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Body size and sexual selection in *Heliconius charitonius* and *Heliconius melpomene* (Lepidoptera: Nymphalidae)

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ABSTRACT

The role played by body size in sexual selection was investigated in captive populations of *Heliconius charitonius* and *Heliconius melpomene* butterflies. Mean forewing lengths of the entire population were compared to those of individuals participating in mating and pre-mating behaviors. It was predicted that because fitness in butterflies often increases with size (Klingenberg and Spence 1997), *Heliconius* spp. should choose larger mates. Sexes did not differ in size for either species (*H. charitonius*: Males = 41.14 mm \pm 2.41, n = 57; Females = 41.28 mm \pm 3.40, n = 48. *H. melpomene*: Males = 36.29 mm \pm 2.54, n = 30; Females = 36.01 \pm 1.82, n = 38). Moreover, there were no differences in size for any of the precopulatory behaviors seen compared to those for the general populations. No evidence of assortative mating was found when comparing pairs of males and females in later stages of courtship (p = 0.622, R² = 0.0193, n = 30). Matings were infrequent, but showed no size difference except for *H. melpomene* males, who were significantly smaller (34.45 mm \pm 1.79, n = 13, t = 2.714, p = 0.011, d.f. = 32). Therefore, mating in these two species of *Heliconius* seems to be independent of body size. Perhaps body size does not impact fitness, or other factors, such as chemical defense, agility or age are more important fitness indicators in these species.

RESUMEN

Se investigó el papel del tamaño del cuerpo en la selección sexual investigado en poblaciones cautivas de mariposas de la especie *Heliconius charitonius* y *Heliconius melpomene*. Comparé los promedios de las longitudes de las alas de todas las mariposas que estaban copulando y que tuvieron comportamiento de cortejo. Yo había predicho que *Heliconius* spp. debería de escoger compañeros más grandes porque el éxito reproductivo de las mariposas aumenta con el tamaño del cuerpo (Klingenberg y Spence 1997). Los promedios de las longitudes de los sexos no fueron diferentes (*H. charitonius*: Machos = 41.14 mm \pm 2.41, n = 57; Hembras = 41.28 mm \pm 3.40, n = 48. *H. melpomene*: Machos = 36.29 mm \pm 2.54, n = 30; Hembras = 36.01 \pm 1.82, n = 38). También, no hubo diferencias en los tamaños de los cuerpos entre las mariposas que estaban copulando o haciendo conductas de cortejo y los de la población promedio. No hubo diferencias de las copulaciones cuando comparé parejas de machos y hembras en las etapas adultas (p = 0.622, R² = 0.0193, n = 30). Las copulaciones no fueron frecuentes, pero no demostraron diferencia en el tamaño del cuerpo, excepto para machos de *H. melpomene* que fueron significativamente más pequeños (34.45 mm \pm 1.79, n = 13, t = 2.714, p = 0.011, d.f. = 32). Por eso, las copulas de las dos especies de mariposas *Heliconius* parecen independientes del tamaño del cuerpo. Tal vez, el tamaño del cuerpo no afecta la propiedad de las mariposas, u otros factores como las defensas químicas, la agilidad, o la edad son más importantes para indicar el éxito reproductivo en estas especies.

INTRODUCTION

The frequency of certain traits in a population can increase or decrease depending on how attractive the trait-bearer appears to potential mates (Alcock 2005). Such intersexual selection may occur through male or female choice, but female choice is usually stronger due to their larger investment in offspring (Trivers 1972). While females may select for greater fitness in males, they sometimes select for traits that appear to be completely neutral with regard to fitness. Through female choice alone, these neutral traits become fitness enhancing for males and increase in frequency through runaway selection (Wiley 1994). Even maladaptive traits may increase in a population through intersexual selection. This is called the handicap principle, in which traits giving males a handicap are preferred because they advertise his ability to survive in spite of it (Krebs and Davies 1981).

