LOCOMOTOR MIMICRY IN BUTTERFLIES

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ABSTRACT

Unpalatable insects often display a warning through the use of a pattern or color to alert their predator that they are distasteful. It may take a predator several tastes to associate the signal with an unpleasant experience but will eventually cease to attack. For those insects that are edible and easy-to-catch, natural selection has allowed for the evolution of mimicry. These easy-to-catch, edible prey species have evolved to ‘mimic’ another edible species but which is more difficult for the predator to capture. Locomotor mimicry is generally described as the movement behavior of unpalatable prey. It is the result of two distantly related prey species, with similar behavior, possessing morphological, physiological and biomechanical traits that are similar to each other. It may also be a result of escape or unprofitable prey mimicry between palatable species that are similar.

While there are many insects that utilize mimicry for survival, butterflies have received much attention and study. In this paper, three different experiments will be analyzed to expose the process through which locomotor mimicry has evolved, to show how this phenomenon has been discovered as well as give an example of how one butterfly uses locomotor mimicry. The first study that will be discussed involves the evolution of positions of centres of mass among groups of Heloconius butterflies. The second study shows how the Heloconius species has also been researched extensively to explain the pitching oscillations of the body and the wing-beat frequency (WBF) in an attempt to determine if that might converge with the body size and aid in survival. The third
study is about a small butterfly, a pierid (Alfalfa butterfly), in which it is the model for the short-horned grasshopper providing an edible food source. The benefit for the mimic, the grasshopper, in this case is that its model, the pierid, efficiently escapes attack and therefore is often not pursued resulting in protection for the mimic. Even though there has been extensive research carried out concerning locomotor mimicry, there has been criticism on its validity. The conciseness of the theory has been questioned as well as the realism of insect’s ability to evolve based their degree of difficulty of being captured.

**INTRODUCTION**

Mimicry is the phenomenon that occurs when an organism resembles a second organism, or the model, and benefits from this resemblance by deceiving a third organism (Allen & Cooper, 1995). There are two basic types of mimicry in prey species: Batesian and Mullerian mimicry named after the two naturalists Henry Walter Bates and Fritz Muller. H.W. Bates (1862) proposed that palatable butterfly species copied the appearance of poisonous butterflies and birds and selected for resemblance whereas Franz Muller (1879) demonstrated mathematically that many unpalatable species could gain protection by converging visually on a single form. These concepts are the basis for the traditional mimicry theory. Simmons and Weller (2002) state that Batesian mimics are palatable species that imitate noxious species and Mullerian mimics are unpalatable species that converge on a single appearance.

The evolution of mimicry in regard to prey motion can be considered in three areas: anti-apostatic selection, locomotor mimicry and escape mimicry (Srygley, 2000). Srygley (2000) states that anti-apostatic selection arises when prey are at very high densities or when prey are Mullerian mimics in which case, motion may also play an
important role in strengthening selection against odd individuals and thus explaining locomotor mimicry between Mullerian mimics. Locomotor mimicry is the result of two distantly related prey species, with similar behavior, possessing ‘morphological, physiological and biomechanical traits that are similar to each other’. Although locomotor mimicry is thought to occur in Batesian mimics, there are important limitations to consider due to selection by the predator for the prey that may inhibit it’s ability to escape if detected. Therefore, locomotor mimicry may also be a result of escape or unprofitable prey mimicry between palatable species that are similar. (Srygley, 2000) According to Srygley (1994), “Locomotor mimicry is the similarity in swimming, walking or flying of distantly related animals, and the associated similarity in form and physiological function, including biomechanical or neuromuscular functions.”

