

Dorsal Forewing White Spots of Male *Papilio polytes* (Lepidoptera: Papilionidae) not Maintained by Female Mate Choice

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Revised: 11 December 2017 / Accepted: 17 December 2017 /

Published online: 12 January 2018

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Abstract Palatable animals sometimes mimic the color patterns of noxious animals to gain protection from predators. This phenomenon, known as Batesian mimicry, is seen in many butterflies of the genus *Papilio*, and in some species the mimicry is limited to females. Although female-limited Batesian mimicry has been hypothesized to be caused by females preferring to mate with non-mimetic males, this hypothesis is rarely tested. In this study, we tested whether female mate choice is driving female-limited Batesian mimicry in *Papilio polytes*. Males have white spots on the dorsal forewings, which are absent in mimetic female sand in the toxic model, *Pachliopta aristolochiae*. Hence, we conducted mate choice experiments to examine whether these white spots are important to females. We offered females a choice of males with intact dorsal forewing white spots and males with artificially blackened dorsal forewings, resembling the model. Females did not show a preference for males with the white spots, suggesting that they are not being maintained by female mate choice. Future studies should investigate the presence of female mate choice on other parts of males' wings to further understand the role of female mate choice, as well as explore other factors driving female-limited mimicry in these butterflies.

Keywords Female mate choice · *Papilio polytes* · sex-limited mimicry · Batesian mimicry

Body coloration plays a key role in survival of prey animals, such as in reducing their likelihood of being eaten by predators. In some noxious prey animals, survival is tied to the display of bright and contrasting (i.e. aposematic) colors that warn potential predators that they are unpleasant or dangerous and therefore unprofitable prey (Poulton

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1890; Rojas et al. 2015). For example, many species of highly poisonous frogs in the Dendrobatidae family have various bright colors on their skin such as red, yellow, and blue-green (Summers and Clough 2001). Predators then associate the bad experience from previous encounters with the protected prey, to its aposematic coloration and learn to avoid them (Davies et al. 2012; Rojas et al. 2015).

In some cases, several co-existing noxious species resemble each other and share similar aposematic coloration so that predators that encounter one noxious species learn to avoid the others as well, which is a phenomenon known as Müllerian mimicry (Müller 1879). An example of such mimicry is found in *Heliconius* butterflies, whereby several distasteful species have similar wing color patterns (Mallet and Gilbert 1995; Meyer 2006). However, there are also cases whereby harmless species (the mimics) resemble the aposematic coloration of co-existing noxious species (the models) to gain protection from predators, a phenomenon known as Batesian mimicry (Bates 1981). For example, harmless or mildly venomous snakes in the Aniliidae and Colubridae families have similar colors as the highly venomous, brightly colored coral snakes in the Elapidae family. These mimics receive protection from predators that avoid coral snakes because predators cannot distinguish models from mimics (Savage and Slowinski 1992).

Batesian mimicry is also seen in many swallowtail butterflies (family Papilionidae) of the genus *Papilio*. Interestingly, there is a high diversity in Batesian mimicry in these butterflies, whereby mimicry can be limited to one sex or found in both sexes, and the butterflies can be monomorphic or polymorphic (Kunte 2009). For example, in *Papilio clytia*, both sexes are mimetic and polymorphic, mimicking either *Euploea core* or *Tirumala limniace* butterflies, both of which are distasteful (Wynter-Blyth 1957). In another species, *Papilio dardanus*, mimicry is female-limited whereby males are monomorphic and non-mimetic, but females exist in at least 14 different forms, with most forms mimicking different species of distasteful butterflies (Nijhout 2003). Moreover, some species which show female-limited polymorphism such as *Papilio dardanus* and *Papilio polytes* also have non-mimetic females in the population (Nijhout 2003; Revathy and Mathew 2014).

