

Overnight perching aggregations of the aposematic Pipevine Swallowtail (*Battus philenor*: Lepidoptera: Papilionidae): implications for predation risk and warning signal use

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Abstract. Aposematic butterflies, those that are unpalatable and warningly colored, may aggregate during overnight perching to reduce the risk of predation. The conditions under which they aggregate and the postures assumed by perching butterflies may indicate how aggregations are a useful defense against predators, including the use of the warning signal. Additionally, studying these aggregations allows for a better understanding of the conditions under which their warning signal may be used. We investigated the overnight perching behavior of the aposematic Pipevine Swallowtail (*Battus philenor*) in both the field and in an enclosure. We found that the butterflies begin perching very close to sunset, when their blue iridescent warning coloration may still be effective, and the aggregations consist of between two and 21 individuals, which may accelerate warning signal learning by naïve predators. In both the field and enclosure, aggregated butterflies perched with the plane of their wings surfaces in parallel which suggests they perch in ways that increase the size of the warning signal. Additionally, *B. philenor* individuals perch in conspicuous locations which may facilitate warning signal detection, learning, and recognition. Our investigations of *B. philenor* aggregations lend support to the hypothesis that aposematic butterflies aggregate to increase the effectiveness of the warning signal against visually hunting predators.

Keywords: Warning coloration, aggregations, perching, *Battus philenor*

INTRODUCTION

Aggregations of aposematic animals, such as the overwintering and overnight aggregations of Monarch and *Heliconius* butterflies, are thought to provide enhanced protection against visually hunting predators (e.g. Turner, 1975; Sillén-Tullberg & Leimar, 1988; Gamberale & Tullberg, 1998). When aposematic butterflies aggregate, individual risk of predator attack can decrease through several mechanisms (Mappes & Alatalo, 1997; Gamberale & Tullberg, 1998; Lindström *et al.*, 1999). First, regardless of whether a predator's association of unpalatability with warning coloration is learned or innate, aggregations

can present a larger and, so, more effective warning signal (Gamberale & Tullberg, 1996a,b; Gamberale-Stille & Tullberg, 1999; Forsman & Merilaita, 1999). Second, aggregations may facilitate learning by naïve predators by 1) providing the opportunity for predators to see warningly colored individuals during or immediately following perception of distastefulness (Gagliardo & Guilford, 1993; Alatalo & Mappes, 1996), or 2) allowing predators to sample more prey in each encounter (Sillén-Tullberg & Leimar, 1988; Riipi *et al.*, 2001). By accelerating the learning process, fewer butterflies will be attacked and the individual risk for butterflies in the aggregation is reduced ("dilution effect"; e.g. Bertram, 1978; Foster & Treherne, 1981). All these mechanisms rely on the predators seeing the butterflies and therefore may not be in force after dark for overnight aggregations.

Aggregations may also reduce the risk of attack by predators without the influence of the warning coloration. A naïve predator that attacks a group of aposematic butterflies may leave the aggregation after determining that prey are unpalatable (Alatalo & Mappes, 1996; Riipi *et al.*, 2001) and the risk of an individual being attacked is again reduced through the dilution effect. Predators will also be less likely

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to encounter aggregated prey than solitary prey scattered throughout an area, because a finite amount of prey aggregated into larger groups will form fewer groups, decreasing the chance of encountering prey (Turner & Pitcher, 1986; Ioannou *et al.*, 2011).

With these potential benefits in mind and in order to better understand the conditions under which warning signals are used, we made observations on the dynamics and structure of overnight aggregations in the Pipevine Swallowtail butterfly, *Battus philenor* (Linnaeus, 1771). We suspected that *B. philenor* adults may aggregate because of their unpalatability, anecdotal reports of overnight aggregations (Scott, 1992; J. Fordyce and L. Gilbert, pers. comm.), and reports of feeding aggregations (Otis *et al.*, 2006). In March 2009, during a search for perching adult *B. philenor*, we observed overnight aggregations in the Mazatzal Mountains of Arizona, USA, and used this as an opportunity for further study of *B. philenor* overnight perching over two months. However, field observations were limited by access to the butterflies and so we expanded our observations and understanding of the aggregations by studying *B. philenor* perching behavior in an enclosure.

