviation

<table>
<thead>
<tr>
<th>Perch location</th>
<th>Wing position</th>
<th>n</th>
<th>Body posture parameter</th>
<th>$\bar{\theta} \pm AD$</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>On ground</td>
<td>Open</td>
<td>23</td>
<td>Pitch</td>
<td>30.0 ± 6.78</td>
<td>20–40</td>
</tr>
<tr>
<td></td>
<td></td>
<td>23</td>
<td>Roll</td>
<td>0.43 ± 5.12</td>
<td>−9–10</td>
</tr>
<tr>
<td></td>
<td></td>
<td>23</td>
<td>Yaw</td>
<td>177 ± 25.9</td>
<td>126–242</td>
</tr>
<tr>
<td>On ground</td>
<td>Closed</td>
<td>25</td>
<td>Pitch</td>
<td>25.6 ± 8.88</td>
<td>14–51</td>
</tr>
<tr>
<td></td>
<td></td>
<td>24</td>
<td>Roll</td>
<td>−0.12 ± 7.68</td>
<td>−17–14</td>
</tr>
<tr>
<td></td>
<td></td>
<td>24</td>
<td>Yaw</td>
<td>182 ± 39.6</td>
<td>78–302</td>
</tr>
<tr>
<td>Off ground</td>
<td>Closed</td>
<td>39</td>
<td>Pitch</td>
<td>−6.53 ± 16.6</td>
<td>−52–41</td>
</tr>
<tr>
<td></td>
<td></td>
<td>39</td>
<td>Roll</td>
<td>−5.67 ± 20.2</td>
<td>−34–50</td>
</tr>
<tr>
<td></td>
<td></td>
<td>37</td>
<td>Yaw</td>
<td>134 ± 57.5</td>
<td>44–356</td>
</tr>
</tbody>
</table>
general observations were made on the flight paths of conspecifics relative to males and their perches.

**Statistical Analysis**

All angular measurements were made to the nearest degree. Statistical evaluation of all angular measurements, including the calculations of means, angular deviations, tests for uniform distribution and correlation coefficients, were performed using the procedures described in Batschelet (1981). All $r^2$ values given are circular correlation coefficients. Other statistical summaries and comparisons were performed by hand or using Corel Quattro® Pro Version 7 (Corel Corporation, Ottawa, ON, Canada). All statistical comparisons were evaluated at the 0.05 level of significance.

**Results**

**Body Posture Versus Perch Substrate**

Table 1 summarizes postural data for the three most common combinations of perch location and wing position seen in perched males: perched on the ground with the wings open, perched on the ground with the wings closed, and perched off the ground with the wings closed (Rutowski et al. 1994). During a typical morning, males first perch on the ground with their wings open (dorsal basking; Kingsolver 1985), but then at higher temperatures perch with their wings closed over their back to reduce heat load. Males changed to perches off the ground at still higher temperatures and most were then perched with the wings closed. Males that were perched on the ground were categorized into those with the wings closed and those with the wings open to reveal effects, if any, of wing position on body posture.

For all three groups of males, body pitch was non-randomly distributed (Table 1). Wing position had no effect on body pitch when males perched on the ground (Watson–Williams test, $p > 0.05$), but the body pitch of both groups of males on the ground was significantly different from that of males perched off the ground (Watson–Williams test, $p < 0.0005$). In general, the body of a male on the ground was pitched up at about 25–30° relative to horizontal, whereas males off the ground were pitched down about 6–7° below horizontal.

Regardless of perch location or wing position, males perched with their dorso-ventral axis close to the vertical plane (roll = 0°; Table 1). Body roll did not differ significantly among any of the groups (Watson–Williams test, $p > 0.05$).

The results for body yaw relative to the solar azimuth were perplexing (Table 1). Males perched on the ground were significantly oriented facing away from the sun as previously reported (Rutowski et al. 1991). However, contrary to previous results, when males perched off the ground they oriented significantly non-randomly at a mean of 134° away from the sun. This was significantly different from both groups of males perched on the ground (Watson–Williams test, $p < 0.05$). However, because this mean angle is not 180° away from the sun and
because the angular deviation and range associated with this mean are much larger than for the body yaw of males perched on the ground, this appears to be a weak pattern at best.