It is necessary to define profitable and unprofitable prey and the characteristics that distinguish the two types of prey. Srygley (1994) defines unprofitable prey as species that are not pursued because of their defenses (for example those containing noxious chemicals) (Sherratt, Rashed & Beatty, 2003), whereas profitable prey would be prey that is readily pursued because of a lack of natural defense. Unprofitable prey commonly moves slower and more predictably than profitable prey (Sherratt, Rashed & Beatty, 2003). Sherratt et.al. (2003) also explains that profitable prey species evolve to be morphologically identical to the slow moving unprofitable prey through evolved locomotor mimicry but only as a last means to avoid predation. Throughout the paper unpalatable may be used interchangeably with unprofitable and palatable with profitable.
Robert B. Srygley (1994) has identified the three different escape tactics used by butterflies within the species *Heliconius* as ‘evasive flight, distastefulness and mimicry of unprofitable prey’. Srygley (1994) completed a study looking at the position of centre of body mass, wing shape, and positions of centres of wing mass of the *Heliconius* to try to answer two questions pertaining to insect flight and the evolution of locomotor mimicry. First, he was interested in finding out what morphological features may contribute to improved evasive flight performance and maneuverability. Secondly, he was interested in determining which morphological features can be considered reliable in deterring predators from unprofitable prey. A study done by Chai and Srygley (1990) had already determined that unpalatable butterflies have longer and thinner bodies as compared to palatable butterflies of the same type but Srygley (1994) wanted to continue this research to explain the evolution of locomotor mimicry.

In this study by Srygley (1994) they began by collecting adult butterflies from forests of several countries and then used these adults to establish the greenhouse stock. It was then necessary to classify the butterflies by species into one of six groups based on common taxonomic lineages. After species classification, the butterflies were furthered classified into one of 11 mimicry groups using wing color and pattern as criteria. They also needed to determine palatability. Butterflies were presented to a rufous-tailed jacamar and then palatability was figured as the percentage eaten over the total presented to the jacamar. Next, some of the butterflies were killed and from these they took several measurements including body mass, body length, diameter of the thorax and the wing length. They also needed to measure the lengths and masses of the head, thorax and
abdomen once the legs and wings were removed. They took some estimates of other morphological characteristics including averages of the body diameter, wing thickness and wing chord and the virtual wing mass. They also used a procedure to estimate the position of the centre of body mass based on the mass and lengths of the separate body segments.

Srygley (1994) was able to conclude that the most appropriate indicators of mimicry and palatability are the positions of the centres of body and wing mass whereas wing shape is not an appropriate indicator. In the mimicry groups of more palatable species, the centres of mass were positioned nearer to the wing base, which was found to increase the flight speed and ability to turn. The palatable butterflies have evolved so that they have selected for body morphology that allows for increased flight speed and ability to turn whereas the unpalatable species have selected for body morphology that inhibits their flight performance.

**PITCHING OCCILLATIONS AND CONVERGENCE IN WING-BEAT FREQUENCY IN HELICONIUS BUTTERFLIES**

Srygley (1999) continued to expand on the previous research that he had accomplished, such as the experiment described in the previous section. In the previous experiment Srygley (1994) found that in the mimicry groups of more palatable species, the centres of mass were positioned nearer to the wing base, which resulted in increased flight speed and ability to turn or maneuver. From this analysis, Srygley (1999) was able to create a second hypothesis of locomotor mimicry, which stated, “Convergent selection on flight behavior may reduce morphological difference of species within mimicry groups arising from distantly related lineages. Convergences in centres of mass within mimicry groups were predicted to result in convergences in oscillations of the body and
Srygley (1999) compared four *Heliconius* species concentrating on the morphology and kinematics of the two mimicry pairs. Srygley identified three morphological features that best represented three character groups by using principle component analysis. He identified the position of the centre of body mass, which is the character group that influences flight speed and the ability to turn or maneuver. He also identified the centre of wing area as related to wing shape, which is the character group that influences lift and drag created by the wings. The third feature identified was the position of the centre of wing mass, which affects the acceleration and deceleration. These characteristics differed among species within lineages and were comparable among the species within the mimicry groups.

Srygley (1999) began this experiment by collecting the butterflies and then categorized the specimens based on species and gender. He needed to rear some of the species so that he had an adequate number of males and females. The butterflies were flown through a tube for a number of sequences and videotaped to watch the flight patterns. After the completion of videotaping, the specimens were frozen and flight-related morphological features were measured and recorded (as done in Srygley’s (1994) previous experiment). He identified the characteristics of the three suites mentioned previously including position of centres of body mass, position of centres of wing mass, and wing shape. It was also necessary to include the body’s rotational inertia because it was a measure of the oscillating body frequency. Wing loading (body mass over wing area) and sweep area (the arc swept by the wings times wing length squared) were
calculated as two predictors for flight kinematics and aerodynamics. From this they selected the flight sequences that were smooth and uninterrupted and calculated the kinematics for each sequence.