B. philenor is distasteful to predators due to the sequestration of aristolochic acids by the larvae (Sime *et al.*, 2000; Fordyce *et al.*, 2005). The ventral hindwing surface functions as a warning signal (Brower, 1958; Codella & Lederhouse, 1990) and displays both iridescent blue and orange spots (Fig. 1; Rutowski *et al.*, 2010). Both the iridescent blue and orange spots are recognized by predators as a warning signal and the most common predators of *B. philenor* in Arizona are insectivorous birds (Pegram *et al.*, unpublished observations).

We aimed to better understand how aggregations may reduce the risk of predation as well as the environmental conditions under which the warning coloration may be used by pursuing answers to four questions. First, do aggregations form and disband at times of day when visually hunting predators are active and when the warning signal is effective? If so, we expect that butterflies would aggregate before sunset or when ambient light is still available and disband after sunrise. Second, do aggregations form in locations that facilitate learning and recognition? To facilitate learning and recognition, we expect butterflies to perch in locations that make them conspicuous. Third, do butterflies position themselves in a way that increases the size of the warning signal? If so, we predict that the butterflies will orient themselves so that more wing surfaces are visible to an approaching predator. Finally, does the size of aggregations indicate that the butterflies aggregate to facilitate warning signal learning? If this



Figure 1. A *B. philenor* perched after sunset and illuminated with only indirect solar radiation. Even without the solar orb present in the sky, the blue iridescence of the ventral hindwing is visible.

is the case, we expect that there are more butterflies in aggregations than the number of butterflies required to be sampled by the predator for the predator to learn. Answers to these questions will help us to determine why these animals aggregate and how aggregations may influence the effectiveness of the warning signal.

MATERIALS AND METHODS

Field observations

We observed overnight aggregations of *B. philenor* from March to May 2009 at the confluence of Mesquite Wash and Sycamore Creek in the Mazatzal Mountains of Arizona, USA (N 33°43.784', W 111°30.997'; Fig. 2). Here, the riparian vegetation includes Sycamore (*Platanus wrightii*), Willow (*Salix* spp.), and Cottonwood (*Populus fremontii*) trees. The streamside area in which we made our observations was approximately 9000 m². On observation days, we arrived at the field site before sunrise or sunset and visually scanned trees with binoculars until we spotted *B. philenor* individuals.

Because some of the benefits of aggregation, such as increased signal size, can be realized with only two individuals, we considered two or more *B. philenor* butterflies perched together to be an aggregation. For each aggregation found, we determined how many individuals were clustered together (within a cubic



Figure 2. Riparian forest at the confluence of Sycamore Creek and Mesquite Wash in Arizona where aggregations of *B. philenor* were observed.

area of about 2 m on a side) and recorded the time at which the aggregation was first observed. On two mornings, we also recorded the time at which each individual left the aggregation. We obtained the sunrise or sunset time for each observation day from the NOAA calculator (<http://www.srrb.noaa.gov/highlights/sunrise/sunrise.html>), and compared all observed times to sunrise (for morning observations) or sunset (for evening observations).

We estimated height from the ground to the lowest butterfly for each aggregation using a known height as a reference. For 20 aggregations, we observed the orientation of each butterfly with binoculars and described it as the compass bearing of the azimuth of the line going from the wing tips to the body of the butterfly. This was always done before we observed any movement in the morning and after no more movement was observed in the evening.

To better understand how aggregations form and the activity around the time in which they perch, on four evenings we also counted individuals flying amongst the trees (at least 3 m above ground) every 15 minutes from a distant observation point that allowed us to observe the whole stand of trees. We stopped recording around sunset to observe the aggregations from a closer vantage point and take the above measures. Throughout the study, we also took notes on any interactions we observed among the butterflies.

Enclosure study

Due to limitations of the field study, in the summer of 2011 we also investigated the perching aggregations of *B. philenor* in a 10 m wide x 24 m long x 4.5 m high enclosure, the Maxine and Jonathan Marshall Butterfly Pavilion at the Desert Botanical Garden in Phoenix, AZ, USA. This enclosure is covered with 65% shade cloth and contains a large variety of vegetation and nectar sources, including Mexican Orchid trees (*Bauhinia mexicana*) and *Lantana* spp., but no hostplant. We populated the pavilion with lab-raised *B. philenor* that were either collected as eggs or larvae from the field site described above, or as eggs from females that mated in this pavilion and oviposited in the lab. Animals were raised to adulthood in an environmental chamber as described in Rutowski *et al.* (2010). We released individually marked *B. philenor* adults into the pavilion within 0-4 days of eclosion, and maintained a population of 6-20 individuals in the enclosure throughout the study. We always released butterflies at least two hours before sunset. The butterflies were an unstructured mix of males and females, and we recorded the sex of each before release.