One trait many organisms use to assess a mate's potential fitness is body size. Survivorship and fecundity are often increased when an organism's body size is larger. A classic example is that larger finches in the Galapagos are sexually selected because of the increase in fitness with beak size (Ridley 1993). In seed beetles (*Stator limbatus*), larger females and males are also favored by sexual selection. Larger females are favored for their ability to lay more eggs than smaller females. Larger males can continue courtship displays and hold territory longer than small ones, as well as produce more ejaculate, meaning the female mates less often (Savalli and Fox 1998).

Butterflies are insects in which intersexual selection plays a large role, especially in terms of body size. In most butterfly species, males initiate courtship and are aggressive and persistent at locating and courting females. Females are often distracted, coy, or effective at rejecting males and must be receptive to males' courtship displays in order for copulation to occur (Silberglied 1989). Female butterflies thus get to be choosy with mates, and most prefer dominant males with high status, large wing size, ability to forage well, good survival skills, and peak physical condition (Savalli and Fox 1998). Male butterflies may also choose to court larger females because female size usually correlates positively with egg size, increasing the survivorship of offspring (Wiklund, Karlsson, and Forsberg 1987). It has been found in *Pieris protidice* (Pieridae) that both males and females prefer larger mates. In this species, large males deposit larger spermatophores, which are readily accepted by large females who can create larger offspring (Scott 1986). However, because butterfly lifetimes are short, the cost of being large means having to spend more time developing, thus slowing generation time and increasing exposure to parasites and predators. Therefore, optimal size is not necessarily maximum size (Klingenberg and Spence 1997).

Much has been made of color and its impact on intersexual selection in the mating patterns of butterflies in the genus, *Heliconius* (Jiggins et al. 2001). Variable populations of *H. melpomene* and *H. erato* seem to favor red colors. However, little is known about the impact of size of *Heliconia* spp. The purpose of the present study is to investigate the impact of wing size on mating preferences of *Heliconius charitonus* and *Heliconius melpomene* butterflies. If *Heliconius* spp. follow the pattern of other butterflies, both males and females should choose larger mates. Further, if other traits like development time counter sexual selection, the optimal size (here regarded as the population mean) may be considerably smaller than that preferred.

MATERIALS AND METHODS

Study Organism

Heliconius charitonius and *Heliconius melpomene* (Lepidoptera: Nymphalidae) are butterflies of one of the most conspicuous butterfly genera in the Neotropics, because of distinctive color pattern and longevity. All *Heliconius* butterflies use hostplants in the family Passifloraceae, making them distasteful to predators. Many are members of mimetic pairs to advertise this fact. *Heliconius charitonius* have black wings with yellow stripes on both wings (Figure 1), and are not part of a mimetic pair. Forewing size can range from 29-47 mm. *Heliconius melpomene* butterflies have black wings with a red stripe on the forewing and yellow on the hindwing (Figure 1), mimicking that of *H. erato*. Forewing length in *H. melpomene* can range from 31-40 mm (DeVries 1987).



a.



b.

FIGURE 1. Photographs of the studied *Heliconius* butterflies. On the right, *Heliconius melpomene* (a.) and on the left, *Heliconius charitonius* (b.).

Study Site

The present study was conducted in the butterfly rearing garden of Amabelis Arguedas in Santa Elena de Monteverde, Costa Rica. The garden is located at about 1300 m in the Premontane Moist Forest life zone (Holdridge 1967). The garden measures 18 x 24 m in area and contains different species of Passifloraceae as the dominant vegetation. Passifloraceae is the larval food plant for *Heliconius* spp. (DeVries, 1987). There were also numerous nectar sources for butterflies in the garden, including *Lantana camara* (Verbenaceae), *Pentas lanceolata* (Pellicieraceae), and *Psychotria elata* (Rubiaceae). Multiple flowers of these plants were injected daily with five milliliters of flat 7-UP, essentially a 20% solution of sugar water, to assure adequate food. The west end of the garden received full sun during the hours of observation while the east end was highly shaded. Observations in the garden were made on sunny days in the late dry season, during the last days of April and the first week of May, 2007.