Papilio polytes is among one of the *Papilio* swallowtail butterflies that exhibits female-limited Batesian mimicry and mimetic polymorphism. Males of this species are monomorphic and have an ancestral non-mimetic wing pattern, whereas females are polymorphic and exist in non-mimetic and mimetic forms (Kunte 2008; Revathy and Mathew 2014) (Fig. 1). The non-mimetic form, called form *cyrus*, has male-like wing patterns. The two mimetic forms, form *stichius* and form *romulus*, are mimics of distasteful butterflies *Pachliopta aristolochiae* and *Pachliopta hector*, respectively (Revathy and Mathew 2014). In Malaysia and Singapore, females only exist in forms *cyrus* and *stichius* (Kirton 2014). The mimetic females of *Papilio polytes* not only have similar wing patterns to the distasteful model, but also display behavioral mimicry by having similar flight behavior as the model (Kitamura and Imafuku 2010). The mimetic females of *P. polytes* were experimentally shown to be avoided by avian predators that previously consumed the distasteful *P. aristolochiae*, showing that this mimetic pattern has a selective advantage (Uesugi 1996). Questions have thus been raised on why males remain non-mimetic and why non-mimetic females remain present in the population.

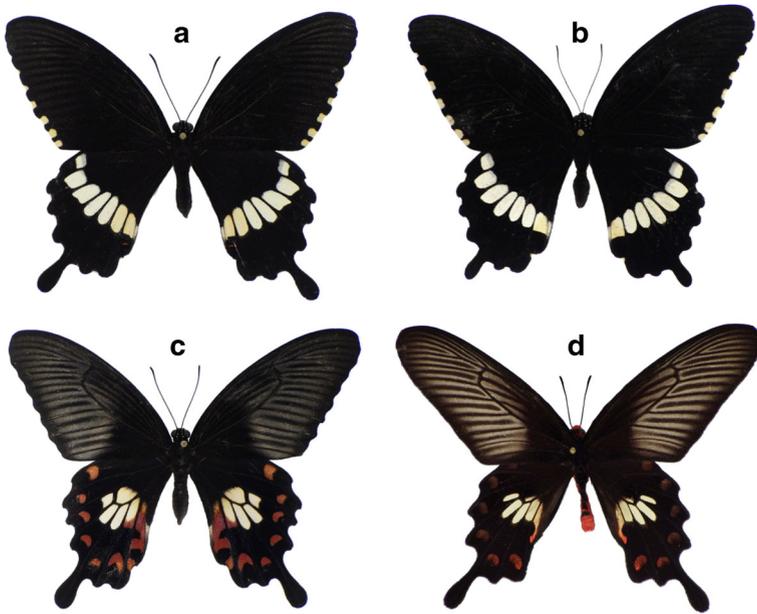


Fig. 1 *Papilio polytes* exhibits female-limited Batesian mimicry. In Singapore, females exist in two forms: form *cyrus* (a), the non-mimetic form that has male-like wing pattern, and form *stichius* (c), the mimetic form that mimics *Pachliopta aristolochiae* (d), a distasteful butterfly species. Males are monomorphic and non-mimetic (b). Only dorsal wing surfaces are shown

Negative frequency-dependent selection has been hypothesized to promote mimetic polymorphism in some Batesian mimics. If the abundance of mimics is high relative to models, the chance of predators encountering and consuming a palatable mimic instead of a toxic model is higher. This hampers predators from associating bright colors with unpalatability, reducing the effectiveness of the warning signal and of the mimicry associated with it. Evolution of polymorphism in Batesian mimics is thus promoted because the low abundance of each mimetic form increases the fitness of each form (Huheey 1964; Mallet and Joron 1999; Ruxton et al. 2004). Although this theory is a possible explanation for the presence of non-mimetic forms within a palatable species, it alone is insufficient to explain why Batesian mimicry is usually limited to females rather than males.

Mate preference has been hypothesized to contribute to female-limited mimicry and the presence of non-mimetic females. On the one hand, male preference for non-mimetic females was suggested to maintain the number of non-mimetic females in the population (Burns 1966). On the other hand, female preference for males with non-mimetic wing patterns was suggested to cause males to retain their non-mimetic patterns (Turner 1978). However, although wing color patterns are known to affect mating success, and mate choice has been found to be linked to wing pattern sexual dimorphism in various butterfly species (Davis et al. 2007; Kemp 2007; Kemp 2008; Morehouse and Rutowski 2010; Prudic et al. 2011), the relationship between mate choice and female-limited mimicry has rarely been tested.