To facilitate the assessment of the distribution of perched butterflies within the pavilion, we created a map of the interior of the enclosure, plotted on it the

location of perched individuals, and noted whether they perched in aggregations or individually. As with the field study, we defined an aggregation as two or more individuals perched within a cubic area of approximately 2 m on a side.

We measured the height of each perched individual with a tape measure. Also, as in the field we described the orientation of perched butterflies using the compass bearing of the azimuth of the line going from the wing tips to the body of the butterfly. These measurements in the enclosure are likely to be more accurate than those made in the field because we were able to more closely observe the butterflies.

We also focused on the formation and disbanding of aggregations. On five evenings, we plotted the location and recorded the height of every perched individual every five minutes, starting a half hour before sunset and ending a half hour after sunset. To understand how the aggregations disband, on five mornings, we recorded when each individual left the perch. We started this at sunrise and ended one hour after sunrise. In addition, we made qualitative observations on flight behavior and interactions among individuals forming aggregations at night or disbanding in the morning.

Statistical analysis

To determine whether perching individuals in the field and enclosure were oriented in a haphazard fashion we used circular statistics (Batschelet, 1981) using Oriana v.3 (Kovach Computing Services, Anglesey, Wales). We calculated: the mean angle; the Rayleigh statistic, which determines if the orientations are significantly different from random orientations; and the *V* test, which tests whether the butterflies were significantly clustered around specific compass bearings, with 180° and 0° as the given angles. We chose 180° and 0° as the given angles because we hypothesized that the butterflies may be perching with their wing surfaces perpendicular to the rays of the rising and setting sun. For the enclosure, we first sorted the orientation observations into those that were taken from aggregations and those that were taken from butterflies perched individually. We then calculated the mean orientation angle for each individual and ran the tests described above on these mean angles to control for multiple measurements on the same individual.

We determined whether height and propensity to aggregate were consistent among individuals using repeatability calculations. We calculated the repeatability (or *r*) and *p*-values (with a significance of 0.05) using one-way ANOVAs and the calculations described in Lessells and Boag (1987). To determine

whether individuals were consistent from day to day in their orientation, we used second-order circular statistics on the mean vector lengths, because linear statistics are not appropriate for angular measurements (Batschelet, 1981). We calculated the mean vector length for each individual using Oriana v. 3 (Kovach Computing Services, Anglesey, Wales) and then compared the distribution to the circular uniform distribution using the Kolomogorov's one-sample test (Batschelet, 1981).

The number of males and females in the enclosure on any given day was not equal. Therefore, to determine whether males and females perch in aggregations at the same rate, we used a t-test to compare the observed number of males in each aggregation to an expected number of males in each aggregation based on the sex ratio in the enclosure and the total number in the aggregation.

RESULTS

Field observations

We recorded data on 27 natural aggregations from 12 March – 5 May 2009 during 13 field visits (six in the early morning and seven around sunset). Nine of the aggregations were found at dusk and 18 were found at dawn. All aggregations were either found at the top or the outer edges of deciduous trees (Fig. 3). Heights ranged from 5.4 m – 10.6 m (mean = 7.9 m). Individuals started arriving at the site and flying around about 1 hour before sunset, and started to settle right around sunset. Counts of individuals in each aggregation ranged from 2-21 (mean = 5.8). Additionally, we found 10 individuals perched alone (10.5% of all butterflies observed), but our efforts in the field were focused on finding aggregations and so could easily have missed many solitary perchers. By 5 May, the trees had leafed out to an extent that made it difficult to scan for perched butterflies. We also found aggregations during future trips to the field site during other parts of the year when *B. philenor* was active (approximately March - October) suggesting that aggregations are not seasonal.

Aggregated butterflies measured in the field (*n*=85), were significantly oriented with the mean at 215° (Rayleigh: $z=13.9$, $p<0.001$; Fig. 4). We also did a *V*-test, which measures whether the observed orientations are clustered around a given angle. The *V*-test for 180° was significant ($p<0.001$) while the *V*-test for 0° was not ($p>0.999$), which means that the orientations of the butterflies were significantly clustered around 180°, that is their wings tended to point to the north.