Rearing, Marking and Releasing Butterflies

Ninety *Heliconius melpomene* pupae were ordered by the Monteverde Butterfly Garden, sent to Amabelis, and hung on straight pins in a screened-in box near her butterfly garden until they emerged. The sexes and forewing sizes of the butterflies were recorded upon emergence and individuals were then released into the garden. Forewings were measured with calipers to the 0.01 mm on the longest possible part of the forewing. Each of about 70 *H. melpomene* butterflies measured for this “garden census” was marked with a *Sharpie* permanent paint pen before releasing it into the garden. Small marks were made in yellow paint pen on the yellow stripe of the right hind wing. The yellow paint pen was a slightly darker yellow than that of the wing stripe, so it was noticeable to me for counting reasons, but not conspicuous to other butterflies, so it would not impact sexual selection.

The most numerous butterfly species present in the garden was *Heliconius charitonius*. Before beginning the experiment, a butterfly net was used to capture as many *H. charitonius* in the garden as possible. A total of 105 *H. charitonius* were caught, sexed, marked, and their forewings were measured. Marks were made with the same paint pen in the same place on the hind wing as in the *H. melpomene*. Judging by the number of marked versus unmarked individuals observed toward the end of the study, I would guess that the census captured over 90% of the garden’s *H. charitonius* population.

Behavioral Observations

After all *H. melpomene* were released into the garden, mating behavior of both species was observed. Observations were made for four hours every day from April 29 until May 9, 2007, between the hours of 9am and 1pm. When pre-mating behavior was observed, the individuals involved were caught, sexed, and measured as before. If these butterflies had not yet been measured, I marked them and included their measurements in the garden census as well as the observational data. Butterflies were caught one couple at a time, in order to keep track of partner relationships. When a pair of butterflies was observed *in copula*, they were not caught, and measured while on the leaf on which they were found.

Pre-mating activity was determined to be composed of the following five separate behaviors: approach, chasing, courtship, copulation, and rejection. Circling was another included behavior, but was only observed in *H. charitonius*. Approach was considered to be when a male butterfly made a straight, purposeful flight toward a female butterfly. Chasing followed the approach if the female was receptive and the male pursued her closely. Courtship began when a female settled on a leaf and a male fluttered above her, forcing her wings downward. Three stages of what I will collectively call “courtship” proceed after that, during which the male landed next to the female, moved to face her, then moved again to her side and touched his abdomen to hers. Copulation started when the male turned to face the opposite direction of the female and occurred for one to three hours. When disturbed while *in copula*, male *Heliconius* carried the female to a more secure location. Rejection occurred when a female flapped her wings or lifted her abdomen at the male during any of the above activities and he immediately backed-off.

During circling, a *H. charitonius* couple would fly together and the male would fly over and under the female in a circular motion.

RESULTS

I was able to census a total of 173 butterflies in the garden for the experiment, 105 *H. charitonius* and 68 *H. melpomene*. Overall, male and female butterflies were found to be the same size in both the *H. charitonius* population (paired t-test; $t = 0.238$, $p = 0.812$, $d.f. = 83$), and the *H. melpomene* (paired t-test; $t = 0.510$, $p = 0.612$, $d.f. = 51$). *Heliconius melpomene* individuals were smaller on average, $36.15 \text{ mm} \pm 2.18$, than *H. charitonius*, $41.21 \text{ mm} \pm 2.91$, and also had a smaller range of sizes, 31.36 mm to 43.60 mm for *H. melpomene* and 29.04 mm to 46.58 mm for *H. charitonius*. To investigate evidence for sexual selection and non-random mating regarding body size, the overall populations of both species were compared to those of each sex observed exhibiting each behavior (Figure 2).