Srygley (1999) was able to conclude that there was convergence among the *Heliconius* pairs in the position of centres of body mass, position of centres of wing mass, and wing shape in addition to the basic morphological features, such as wing pattern and coloration, associated with mimicry. More importantly this was the first study to identify the convergence with wing-beat frequency. Because of this demonstration of convergence within mimicry groups, locomotor mimicry allows the opportunity to look at the adaptation of form as compared to the slower flight movements. The evolution of the convergence of body size may be a result of the convergence of the wing-beat frequencies. This study provided the preliminary steps to understanding the convergence with morphological and kinematic features of the *Heliconius* butterflies.

**PIERID AND GRASSHOPPER MIMIC**

To date, there has only been one published study that has researched the connection between a pierid or alfalfa butterfly and the short-horned grasshopper. In this study performed by Balgooyen (1997) the grasshopper is a mimic of the alfalfa butterfly, proving an unusual form of evasive mimicry. In a system such as this, the protection gained by the mimic results from appearance, predator learning and retention, and the ratio of model (pierid) to the mimic (grasshopper) in the environment. The reason that this is such an unusual form of evasive mimicry is that ‘instead of the mimic evolving to look like a toxic or irritating model, the mimic resembles a model that exhibits efficient escape’ (Wickler, 1968; Balgooyen, 1997). That is, the mimic has gained an advantage
by being associated with a model that is too difficult and too expensive energetically to pursue and capture.

There were three objectives to this study by Balgooyen (1997): 1) the comparative evasion index by difficulty of capture, 2) the relative densities of pierid models and acridid (grasshopper) mimics, and 3) the edibility of the pierid butterfly model by a predator. Objective 1 was carried out using a standard insect net to selectively capture flying A. conspersa grasshoppers and C eurytheme butterflies to determine if there was a difference in difficulty of capture. The butterflies were more difficult and required more energy to capture because of the quick and sharp directional way that it flies. Objective 2 was carried out by walking and counting Colias eurytheme and Arphia conspersa flying on or off of transects and it was determined that the grasshoppers were more abundant than the butterflies. Finally, objective 3 was carried out by feeding stunned butterflies to captive kestrels to see if they would consume the butterflies and it resulted in complete consumption of all the butterflies fed to the kestrels. It was concluded that this experiment supports evasive mimicry because of the consumption of the pierid without apparent distaste and because of the erratic flight when under attack by the kestrels. This proves that the risk of predation is lowered for the grasshopper by mimicking its evasive model, the pierid.

**CRITICISM OF THE LOCOMOTOR MIMICRY THEORY**

Robert B. Srygley has conducted a majority of the recent research on locomotor mimicry. On his website [http://users.ox.ac.uk/~zool0206/locomim.html](http://users.ox.ac.uk/~zool0206/locomim.html) he makes the following statement, “I research locomotor mimicry in butterflies. Ultimately, I am interested in identifying the adaptations in morphological design and physiological
processes that are relevant to flight. I believe that we can use evolutionary convergence via selection on mimicry to test whether attributes that have been identified through biomechanical and aerodynamic theory are truly relevant to flight behaviors.” While Srygley has dedicated his time to this cause, others have responded to his research with criticism of the validity as well as the conciseness of the theory. Brower, A.V.Z. (1995) responded with criticism to the paper Srygley (1994) published saying that it was ‘unparsimonious’.

Brower’s (1995) criticism of Srygley’s (1994) hypothesis of locomotor mimicry is based on two questions. The first question addresses the issue of the ‘existence of mimicry between palatable and unprofitable prey as disputed on theoretical and empirical grounds’. He asks if this is a plausible phenomenon and whether or not is has been proven to happen in nature? His second question addresses that ‘correlations of phenotypic characters used to support alternative adaptive peaks for palatable and unpalatable butterflies are criticized for failing to account for phylogenetic relationships’. Brower proposes an alternative hypothesis based on ‘phylogenetic constraint in the evolution of morphological characters associated with predator avoidance’.