In this study, we investigated the relationship between female mate choice and the evolution of female-limited Batesian mimicry in *P. polytes*. Males of this species hover in front of females during courtship, displaying only the dorsal side of their wings to females

(personal observation). Therefore, the dorsal wing patterns are likely important in sexual signaling. On the dorsal side, there are several differences between the wing patterns of males and mimetic females. For example, males have white spots on the edge of their forewings while mimetic females and *P. aristolochiae* models lack these white spots; males have hindwings that are mostly black with a white band that extends across the hindwing, while females have red spots near the edge of hindwings and a circular white patch on the inner side of hindwings (Fig. 1). We hypothesized that these differences in wing pattern are due to female mate choice, whereby females exert sexual selection pressure on the male wing pattern and therefore cause males to remain non-mimetic. Hence, we conducted mate choice experiments to investigate whether male *P. polytes* with a partially altered dorsal wing pattern to resemble mimetic females are less successful in mating. By offering females a choice of males with intact dorsal forewing white spots and males with artificially blackened dorsal forewings, we examined whether the white spots on the dorsal forewings of males are being maintained by female mate preference. We chose to focus our investigation on the white wing spots of forewings because similar pattern elements have been shown to be very important in female mate choice in *Bicyclus anynana* butterflies, namely the white UV-reflective centers in the dorsal forewings of males and females (Prudic et al. 2011; Robertson and Monteiro 2005).

Materials and Methods

Origin of Animals

Pupae of *P. polytes* from the forms *cyrus* and *stichius* were imported from “Entopia by Penang Butterfly Farm” (Penang, Malaysia). Upon eclosion, each individual was marked on its right ventral hindwing with a serial number using a black Staedtler Lumocolor fine point permanent marker (Staedtler, Nuremberg, Germany). Males and females were kept in separate cages until they were used in mate choice experiment. All butterflies were given *ad libitum* access to a 10% sugar solution via artificial flowers made from pipette tips that contained the sugar solution and yellow and red PVC tape shaped into outer petals.

Wing Color Manipulation

Males were randomly assigned into an experimental group and a control group and were both painted with a black Sharpie fine point permanent marker (Newell Brands, Hoboken, NJ, USA) at least one hour before the experiment. Males assigned to the experimental group had the white spots on the dorsal forewings painted black. To control for the scent of the paint and the handling process, males assigned to the control group were handled in the same way, but the paint was applied on the black regions in between the white spots on the ventral forewings (Fig. 2).

Mate Choice Experiment

Experiments were conducted in a 1.5 m × 1.5 m × 1.3 m flight cage containing a pot with a lime plant (*Citrus* sp.), which is the host plant of *Papilio polytes* larvae

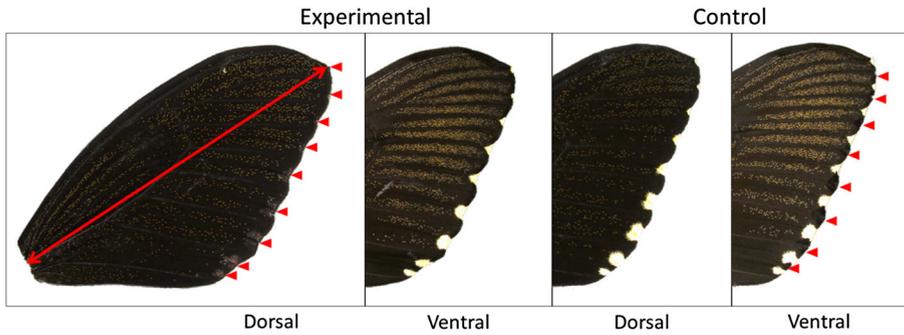


Fig. 2 In experimental males, the white spots on the dorsal forewings were painted black. In control males, the paint was applied on the dark areas between the white spots on the ventral forewings. The red triangles indicate where the paint is applied. Forewing length was measured from the wing apex to the wing base, as indicated by the two-headed arrow, as a proxy for size