Heliconius charitonius males

Heliconius charitonius males in the butterfly garden ranged from 32.90 mm to 45.64 mm , with an average size of $41.14 \text{ mm} \pm 3.40$ ($n = 57$). Males that were observed approaching conspecific females had forewing sizes of $40.45 \text{ mm} \pm 2.26$, not significantly different from those of the average *H. charitonius* male (Figure 2a; paired t-test; $t = 1.28$, $p = 0.203$, $d.f. = 54$). Males caught chasing females were of similar size, $40.77 \text{ mm} \pm 2.21$, (Figure 2a; paired t-test; $t = 0.644$, $p = 0.523$, $d.f. = 39$) and chased females of their own size most often, $40.73 \text{ mm} \pm 2.32$. Figure 2a shows that males that rejected females were also of average size, $41.68 \text{ mm} \pm 1.67$, in *H. charitonius* (paired t-test; $t = 0.664$, $p = 0.525$, $d.f. = 8$). Surprisingly, the same was true for males that were rejected by females (Figure 2a; $40.64 \text{ mm} \pm 2.60$, paired t-test; $t = 0.489$, $p = 0.639$, $d.f. = 7$). Rejection by females seemed to be more dependent on how the male approached than on his size. Participation in “courtship” was also by males whose wings were not significantly smaller or larger than average, $41.25 \text{ mm} \pm 0.83$, (Figure 2a; paired t-test; $t = 0.240$, $p = 0.813$, $d.f. = 22$), as was participation in circling behavior, $40.79 \text{ mm} \pm 2.81$, (Figure 2a; paired t-test; $t = 0.507$, $p = 0.615$, $d.f. = 29$). It was observed that almost all of the *H. charitonius* males in the garden were participating in pre-mating behavior.

Heliconius charitonius females

Forewing size for female *H. charitonius* butterflies used in this study ranged from 29.04 mm to 46.58 mm , with an average size of $41.28 \text{ mm} (\pm 2.41 \text{ mm}, n = 48)$. *Heliconius charitonius* females that were approached by males had average forewing sizes, $41.59 \text{ mm} \pm 2.00$, (Figure 2b; paired t-test; $t = 0.460$, $p = 0.647$, $d.f. = 61$), as did females that were chased after the approach ($40.73 \text{ mm} \pm 2.32$; Figure 2b; paired t-test; $t = 0.771$, $p = 0.444$, $d.f. = 48$). Females that were rejected by males had a significantly smaller forewing, $36.08 \text{ mm} \pm 5.55$, than females of the average population (Figure 2b; paired t-test; $t = 2.415$, $p = 0.046$, $d.f. = 7$). However, since only seven of them were observed being rejected, small sample size must be kept in mind when interpreting this result.

These data may also have been skewed by the rejection of one extremely small female (29.06 mm), because some of the others are above average. The forewing length of *H. charitonius* females caught rejecting males had a mean value of 41.94 mm \pm 3.17, which was just about average (Figure 2b; paired t-test; $t = 0.484$, $p = 0.641$, d.f. = 8). Females being courted by males of *H. charitonius* were not significantly different-sized than average females, 42.49 mm \pm 2.04, (Figure 2b; paired t-test; $t = 1.096$, $p = 0.295$, d.f. = 12). It can be seen in Figure 2b that *H. charitonius* females being circled by males also had average forewing sizes (paired t-test; $t = 0.164$, $p = 0.869$, d.f. = 58).

***Heliconius melpomene* males**

The body size of these males was found to be slightly smaller than either sex of *H. charitonius* ranging from 31.98 mm to 43.60 mm with an average size of 36.29 mm (\pm 2.54 mm, $n = 30$). *Heliconius melpomene* males observed approaching females had average forewing lengths of 35.56 mm \pm 1.73 (Figure 2c; paired t-test; $t = 1.11$, $p = 0.272$, d.f. = 36). Males that continued after the approach to the chase did not differ significantly in size than the overall population either, 35.81 mm \pm 2.22, (Figure 2c; paired t-test; $t = 0.679$, $p = 0.501$, d.f. = 40). Males that rejected females in *H. melpomene* had a mean wing length statistically equal to the average, 36.67 \pm 0.52, (Figure 2c; paired t-test; $t = 0.706$, $p = 0.489$, d.f. = 17). Females of this species rejected small and large males, the mean rejected male size being 35.63 mm \pm 3.42, not significantly different from average (Figure 2c; paired t-test; $t = 0.335$, $p = 0.769$, d.f. = 2). Participation in “courtship” happened in average sized, 35.18 mm \pm 2.15, *H. melpomene* males as well, (Figure 2c; paired t-test; $t = 1.117$, $p = 0.296$, d.f. = 8). No circling behavior was observed in the *H. melpomene* species, but forewing sizes of these males *in copula*, 34.45 mm \pm 1.79, were significantly less than those of the overall male population, (Figure 2c; paired t-test; $t = 2.714$, $p = 0.011$, d.f. = 32). Even though males copulating were only about two millimeters smaller than the average male, all but three of the 13 copulating males were indeed smaller than average, some by more than five millimeters.