**Body Roll Changes with Body Yaw**

The observed variation in body roll may be explained in the following way. Previous studies of thermoregulation in butterflies suggest that closing the wings over the back minimizes the surface area of the wings and body exposed to solar radiation and thereby heat load when ambient air temperatures are high (Kingsolver 1985; Heinrich 1993). To further minimize wing surface exposed to the sun, when yaw is not directly away from the sun, body roll may be adjusted so that the edges of the wings closed over the back point at the sun. Consistent with this idea, body yaw and roll in males perched with the wings closed were significantly correlated (Fig. 2: on ground, $r^2 = 0.164$, $n = 24$, $p < 0.05$; off ground, $r^2 = 0.167$, $n = 37$, $p < 0.005$). If a male with his wings closed was turned facing to the left of the bearing directly away from the sun, his body was likely to be rolled to the left (counterclockwise) and vice versa.

Do males point their wings directly at the sun? That is, given his body yaw and the current solar elevation, is a male’s body roll precisely adjusted to minimize the solar radiation hitting the wings? Using equations in Findlay et al. (1983), I calculated for each male the expected body roll that would point his closed wings straight at the sun given his body yaw and the solar elevation measured at the time the postural observations were made. I then compared this expected body roll to

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**Fig. 2:** Relationship between body roll and body yaw relative to the solar azimuth for males perched on and off the ground
the observed body roll using rank circular correlation (Fig. 3). Observed and expected values were not significantly correlated for males on the ground ($r^2 = 0.054$, $n = 24$, $p > 0.4$), but they were for males off the ground ($r^2 = 0.182$, $n = 35$, $p < 0.005$). These results suggest that, although males that are not facing directly away from the sun do roll their body toward the sun, only for males perched off the ground is the magnitude of the roll strongly determined by their orientation relative to the sun.

Head Posture Relative to Body Versus Perch Substrate

During the observations of body posture, I noted that both body pitch and roll varied considerably and that the orientation of the head relative to the body might vary with body posture in a way that suggested body orientation alone was

Fig. 3: For males perched (a) on and (b) off the ground, a comparison of observed body roll with that expected if, given the solar elevation and a male’s yaw relative to the sun, his wings were pointed directly at the sun. Each data point shows the expected and observed body roll for a male perched (wings closed) in a particular orientation relative to the sun. In each graph, the solid line shows the expected relationship if observed roll perfectly matched expected roll.
not a good indicator of the alignment of the visual system in space. Because wing position had no effect on male body position, I treated all males perched on the ground as a single data set in this part of the analysis.

Head roll was negatively correlated with body roll (Fig. 4). This means that the orientation of the head is adjusted so that the dorso-ventral axis of the head remains closer to vertical than if the adjustment was not made. This compensatory counter-rotation of the head occurs in both males perched on the ground ($r^2 = 0.284, n = 20, p < 0.01$) and males perched off the ground ($r^2 = 0.696, n = 22, p < 0.001$), although the compensation is more complete for males on elevated perches.

Similarly, when perched off the ground, head pitch is significantly negatively correlated with body pitch (Fig. 5; $r^2 = 0.620, n = 22, p < 0.001$). This has the effect of keeping the equator of the head closer to horizontal than it would otherwise be. This relationship was not observed in males perched on the ground (Fig. 5; $r^2 = 0.140, n = 18, p > 0.05$).

No adjustment of head yaw was found as orientation relative to the sun varied when males were perched both on the ground ($r^2 = 0.076, n = 21, p > 0.05$).

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**Fig. 4:** Relationship between body roll and head roll relative to the body for males perched (a) on and (b) off the ground. The slope of the solid line is that expected if head roll relative to the body was the reciprocal of body roll. This relationship would keep the head midline vertical independent of body roll.
Fig. 5: Relationship between body pitch and the pitch of the head relative to the body for males perched on and off the ground. The solid line shows the relationship expected if the anterio-posterior head axis was always horizontal no matter what the body pitch, i.e. head pitch relative to the body was the reciprocal of body pitch.

and off the ground ($r^2 = 0.098$, n = 19, p $> 0.05$). Moreover, observations with the naked eye and motion picture films made at 70 frames s$^{-1}$ revealed no tracking of targets (rock, intruding males, or females) prior to departure from the perch.