Figure 3. An aggregation of six *B. philenor* high in a tree in the morning just before the animals disbanded. Note that three of the animals are dorsal basking.

Enclosure study

In June and July of 2011, we observed the overnight perching behavior of *B. philenor* in 38 visits to the enclosure on 33 different days, on some days visiting both in the morning and the evening. Our observations in the enclosure, as in the field, revealed individuals perching within aggregations as well as individuals perching alone (not within about 2 m of another butterfly). The mean percentage of individuals aggregating was 43% over all nights with a maximum of 65% on 21 July 11 and a minimum of 0% on 27 June 11 when only six individuals were present in the enclosure. The mean size of aggregations was 2.8, ranging from two to six individuals, and aggregations were composed of both males and females. The sex ratio of these aggregations was not biased toward either sex (t-test, $p = 0.464$).

Butterflies perched in aggregations ($n = 57$ individuals, 144 observations) were significantly oriented (Rayleigh test $z = 8.398$, $p < 0.001$) with a mean angle of 227.14° (Fig. 4). Also, as in the field, the orientations of aggregated individuals were significantly clustered around 180° (V-test, $v = 0.261$, $p = 0.003$) but not 0° ($v = -0.261$, $p = 0.997$), that is, with their wings pointed toward the north. Interestingly, butterflies perched individually (not in aggregations; $n = 57$ individuals, 173 observations) were not significantly oriented overall (Rayleigh test $z = 0.402$, $p = 0.669$; Fig. 4). In the enclosure, butterflies perched at heights ranging from 0.05–3.9 m (mean = 2.02 m), much lower than in the field and no doubt constrained by the height

of the pavilion's roof. As in the field, aggregations were found at the top or outer edges of trees and plants (Fig. 5), but were also found on the shade cloth and other structures within the pavilion.

In the enclosure, we could identify individuals and therefore determine repeatability or consistency in perching behavior among individuals. We found height ($r = 0.967$, $p < 0.001$) and whether they perched in aggregations or individually ($r = 0.814$, $p < 0.001$) to be consistent among individuals. However, orientation angle was not consistent among individuals (Kolmogorov's one-sample test; $T = 0.717$, $p = 0.762$).

We noticed that during their search flights in the evenings, individuals often landed on multiple perching spots before settling on a final perch between a half hour before sunset and a few minutes after sunset. Movements varied from slightly shifting their orientations to leaving for a new perching location up to several meters away. The mean number of times an individual landed on a perch before their final location was 3.1 (min = 0, max = 6). We also noticed that individuals already perching within an aggregation sometimes left after another butterfly arrived and flew around the perch, interacting with those already perched. Our observations ended about 45 minutes after sunset and, on 13 nights, we made observations the following mornings. On two occasions out of the 13, we found that the individual moved overnight and, on eight occasions, we were not able to find the individual anywhere in the pavilion and suspected they were attacked overnight. All of these individuals were perched alone. Predation may have been due to lizards (*Sceloporus* spp.) or roof rats (*Rattus rattus*), which were both spotted in the enclosure.

In the mornings, individuals opened their wings to bask, made small movements, or took off from their perches starting from a few minutes to one hour after sunrise. Most individuals moved to a different perching location after leaving their original night perch. We counted the number of perches until an individual started flying continuously or began feeding. The mean number of perches that individuals made after leaving their night perch was 1.4 (min = 0, max = 4). Aggregations disbanded one individual at a time, similar to how they formed. The shortest time from the first individual leaving to the last departure was 17 minutes for an aggregation of two individuals and the longest time from the first individual leaving to the last departure was 48 minutes for an aggregation of four individuals. However, we never observed any interactions between individuals within an aggregation during disbanding.