***Heliconius melpomene* females**

Female *H. melpomene* forewings were measured to be between 31.36 mm and 40.18 mm, with an average size of 36.01 mm (\pm 1.82 mm, $n = 38$). Females approached by males were average sized, 35.79 mm \pm 1.99, (Figure 2d; paired t-test; $t = 0.353$, $p = 0.728$, d.f. = 21). Average sized females in *H. melpomene*, 36.24 mm \pm 1.47, (Figure 2d; paired t-test; $t = 0.529$, $p = 0.599$, d.f. = 44), were caught being chased by males slightly smaller males 35.81 mm \pm 2.22. Unlike in *H. charitonius*, *H. melpomene* females rejected by males were not significantly smaller than average, 34.66 mm \pm 0.94, (Figure 2d; paired t-test; $t = 2.186$, $p = 0.117$, d.f. = 3). Females of all sizes were caught rejecting males, mean size being equal to 37.30 mm \pm 2.55, (Figure 2d; paired t-test; $t = 0.861$, $p = 0.479$, d.f. = 2). Females courted on a leaf were not found to be significantly different in wing size than the average female, 36.31 mm \pm 0.66, (Figure 2d; paired t-test; $t = 0.734$, $p = 0.475$, d.f. = 14), yet observation of this behavior was very rare. Forewing size of *H. melpomene* females *in copula* was less than average by more than one millimeter, 34.81

mm \pm 1.81, very close to being statistically significantly smaller than average (Figure 2d; paired t-test; $t = 2.063$, $p = 0.051$, d.f. = 21). As in the *H. melpomene* males, all but three of the 13 copulating females observed were below average size.