(Revathy and Mathew 2014), and a pot with a Lantana plant (*Lantana* sp.), for extra nectar, in an outdoor shed with a transparent glass roof (Fig. 3). Males used were between two to six days old and females used were between two to nine days old. Five virgin males from each experimental group and five virgin females were released into the flight cage at 0900 h and provided with *ad libitum* access to 10% sugar solution via artificial flowers as described above as well as the Lantana plant. The cage was observed at 15 min intervals. Each mating pair was removed from the cage and immediately replaced with a virgin female and a virgin male from the corresponding experimental group. In the event that there were no more males for replacement, a male from the other group was removed from the cage to maintain the ratio of experimental to control males at 1:1. The experiment was suspended at 1600 h by removing all unmated females from the flight cage and resumed at 0900 h the following day. Observations were made between 20



Fig. 3 Flight cage (1.5 m × 1.5 m × 1.3 m) used for the mating experiment

December 2016 and 14 February 2017. All individuals were euthanized by freezing at the end of experiment.

Wing Size Measurements

Larger male butterflies may have higher mating success (Elgar and Pierce 1988), and males may select females purely on the basis of body size, an indicator of fecundity (Rutowski 1982). To make sure males from each treatment group had similar sizes, and to test for any effect of male or female wing size on mating outcome, we measured forewing length in males and females as a proxy for butterfly size, from the wing apex to the base (Fig. 2) to the nearest 0.01 mm using a Mitutoyo digital caliper.

Wing Color Measurements

To assess the effect of painting the males' wings, reflectance spectra of the intact white spots, painted white spots, and black regions between white spots on the dorsal forewings were measured using an Ocean Optics USB2000 + XR fiber optic spectrometer (Florida, USA) with a deuterium-halogen tungsten lamp as the illumination source. The illuminating and detecting fiber was positioned at 90° to the plane of the wing. All spectra were measured relative to a white Ocean Optics WS-1 reflectance standard. Reflectance spectra of averaged reflectance values ($N = 6$) were then plotted using the R package *pavo* (Maia et al. 2013).

Statistical Analysis

Chi-square tests were conducted to assess whether females mated non-randomly with each type of male. Independent t-tests were conducted to compare the sizes of (i) control versus experimental males; (ii) mated versus unmated males; and (iii) females that mated with control males versus females that mated with experimental males. Shapiro-Wilk tests were used to check for normality of data. Size measurements are presented as mean \pm SD.

Results

Wing Color Manipulation and Male Wing Size

Reflectance data showed that black paint greatly reduced the reflectance of the dorsal white spots of experimental males, causing the spots to display similar reflectance spectra to the natural black color in the regions between the spots (Fig. 4). The paint, thus, created a uniform black pattern on the dorsal forewings of experimental males as seen in mimetic females.

We confirmed that our random assignment of males to the two treatment groups produced groups with similar average wing size (forewing length: control = 44.47 ± 1.68 mm, experimental = 43.63 ± 2.32 mm, $t = 1.62$, $p = 0.11$). Therefore, males from both treatments had similar sizes.

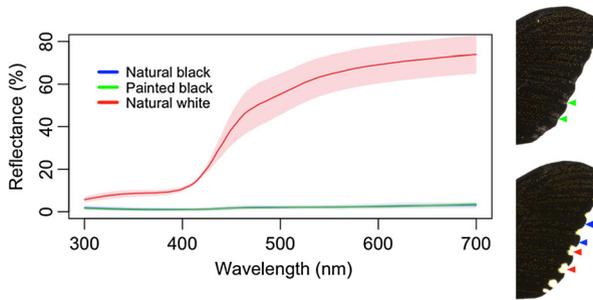


Fig. 4 Reflectance spectra of dorsal white spots (red line), painted white spots (green line), and the black regions between dorsal white spots (blue line). The lines represent the mean values, while the shaded regions represent the standard deviation of the spectral data ($n = 6$ for each type). The green line and blue line are very close together and overlap each other because the black paint has very similar reflectance spectra as the natural black colour at the regions between the dorsal white spots

Mating Outcomes

A total of 112 butterflies were used in this experiment, resulting in 34 successful mating pairs (Fig. 5). Copulation between virgin individuals under our experimental conditions lasted for at least 40 min (personal observation).