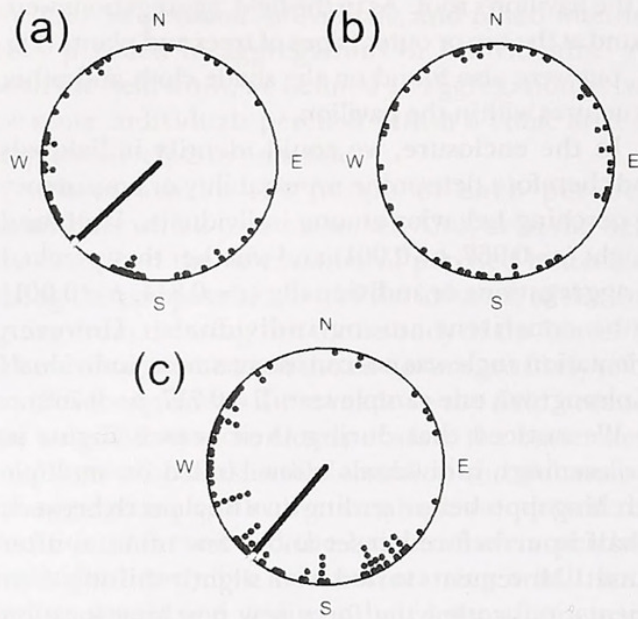


Figure 4. Orientation of a) aggregated butterflies in the enclosure, b) butterflies perched individually in the enclosure, and c) aggregated butterflies in the field. For the field observations, each dot represents one butterfly orientation, measured as the azimuth of the line going from the wing tips to the body. For the enclosure observations, these are averaged for each individual, so that each dot represents an individual. Butterflies in aggregations were significantly oriented (mean vector = 227° in (a) and 215° in (c)). The azimuths of the sunsets during measurement periods ranged from 270° to 299° and from 62° to 90° for sunrise.

DISCUSSION

In this study we set out to answer four questions about *B. philenor* aggregations and how they might influence predation rates: when and where the butterflies aggregate, the way the butterflies position themselves, and the size of the aggregations.

Do aggregations form and disband at times of day when visually hunting predators are active and when the warning signal is effective?

Insectivorous birds, the most common predators of *B. philenor* in Arizona, are active throughout the day, but may hunt more intensely around sunset or sunrise (e.g. Morton, 1967; Hutto, 1981). We found that *B. philenor* started perching around sunset but left their perches well after sunrise, which may indicate they are perching when their predators are most active.

The timing of the formation and disbanding of aggregations is likely to influence the effectiveness of warning coloration. The transmission and perception

of color signals are influenced by light environment (Endler, 1990; 1993). Under low light conditions, color signals become difficult to discriminate by birds (Cassey, 2009). Therefore, whether or not the solar orb is still present in the sky influences if and how predators learn or recognize the warning signal. The formation of aggregations around sunset or after the sun had set could limit the effectiveness of the visual signal. However, during field observations, the iridescent blue of the ventral hindwing was visible to the human eye even for some time after sunset but while there was still skylight (Fig. 1). This may be an advantage of displaying an iridescent warning signal. We also found that aggregations disbanded well after sunrise, so the warning coloration may be more effective at deterring insectivorous birds in the morning than in the evening.

Additionally, aggregating individuals may benefit from reduced predation through dilution or fewer predator encounters, as discussed earlier. Therefore, even though the aggregations are forming after sunset and diffusely reflecting warning colors may not be effective, iridescent warning colors may still be effective and aggregations may still reduce the risk of predation.

Do aggregations form in locations that facilitate learning and recognition?

A more conspicuous and larger signal may facilitate predator learning and recognition of a warning signal (Guilford, 1986; Gamberale & Tullberg, 1996b; Gamberale-Stille & Tullberg, 1999; Forsman & Merilaita, 1999; Gamberale-Stille, 2001; Prudic *et al.*, 2007). We found that *B. philenor* aggregations in the field average 5.8 individuals and form very high in trees. The area in which our observations took place is surrounded by mountains, and the sunshine clearly hits the tops of the trees first. This may allow for both the diffusely reflecting and iridescent warning colors to be effective earlier, as light becomes available to reflect off of the wings. Higher perching locations may also discourage predation by nocturnal, ground dwelling animals that may not be visually oriented and therefore not deterred by the warning coloration. In the enclosure, the average height of perching was only about 2 m off the ground but was likely constrained by the fact that the maximum height in the enclosure is only 4.5 m. We also found that aggregations were often formed on the outer edges of trees, which may also increase conspicuousness and, thus, warning signal effectiveness.