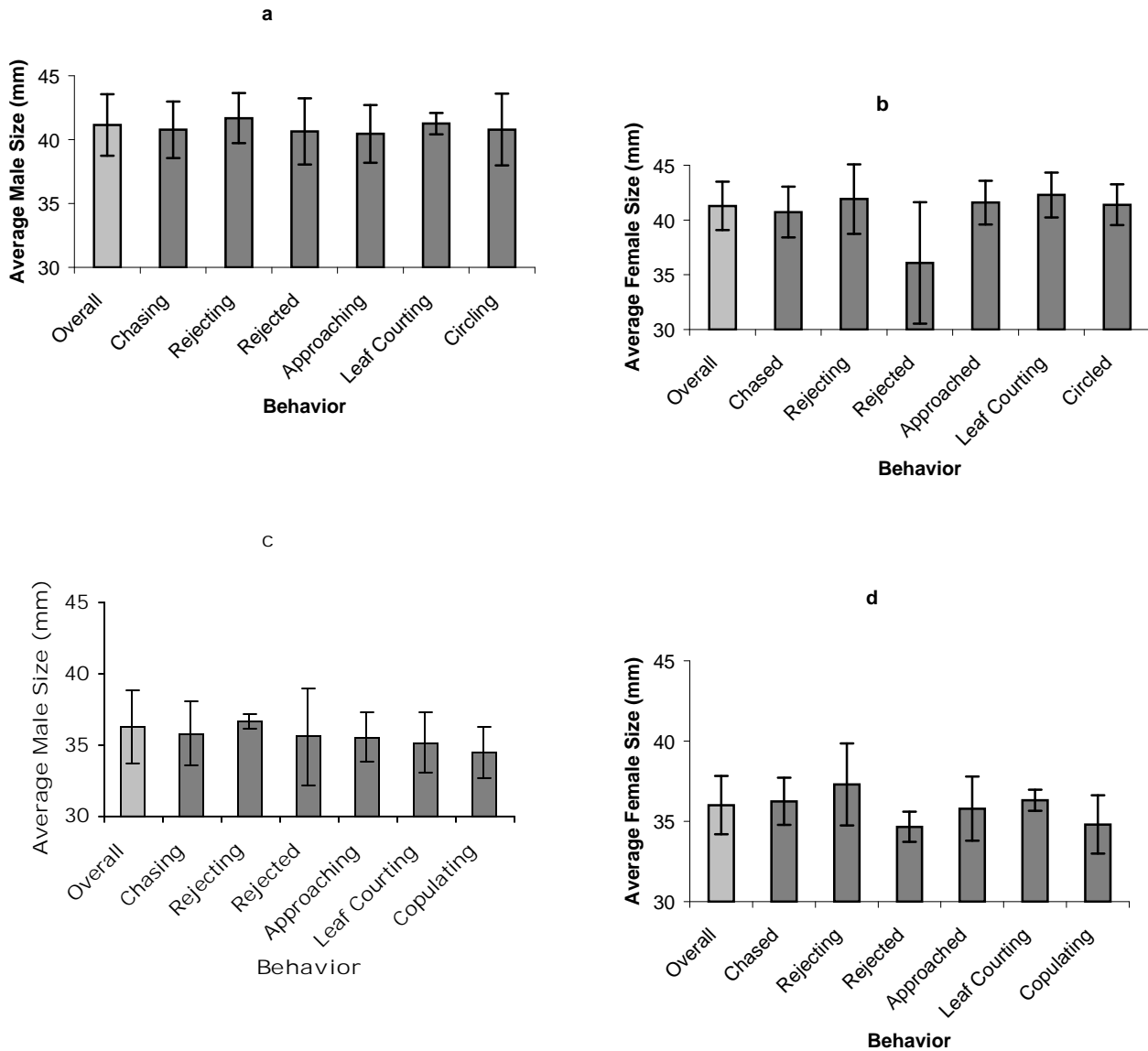


FIGURE 2. Average forewing size vs. behavior, a: male *H. charitonius*, b: female *H. charitonius*, c: male *H. melpomene*, d: female *H. melpomene*. None of the average sizes of butterflies participating in any pre-mating behavior were significantly different than the overall average population size, except copulating males of *H. melpomene* (c; paired t-test; $t = 2.714$, $p = 0.011$, d.f. = 32) and rejected *H. charitonius* females (b; paired t-test; $t = 2.415$, $p = 0.046$, d.f. = 7).

Regression Tests

A regression test was used to analyze the size relationship between males and females copulating for *H. melpomene* and circling for *H. charitonius*, because no *H. charitonius* copulations were observed (Figure 3). Although circling does not signify as close of a mating relationship between butterflies as copulation, it still signifies a relationship because both individuals have to participate. Circling relationships between couples of the *H. charitonius* population analyzed did not show any significant correlation (Figure 3a; $p = 0.622$, $R^2 = 0.0193$, $n = 30$). Even though copulating *H. melpomene* individuals were smaller than average, no correlation was found between copulating *H. melpomene* butterflies because of the way these couples were paired (Figure 3b; $p = 0.986$, $R^2 = 3 \times 10^{-5}$, $n = 26$). Thus, both species of butterflies were found to show interest in mates without regard to forewing size, and neither showed assortative mating according to body size.