**Flight Paths**

In general, the flight paths of conspecifics were within 2–3 m and straight along the face of vegetation near or on which males perched. The flight altitude of such conspecifics averaged ($\pm$ SD) 0.89 $\pm$ 0.26 m (range = 0.5–1.5 m, n = 23). Presumably this includes both males and females, as the sex of these butterflies cannot be reliably determined when they are on the wing. Resident males on patrol flights in their perching site flew 0.80 $\pm$ 0.17 m (range = 0.5–1.1 m, n = 29) above the ground. The flight altitudes of these two groups did not differ significantly ($t = 1.39$, df = 37, p $> 0.15$). Also, the flight altitude of these groups combined did not differ significantly from the average height of males perched off the ground (0.87 $\pm$ 0.23, n = 52, Rutowski et al. 1991; $t = 1.19$, df = 108, p $> 0.2$).
Discussion

Body Posture and Perch Location

A number of patterns were evident in the relationship between body posture and perch location in *A. leilia*. Body pitch changed from up 20–30° when males were on the ground to down a few degrees when they were perched on a plant. Why males perch with these specific body pitches in these locations has yet to be determined.

On the ground perched males tended to face away from the sun, i.e. their yaw relative to the sun’s azimuth averaged 180°, but off the ground this tendency was weak or non-existent, as reported previously (Rutowski et al. 1991). The adaptive advantage of facing away from the sun when on the ground is not known.

Body roll averaged 0° in both perch locations. Although it changed with orientation relative to the sun, there is no evidence here that males are lateral basking, i.e. placing the plane of the closed wings perpendicular to the sun’s rays to maximize solar heat gain (Casey 1981; Kingsolver 1985; May 1985; Heinrich 1993). Instead, the wings when closed were pointed at the sun, albeit with little precision, which supports the view that males adjust body roll in ways that reduce solar heat gain. However, the lack of precision is consistent with the results of experiments with thermocouple-implanted models, which suggest that the orientation of the wings relative to the solar rays does not have large effects on the thermal equilibrium attained by these butterflies (Rutowski et al. 1994).

There are two points about the proximate determinants of these patterns in body posture. First, body posture varied around all three axes, but the influences of variation in perch slope and topography on body posture are not known. Secondly, preliminary observations suggest that males fine-tune their body posture during the first few seconds after alighting on the substrate. Hence, the observed differences in the body posture of males on different substrates appear to be due to active adjustments and are not just passive consequences of differences in how males land on different substrates.

Head Position Relative to Body

Although body pitch and roll vary in *A. leilia*, compensatory adjustments in the orientation of the head relative to the body render the orientation of the head relative to gravity far less variable. The mechanisms underlying the positional relationships between head and body have been studied extensively in insects (for reviews, see Hengstenberg 1992, 1993). Both induced and self-generated rotations of the body during locomotion produce compensatory movements in the head that are thought to help stabilize the visual field and minimize motion-induced blurring of images in the eye. Also, the head may be turned voluntarily relative to the body when visually tracking an object of interest. The observed compensatory head positions in *A. leilia* are not a consequence of locomotion or tracking but are more static and perhaps anticipate where conspecifics are likely to appear (see below). What is the source of information about the direction to the horizon used to
position the head? Perhaps the strongest possibility is a dorsal light response in which the top of the head is pointed at the brightest region of the visual field (i.e. the sky) (Hengstenberg 1993).

The compensatory head orientations along with body posture and perch location have implications for how the visual system is oriented relative to conspecific flight paths while the males perch. First, as shown in the ‘Results’ section, males perch off the ground at a height above the ground similar to the typical paths of conspecifics flying through perching areas, and males face out of the plant which directs the frontal acute zone toward that part of space where conspecifics are likely to appear. Secondly, the compensatory rotations of the head about both roll and pitch axes will tend to keep the equatorial acute zone of the eyes in the same plane as the likely flight paths of passing conspecifics. Thus, in this perch location, placement and orientation of the visual system appear to maximize the probability of detecting passing conspecifics.