Females do not appear to have a preference for the presence of white spots on the forewing of males as the number of matings with males from either group was similar. Females mated with 18 control group males and with 16 experimental group males ($\chi^2 = 0.138, p = 0.71$) (Fig. 5a).

Mating patterns also did not correlate with either male or with female size. Males that successfully mated did not differ in size from males that did not mate (mated = $44.41 \pm$

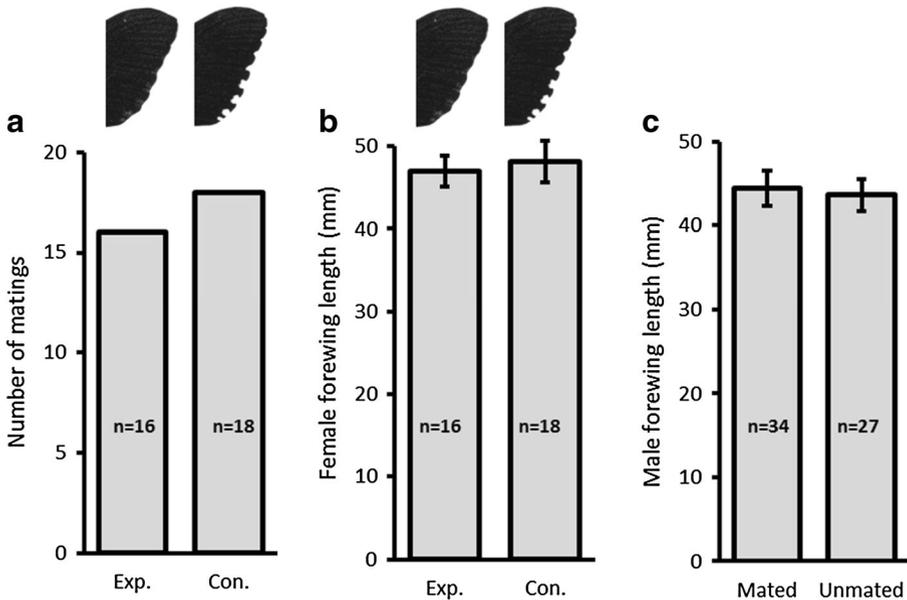


Fig. 5 a Number of mated males from the experimental and control group. b Size of females mated with experimental males versus females mated with control males. c Size of mated males versus unmated males

2.10 mm, unmated = 43.60 ± 1.92 mm, $t = 1.55$, $p = 0.12$), and females that mated with control males were similar in size to those that mated with experimental males (control = 48.14 ± 2.57 mm, experimental = 47.02 ± 1.91 mm, $t = 1.43$, $p = 0.16$) (Fig. 5b,c).

Discussion

Female Mate Choice in *Papilio polytes*

The white spots on the dorsal forewings of *P. polytes* males, a trait that disappeared in mimetic females, but that was retained in males of the same species, is seemingly not maintained by sexual selection via female mate choice. Males with either intact or painted white spots on the dorsal forewings were equally likely to mate. In addition, mated and unmated males were similar in size, suggesting that females do not select males based on wing size and therefore the size of males is unlikely to be a confounder of the results of this experiment.

Experiments on a different *Papilio* butterfly, *P. glaucus*, which also exhibits female-limited Batesian mimicry, had a similar outcome to our experiments. However, more detailed behavioral observations lent some support to the hypothesis that female-limited Batesian mimicry is maintained by female mate choice (Krebs and West 1988). *P. glaucus* females showed no bias in mating outcome when presented with typical yellow-colored non-mimetic males and males with their wings painted black to resemble the mimetic form. However, females solicited more male courtship from yellow males over black males (Krebs and West 1988). In our experiment we did not directly measure or quantify female solicitation towards the two male types, and, like the experiment on *P. glaucus*, did not observe significant differences in mating outcome between the two male forms of *P. polytes*. This suggests either that female *P. polytes* has no preference for the presence or absence of dorsal forewing white spots on the wings of males, or that male behavior, in our experimental cage set-up, is able to override these preferences.