Brower (1995) argues his first question by making four observations that disagree with Srygley’s (1994) work. First, he suggests that the palatability of most of the species may not be known and therefore the insects of that mimicry group may be actually normally unpalatable models. Secondly, he argues that it may be because of the microhabitats the species may converge on like patterns. Third, it is the result of common descent that like color patterns are shared and not because of mimetic convergence. The fourth argument is that large, fast flying butterflies act as a model for
the less aggressive mimic because of the ability of the fast flying butterflies to efficiently escape the predator. Brower demonstrates many examples in the paper that support these four arguments. Through this demonstration he tried to show that ‘mimicry of a palatable but unprofitable model is far less likely than traditional Batesian mimicry of an unpalatable model on theoretical grounds, and that the purported examples of it are poorly supported’. He suggests that more field experiments are needed to really understand these dynamics of complex predator-prey dynamics.

In addressing Brower’s (1995) second question about phylogenetic relationships he feels that the concept of adaptation needs to be considered to grasp the full meaning. He re-examined Srygley’s (1994) results so that he could prove that ‘ignorance of phylogeny can lead to erroneous conclusions about adaptation’. He goes on to argue that adaptive convergence can only be a parsimonious explanation if there is conclusive evidence that like patterns have ‘evolved in phylogenetically independent lineages’. Brower feels that Srygley was misleading in several of his conclusions. He feels that the mimetic pairs of *Heliconius* Srygley (1994) chose were of common ancestry and so they should only constitute as one observation in the statistics of flight morphology characteristics. He also points out how Srygley (1994) admits to the variable group size, which is in violation of the statistical assumption, but maintained strong conclusions from these results. Other examples that Brower argues concerning the conciseness of Srygley’s work suggest the he did not adequately factor out phylogeny from his results, he needs to look at additional taxa to determine if his theories still hold up, as well as other arguments all disagreeing with the work that Srygley (1994) published.
Brower (1995) made a valid attempt to use the information from the last 130 years to support his hypothesis that was based on ‘phylogenetic constraint in the evolution of morphological characters associated with predator avoidance’. He used an abundant number of examples to support his hypothesis and to challenge Srygley’s (1994) conclusions. Brower was able to conclude that the results were misleading because of errors in statistical analysis and that inappropriate attention that was given to the ‘phylogenetic relationships has led to conclusions about adaptation that are unwarranted with respect to his own results and contradicted by previous evidence available in the literature’.

Ruxton, Speed & Sherratt (2004) recently published a paper that questions the realism of an insect’s ability to evolve based their degree of difficulty of being captured. They do not disagree that evasive mimicry is possible but they argue that there are ‘fundamental aspects of it that will limit its possible prevalence in nature’. Ruxton et.al. (2004) used two mathematical models to test the logic of evasive mimicry versus the actuality of this phenomenon to occur in nature. One of the models was used to test Batesian mimicry and the other to test Mullerian mimicry.

In their conclusions they found that evasive Batesian mimicry should be possible if certain criteria are met but there is not current evidence that evasive Batesian mimicry occurs in the field. They also agree that evasive Mullerian mimicry should be possible but there are certain costs associated and they have not found that such costs have been quantified as previous studies have suggested.
CONCLUSION

Locomotor mimicry is a fascinating phenomenon that occurs within many insect species. Locomotor mimicry can basically be interpreted as the mimicry of the movement behavior of unpalatable species. Insects commonly use color patterns as a warning to their predator that they are distasteful. This paper specifically focused on locomotor mimicry in butterflies explaining the evolution of the phenomenon, the notion of convergence of wing-beat frequency with its body size as a survival aid and an example of a pierid butterfly and its mimic, the short-horned grasshopper. Batesian and Mullerian mimicry have established the foundation for the concept of locomotor mimicry. Regardless of the quantity of research surrounding the concept of locomotor mimicry, there has been criticism concerning its validity. Questions have been raised in concern for the conciseness of the theory as well as the realism of insect’s ability to evolve based on difficulty of being captured. Those that question its validity recognize that it is possible but can’t prove that it occurs in the field. Even though there has been question about locomotor mimicry, as more research is carried out, concern and questions should be eliminated and further understanding of this phenomenon will be gained.