On the other hand, when males perch on the ground the situation appears less optimal. Although males compensate at least for body roll by head counterrotation when on the ground, the head faces up at an angle of about 20–30° relative to the horizon and so the equatorial and frontal acute zones intersect the plane of conspecific flight paths. On the ground, males perch facing away from the sun, but their compass position relative to the nearest vegetation is random (Rutowski et al. 1991); so, there is no typical direction in which males face relative to the potential flight paths of conspecifics. Hence, for a male on the ground, conspecifics’ flight paths may often pass through parts of the visual field where acuity is not highest. This is in sharp contrast to the situation for males perched off the ground.

Perches off the ground may therefore be better locations for detecting passing conspecifics than are perches on the ground. However, this conclusion rests on untested assumptions about the structure of the visual field of A. leilia males, and fails to consider that the backgrounds against which conspecifics are viewed are probably very different depending on perch location. From the ground, conspecifics are likely to be viewed as dark objects against the bright, uniformly colored sky. In comparison, from elevated perches, conspecifics will be viewed against spectrally diverse backgrounds of vegetation, soil and sky that have a brightness similar to that of flying butterflies. Uniform, brightly lit backgrounds are generally regarded as better for the detection of small moving objects (Hailman 1977; Labhart & Nilsson 1995) and this advantage may override considerations of visual field placement. To resolve this matter, I am currently engaged in experimental analyses of factors that affect detection of conspecifics by perched males, as well as studies of visual field structure in these butterflies.

The results of this study suggest that when, for thermoregulatory reasons, the perch preferences of males change, a proximate consequence is that the probability of detecting conspecifics changes. A more difficult question has been how mate-locating behavior, thermal tolerances, and visual system structure have interacted in evolutionary time. Males of A. leilia engage in perching to locate mates for only about 3 h each day (Austin 1977; Rutowski & Gilchrist 1988; Rutowski et al. 1996). However, these insects must deal with the thermal environment and
use their eyes in a variety of contexts throughout the entire day. Hence, thermal tolerances and visual system structure are not expected to mirror precisely the demands of mate location alone. In this case, mate detection appears to be constrained by thermal tolerances and visual system structure, which suggests that the overall costs of changing thermal tolerances or visual system structure are higher than the benefits that might accrue from not having to change perches during the morning activity period. However, within the context of these thermal and morphological constraints, the perch, body and head orientation preferences appear to have evolved to be perch-height dependent and to optimize placement of the visual system.

Although there are many species of insects in which males use a sit-and-wait strategy to locate mates, a striking diversity exists in exactly how and where they perch (Thornhill & Alcock 1983), especially among the butterflies (Rutowski 1991). For example, while A. leilia males that perch on vegetation orient for the most part horizontally, facing out of and away from the vegetation, there are other butterflies that consistently perch off the ground on nearly vertical surfaces with either their head down (Hamadryas, Otero 1990; other Asterocampa, Rice 1999) or their head up (Battus philenor, Rutowski et al. 1989; Coenonympha pamphilus, Wickman 1985; Rutowski, pers. obs.). This diversity may prove to be fertile ground for comparative tests of the evolutionary interactions between visual system structure, thermal biology and behavior.

Acknowledgements

Keith Fales, Ofer Eitan, Thad Leffingwell and Mike Demlong provided assistance in the field and laboratory. Barbara Terkanian drew the original illustrations for Fig. 1. Helpful comments on an earlier version of this manuscript were provided by Cole Gilbert. Financial support was provided by grants from the Arizona State University College of Liberal Arts and Sciences and National Science Foundation (BNS 9723160). For all this help, I am grateful.

Literature Cited


Received: June 17, 1999

Initial acceptance: September 18, 1999

Final acceptance: November 24, 1999 (J.-G. Godin)