In addition, our experimental design is not sufficient to dismiss the presence of female mate choice on male wing patterns because there are other sexually dimorphic patterns between males and mimetic females, apart from the forewing white spots, where female mate choice could act upon. Mimetic females have grey bands bordering the veins on the dorsal forewings and red spots near the edges of dorsal hindwings, which are both absent from males (Fig. 1). In addition, males have an extensive white band across the dorsal hindwing, while mimetic females have a more restricted white patch on the same wing surface. Furthermore, although males and non-mimetic females have similar wing patterns, spectrometry showed that the white bands on the dorsal hindwings of males reflect more light in the visible wavelengths and hence appear brighter compared to non-mimetic females (Su 2015). Although females were observed to have no preference for the brightness of the white bands on males' dorsal hindwings (Su 2015), it remains to be tested whether the extent of the white bands and absence of red patches in males are the product of female mate choice. So far there is no study on the visual capability of *P. polytes*, but another *Papilio* species, *P. xuthus*, is known to have five different color receptors that are sensitive to UV, violet, blue, green,

and red, respectively (Arikawa et al. 1987). Assuming that *P. polytes* have similar color receptors, they should be able to perceive these differences in color patterns. Therefore, manipulation of the color patterns on other parts of the males' wings should be performed and mate choice experiments should be conducted to further investigate the role of female mate choice in restricting wing pattern evolution and mimicry to females in *P. polytes*.

Other Potential Drivers for the Evolution of Female-Limited Batesian Mimicry

Apart from female mate choice, the evolution of female-limited Batesian mimicry in *Papilio polytes* and other butterfly species could be explained by two other hypothesized mechanisms: sexual selection via male-male competition and differences in predation rates on males and females.

The hypothesis of sexual selection via male-male competition suggests that wing patterns of males are used in male intrasexual communication, via male-male competitive interactions, preventing the evolution of novel wing patterns, including mimetic ones, in this sex (Pearse and Murray 1982; Silberglied 1984). This hypothesis is supported by a study on *Papilio polyxenes*, which also exhibits female-limited Batesian mimicry. In this species, males with altered wing patterns to resemble mimetic females were found to be less successful in establishing and maintaining a territory than their counterparts with unaltered wing patterns. On the other hand, females were equally likely to mate with males with altered and unaltered wing patterns. These findings suggest that male intrasexual selection, instead of female mate choice, plays a more important role in constraining the evolution of male wing patterns and thus limiting mimicry to females (Lederhouse and Scriber 1996).

For *P. polytes*, however, there are mixed reports on whether males are territorial and, thus, on whether male-male competition could be restricting males of this species from evolving mimetic patterns. Two separate field studies have been conducted in India, with one reporting that males of this species do not show territorial defense (Tiple et al. 2011) and another reporting that they do (Revathy and Mathew 2014). Therefore, the presence of territorial behavior in this species and whether male wing pattern is involved in male-male competition remains uncertain. In our experiments using *P. polytes* populations from Malaysia, we did not observe prolonged male-male interaction during our observations at 15 min intervals.

The hypothesis of sex-specific differences in predation rates suggests that females are more frequently attacked by avian predators and therefore subjected to stronger natural selection pressure relative to males, leading to the evolution of female-limited mimicry. Females carry eggs in their abdomen, causing them to be heavier and less agile in flight compared to males, which could result in heavier predation (Marden and Chai 1991; Ohsaki 1995; Srygley and Chai 1990). In support of this hypothesis is the observation that non-mimetic females of *P. polytes* were found to be more likely to have beak marks on their wings compared to males, indicating females are preferentially preyed upon by birds (Ohsaki 1995). Thus, it is possible that females have indeed been subjected to greater natural selection pressure. This, together with negative frequency-dependent selection pressure, could cause the females alone to evolve mimetic wing patterns.