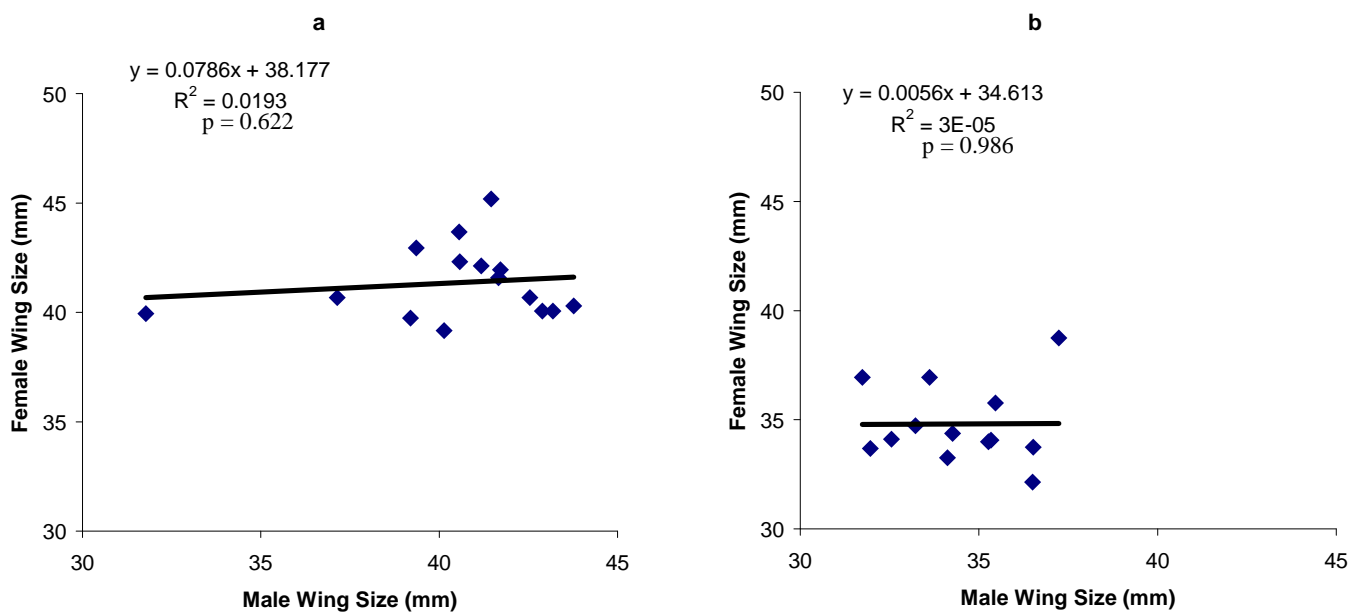


FIGURE 3. No evidence of assortative mating by wing size between male and female (a) *H. charitonius*, or (b) *H. melpomene*. Circling behavior, (a) was used to assess interest in mating in *H. charitonius*. Copulation was used this in *H. melpomene* (b). There was no relationship observed in either species.

Additional Observations

There were some interesting mating observations made during the study that were not quantifiably measured. A male *H. charitonius* was observed *in copula* with a female *H. melpomene*, their sizes were not recorded, but interspecific copulation is a rare occurrence. I thought that I saw other interspecific copulations taking place, but as the frequency of them increased, I learned that there were some mutant *H. melpomene* individuals in the garden that had lost the yellow stripe on the hind wing. This has been known to take place on rare occasions in isolated geographic areas (Silberglied 1989). After learning this information, the five mutant individuals in the garden were incorporated into the study and treated as normal individuals.

DISCUSSION

The findings reported here demonstrate that male and female forewing lengths in *Heliconius* butterfly pairs participating in pre-mating activity are not significantly different than forewing lengths of the overall butterfly population, with the exception of *H. melpomene* copulation. I have also shown that copulating male and female forewing lengths are not correlated in the studied population of *H. melpomene*, and thus they do not exhibit size-based assortative mating. This can also be assumed of the *H. charitonius* populations, which showed no male-female wing size correlation between circling individuals. Contradictory to my prediction, it can be inferred from these results that these two species of butterflies choose mates without regard to wing size.