Despite perching in locations that may facilitate learning and recognition of warning signals through increased conspicuousness and signal size, microclimate could also be a factor driving *B. philenor* perch

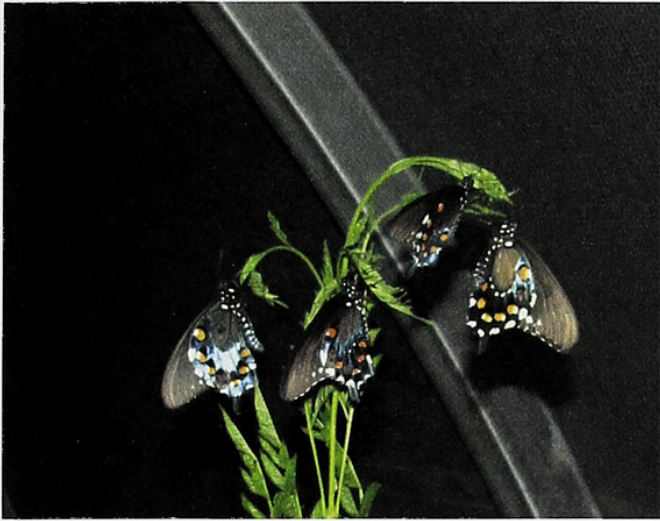


Figure 5. An aggregation of four *B. philenor* in the enclosure taken in the evening.

selection and aggregations. Other butterfly species (e.g. *Danaus plexippus*) choose their perching location based on temperature and protection from wind and precipitation (Brower *et al.*, 2008; Salcedo, 2010). In *B. philenor*, perching high in trees may allow the butterflies to start basking earlier and therefore leave their perch, where they are most susceptible to predation (Rawlins & Lederhouse, 1978; Lederhouse *et al.*, 1987), earlier. An indication that *B. philenor* individuals are seeking specific conditions for perching is found in their evening activity. In the field and enclosure, we regularly observed interactions between perched and patrolling individuals in the trees during the evening. Individuals often settle on several perches before selecting their overnight perch. In the enclosure, most individuals landed on at least one perch before settling on a perch overnight. In the mornings, there is less interaction, but the butterflies still land on several perches before becoming fully active.

Do butterflies position themselves in a way that increases the size of the warning signal?

Butterfly orientation can have several implications for signaling behavior because the iridescent color on the wings will only be visible from certain angles and predators approaching on a path in the plane of the wing surface will not see any of the wing colors. We found that butterflies both within and among aggregations were similar in their body orientation in both the field and enclosure, but that non-aggregated butterflies were not. This suggests that butterflies may aggregate and position themselves to increase the size and, therefore, effectiveness of the warning signal. If

all of the butterflies in an aggregation are facing in the same direction, the warning signal they display is much larger to any potential predator approaching from a direction perpendicular to the plane of the wings and, in general, a larger warning signal is a more effective signal (Gamberale & Tullberg, 1996b; Gamberale-Stille & Tullberg, 1999; Forsman & Merilaita, 1999). An alternative hypothesis is that *B. philenor* butterflies could also be orienting themselves in order to increase the sun rays hitting the wings for warmth, but then we would expect to find that all perched butterflies significantly orient themselves to a direction perpendicular to the sun. This was not the case as butterflies perched individually were not significantly oriented.

Does the size of aggregations indicate that the butterflies aggregate to facilitate warning signal learning?

If a naïve predator is sampling prey from the aggregation and learning to avoid the animals based on the warning coloration, then the number of individual butterflies in the aggregation should increase with the number of prey the predator needs to sample to learn to avoid that prey item (Sillén-Tullberg & Leimar, 1988). For *B. philenor*, one experiment demonstrated that it takes an average of 2.67 butterflies for Blue Jays (*Cyanocitta cristata*) to learn not to attack this species using the ventral surface in a captive setting (Codella & Lederhouse, 1990). Considering the mean size of the observed aggregations was 5.8 for the field and 2.8 in the enclosure, predator sampling during learning could have influenced the size of *B. philenor* aggregations.

CONCLUSIONS

Our study provides information on the environmental conditions in which the warning signal of *B. philenor* is likely to mediate interactions between them and their predators and the ways in which by forming aggregations they may increase the effectiveness of their warning signal. We now know that *B. philenor* forms aggregations, selects postures within aggregations that may maximize the size of the warning signal, forms groups of a size that may facilitate predator learning, perches in locations that may facilitate learning and recognition, and forms aggregations at times during the day when iridescent warning coloration may be effective. Our observations revealed that the iridescence is still visible when the solar orb is not present in the sky, giving us a potential reason for why an iridescent warning signal might evolve. Our observation that the only

animals that disappeared from the pavilion overnight were individuals that were perched individually may also support the idea that *B. philenor* aggregations reduce predation risk.

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