Future Studies

The selection pressures that led to the evolution of female-limited Batesian mimicry are still not fully understood. So far three hypotheses, female mate choice, male-male competition, and sex-specific differences in predation rates, have been proposed, but few attempts have been made to test them. Therefore, more studies are required to test the validity of these hypotheses.

If similar mate choice experiments are to be conducted, by manipulating the pattern in other parts of the males' wings, three improvements on our experimental setup can be made to increase the number of observed matings: adding artificial heat and light sources to increase butterfly activity, placing more plants in the cage to provide more landing sites for the butterflies, and recording the experiments with video.

During most of the duration of the experiment, the butterflies' activity was affected by the weather. Under the experimental setting, they were observed to be the most active when the weather was sunny, especially during the afternoon when temperatures were higher. However, the frequent rain, coupled with long periods of cloudy weather during the period of the experiment, caused the butterflies to be not very active most of the time. This led to infrequent courtship. Therefore, future mate choice experiments should include artificial heat and light sources through the use of heating lamps and full spectrum light bulbs to increase butterfly activity and the occurrence of mating.

In addition, more plants can be placed in the flight cages to provide more resting sites for the butterflies. In order for males to hover in front of females during courtship, there needs to be space in front of each female. However, if the females are resting on the edges of the cage, males cannot hover in front of them. This can affect the males' ability to display their dorsal wing pattern to the females. Thus, future mate choice experiments with similar settings should have more plants placed in the cage to reduce the likelihood of females landing on the edges of the cage.

Furthermore, the experiments can be video recorded. This would help to keep track of the interactions between individuals in the cages and provide more information about any difference in solicitation by the females towards courtship by males from different groups, such as that observed in *P. glaucus* (Krebs and West 1988).

In order to investigate the role of male-male competition in the evolution of female-limited Batesian mimicry, the behavior of male butterflies should be monitored. So far, the presence of territorial behavior in *P. polytes* is still unconfirmed. Studies to confirm this behavior could be done by releasing males in pairs into a study area, followed by observations of their interaction. If the males are confirmed to be territorial, experiments with males with manipulated wing patterns and males with natural wing patterns could then show their relative success rates in establishing territories (Lederhouse 1982; Lederhouse and Scriber 1996).

To test for differences in predation rates on male and female butterflies, field or large aviary studies can be conducted. Rates of beak marks between males, non-mimetic females, and mimetic females of *P. polytes* or other butterfly species which exhibit female-limited Batesian mimicry can be estimated from mark-recapture experiments conducted in the field (Ohsaki 1995), or more directly from observations conducted in large flight cages where avian predators have also been released (Langham 2004). Here the attack behavior of the birds can be observed and the number of successful attacks on the different sexes can be recorded.

Conclusion

Female mate choice has been hypothesized to exert stabilizing selection on male wing patterns and restrict the evolution of Batesian mimicry to female butterflies. However, in our mate choice experiment, we offered female *P. polytes* a choice of males with intact dorsal forewings showing their typical (non-mimetic) white spots and males with artificially blackened dorsal forewings (resembling the female mimetic wings and those of its Batesian model) and found that females mated equally with both male types. This result suggests that the dorsal white spots are not being maintained by female mate choice. Further studies are required to investigate whether female preference exerts stabilizing selection on the color pattern of other parts of the male wings. In addition, male-male competition and differences in predation rates on male and female butterflies should also be explored to test these hypotheses in connection to female-limited wing pattern mimicry in *P. polytes*.

Acknowledgements Work was supported by the Department of Biological Sciences (DBS) Undergraduate research program of the National University of Singapore (NUS) and DBS, NUS R-154-000-608-651 LHK fund. We also thank Entopia by Penang Butterfly Farm for supplying live *Papilio polytes* pupae for this research and Jocelyn L. Q. Wee for assistance with the reflectance spectra measurement and plotting.

Author Contributions Conceived and designed the experiments: XHL and AM. Performed the experiments: XHL. Analyzed the data: XHL. Wrote the paper XHL and AM.

Compliance with Ethical Standards

Conflict of Interest The authors declare that they have no conflict of interest.

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