However, males of the species *H. melpomene* observed *in copula* were significantly smaller than the average *H. melpomene* male, and sizes of their mates, though not significantly smaller, were trending toward this result. One theory to explain the fact that smaller butterflies are copulating more often is that these are the first to emerge from the chrysalis. Because butterflies must reach a certain age before copulation, the older members of the population were experiencing higher fecundity because they had a head start in the mating game (Klingenberg and Spence 1997). Small males may also be able to subdue small, naïve females without much precopulatory ritual, a possible explanation for why this trend was only observed in copulation. According to this hypothesis, it is logical that the same trend was not found in *H. charitonius* because these butterflies were older, thus enough time had passed since emergence that smaller individuals would no longer have any advantage.

It may be suspected from my data that wing size is not a trait the two studied species of *Heliconius* butterflies use in intersexual selection. Perhaps size is unrelated to fitness, or only plays a role in terms of intrasexual selection or natural selection. Intrasexual competition and how body size affects *Heliconius* survivorship would both be interesting to study in the future. It is also possible that no traits play a role in sexual selection and these two species choose mates completely randomly. Another possibility is that other traits, such as motion, odor, and hue may be sexually selected characters more intensely involved in courtship than body size (Crane 1955). In order to gain more insight into intersexual selection among *Heliconius* butterflies, it would be beneficial to study other traits in addition to body size and how they affect *Heliconius* mating preferences, collectively and individually.

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LITERATURE CITED

- Alcock, J. 2005. *Animal Behavior* Eighth Edition, p. 329. Sinauer Associates, Sunderland, Massachusetts.
- Crane, J. 1955. Imaginal behavior of a Trinidad butterfly, *Heliconius erato hydara* Hewitson, with special reference to the social use of color. *Zoologica: New York Zoological Society* 40 (16): 167-196.
- DeVries, P.J. 1987. *The Butterflies of Costa Rica and Their Natural History* p. 193. Princeton, NJ: Princeton University Press.
- Holdridge, L.R. 1967. *Life Zone Ecology*. San Jose: Tropical Science Center, 7-31.
- Jiggins, C.D., Naisbit, R.E., Coe, R. L., and Mallet, J. 2001. Reproductive isolation caused by colour pattern mimicry. *Nature* 411: 302-305.
- Klingenberg, C.P. and Spence, J. 1997. On the role of body size for life-history evolution. *Ecological Entomology* 22 (1), 55–68.
- Krebs, J.R. and Davies, N.B. 1981. *An Introduction to Behavioral Ecology*, pp. 121-131. Sinauer Associates, Sunderland, Massachusetts.
- Ridley, M. 1993. *Evolution*, p.229. Blackwell Scientific Publications, Boston, Massachusetts.
- Savalli, U.M. and Fox, C.W. 1998. Sexual selection and the fitness consequences of male body size in the seed beetle *Stator limbatus*. *Animal Behavior* 55: 473-483.
- Scott, J.A. 1986. *The Butterflies of North America*. Stanford University Press, Stanford, California.
- Silberglied, R.E. 1989. Visual Communication and Sexual Selection Among Butterflies, pp. 207-209. *In* Vane-Wright, R.I. and Ackery, P.R. (Eds). *The Biology of Butterflies*. Princeton University Press, Princeton, New Jersey.
- Sokolovska, N., Rowe, L., and Johansson, F. 2000. Fitness and body size in mature odonate. *Ecological Entomology* 25 (2): 239–248.
- Trivers, R. L. 1972. Parental investment and sexual selection, p. 136-179. *In* Campbell, B. (Ed.). *Sexual selection and the descent of man*, pp. 1871-1971. Aldine-Atherton, Chicago, Illinois.
- Wiklund, C., Karlsson, B., and Forsberg, J. 1987. Adaptive vs. constraint explanations for egg-to-body-size relationships in two butterfly families. *The American Naturalist* 130 (6): 828-838.
- Wiley, R. H. 1994. Errors, Exaggeration, and Deception in Animal Communication. *In* Real, L.A. (Ed.). *Behavioral Mechanisms in Evolutionary Ecology*, pp. 179-181. The University of Chicago Press, Chicago, Illinois.